

# On the vulneravility of food webs to multiple stressors

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## Proposal letter

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### Notes

- In it's current form, I believe that the contribution portion is not good enough
- I wonder whether the qualifications should be more in depth.
- Right now, the letter is 43 words over the word limit.
- Also, this text might be better than the current abstract

### Letter

Evaluating the effects of multiple sources of stress in natural environments has become an increasingly important issue as the effects of intensifying global change and expanding human activities result in complex stress exposure regimes. Even though the non-additive effects of multiple stressors have been investigated empirically for a few decades now, there remains a general lack of theoretical understanding of their impacts on natural systems. In particular, the role of species and their interactions in mediating the effects of multiple disturbances through ecological communities networks, although widely acknowledged, has yet to be formally explored. We propose the first such formal exploration by exhaustively simulating the impacts of all possible pathways of effects on the dynamics of 3-species motifs using Lotka-Volterra models. We uncover that interaction types and species position greatly influence sensitivity to and amplification of multiple disturbances and that indirect pathways of effects are the main cause of non-additive effects. In particular, predators in food chain and omnivory interactions act as both weak entry points (*i.e.* highly sensitive to disturbances) and biotic amplifiers (*i.e.* affected synergistically by disturbances). We then use the simulated sensitivity and amplification scores as heuristics to infer trophic vulnerability of species based on topology and realized pathways of effects in the food web of the Northern Gulf of St. Lawrence, Canada, prior to a groundfish stock collapse in the 1990s. We find that heavily exploited species appear to be the most vulnerable trophically, while fisheries transitioned to insensitive or beneficiary species post-collapse. This contribution is significant and timely for two main reasons. First, from a theory stand point, this is the first exhaustive exploration of mitigation and amplification of multiple disturbances via trophic motifs. Second, we provide a clear link between theory and management by illustrating how

69 our framework can be applied to detect most sensitive species in a real food web exposed  
70 to various stressors. Our group of co-authors is singularly positioned to write this paper.  
71 D. Beauchesne and P. Archambault both have strong backgrounds in environmental assess-  
72 ments in general and cumulative impacts in particular. K. Cazelles and D. Gravel are both  
73 experts in theoretical ecology with strong backgrounds and recognition in the field.

# 1 Abstract

Evaluating the effects of multiple sources of stress in natural environments has become an increasingly important issue as the effects of intensifying global change and expanding human activities result in complex stress exposure regimes. Even though the non-additive effects of multiple stressors have been investigated empirically for a few decades now, there remains a general lack of theoretical understanding of their impacts on natural systems. In particular, the role of species and their interactions in mediating the effects of multiple disturbances through ecological communities, although widely acknowledged, has yet to be formally explored. We propose the first such formal exploration by exhaustively simulating trophic impacts through all possible pathways of effects on the dynamics of 3-species motifs using Lotka-Volterra models. We uncover that interaction types and species position greatly influence sensitivity to and amplification of multiple disturbances and that indirect pathways of effects are the main source of non-additive effects. In particular, predators in food chain and omnivory interactions act as both weak entry points (*i.e.* highly sensitive to disturbances) and biotic amplifiers (*i.e.* affected synergistically by disturbances). We then use the simulations results as heuristics to infer trophic vulnerability of species based on topology and realized pathways of effects in the food web of the Northern Gulf of St. Lawrence, Canada, prior to a groundfish stock collapse in the 1990s. We find that heavily exploited species appear to be the most vulnerable trophically, while fisheries transitioned to insensitive or beneficiary species post-collapse.

## 2 Introduction

Ecosystems worldwide are increasingly affected by a vast array of environmental pressures, commonly referred to as stressors (Boonstra *et al.* 2015; Halpern *et al.* 2019). Pressures may be driven by natural or human-induced biophysical processes such as ocean acidification and warming, or directly from anthropogenic activities such as fisheries. These drivers can be defined as any externality that affects environmental processes and disturbs natural systems. Individually, drivers have been found to impact all levels of biological organization and cause dramatic changes to whole ecosystems. Ocean acidification can reduce coral and mollusk calcification, metabolic, growth and mortality rates, and has been linked to altered carbon fluxes in ecological networks (Fabry *et al.* 2008; Kroeker *et al.* 2013; Bove *et al.* 2019). Fisheries have caused the collapse of commercial species, decreased the mean trophic level in coastal and oceanic environments by targetting large predators and impaired a variety of essential ecosystem services (Pauly *et al.* 1998; Myers & Worm 2003; Worm *et al.* 2006). Rarely do drivers occur individually, and the list of potentially interacting drivers affecting an ecosystem at any given point in time or space can be extensive (Halpern *et al.* 2019). Global changes and local human activities thus result in increasingly intricate environmental stress exposure regimes, compounding the pathways of effects through which natural systems can be impacted (Halpern *et al.* 2019). For example, coral reefs contend with a suite of pressures including fishing, warming temperatures, ocean acidification and water quality that may impact species in contrasting ways (McClanahan *et al.* 2014; Harborne *et al.* 2017). Drivers can then combine to induce complex and sometimes unpredictable effects (Côté *et al.* 2016). Dramatic examples include up to 100-fold increases of the sensitivity of certain organisms to toxicants (*e.g.* pesticides) when exposed to other environmental stressors (*e.g.* parasites; Liess *et al.* 2016) and the reversal of the positive effects of acidification on primary producer biomass by warmer waters in boreal lakes (Christensen *et al.* 2006).

The potential for complex interactions between drivers remains the largest uncertainty when

120 studying or predicting environmental impacts (Darling & Côté 2008; Côté *et al.* 2016).  
121 Interactive drivers effects have thus been extensively investigated to uncover instances of  
122 non-additive effects, *i.e.* when the effect of multiple interacting drivers is greater (synergism)  
123 or lower (antagonism) than the sum of their individual parts. These studies have found non-  
124 additive effects of multiple drivers to be the norm rather than the exception across ecosystems  
125 globally (*e.g.* Darling & Côté 2008; Crain *et al.* 2008; Piggott *et al.* 2015; Jackson *et al.*  
126 2016).

127 Species sensitivity to environmental pressures can be highly variable, which further com-  
128 pounds the complexity of multiple drivers studies. For example, hypoxia decreases overall  
129 habitat quality but has species-dependent effects, ranging from well-adapted (*e.g.* north-  
130 ern shrimp *Pandalus borealis* and Greenland halibut *Reinhardtius hippoglossoides*; Pillet *et*  
131 *al.* 2016) to avoidance behaviour (*e.g.* Atlantic cod *Gadus morhua*; Chabot & Claireaux  
132 2008), and mortality (*e.g.* sessile benthic invertebrates; Eby *et al.* 2005; Belley *et al.* 2010).  
133 Species are also embedded in a complex web of interactions that provides indirect pathways  
134 of effects through which pressures may permeate entire ecological communities (Wootton  
135 2002; Bascompte 2009; Montoya *et al.* 2009; O’Gorman & Emmerson 2009; O’Gorman *et*  
136 *al.* 2012). Indirect effects, *i.e.* when two or more direct effects are linked by a single species  
137 involved in both effects, may be as important of, and propagate faster than, direct effects  
138 (Wootton 1993, 2002; Menge 1995; Yodzis 2000). Empirical examples of trophic cascades are  
139 abundant throughout all types of ecosystems globally (Estes *et al.* 2011). In multi-species  
140 systems, where both direct and indirect effects are operating simultaneously, it is expected  
141 that the effects of environmental pressures will be amplified or dampened through biotic  
142 interactions (Ives 1995; Wootton 2002; Thompson *et al.* 2018). Community dynamics and  
143 how species are embedded in complex networks is therefore likely to affect their sensitivity  
144 to environmental pressures.

145 Confronted with the challenge of managing and preserving complex systems, there is an  
146 urgent need for the development of theoretical frameworks that properly consider the com-

plexities of multiple drivers and ecological networks in ways that are informative to management. From a practical standpoint, single-driver and single-species assessments remain overwhelmingly applied (O'Brien *et al.* 2019), while most multiple drivers studies have typically focused on habitats (*e.g.* Ban *et al.* 2010; Halpern *et al.* 2019). This conveniently circumscribes assessments to a set of tractable units, but it also ignores systems complexity and aggregates biological processes operating at lower levels organization (Halpern & Fujita 2013; Giakoumi *et al.* 2015). Studies have also relied on the use of null models that provide little insights into the mechanisms underlying ecological responses to the effects of multiple drivers (Griffen *et al.* 2016; Jackson *et al.* 2016; De Laender 2018; Schäfer & Piggott 2018). Theoretically, species interactions have long been identified as key components to the sensitivity of whole networks to disturbances (*e.g.* Ives 1995; Wootton 2002; O’Gorman & Emmerson 2009; O’Gorman *et al.* 2012), but the effects of multiple disturbances on networks have yet to be formally explored.

In this paper, we address this issue by exhaustively investigating how multiple environmental pressures permeate complex ecological networks and the role of species and their interactions (*i.e.* food web topology) in buffering against or amplifying the effects of disturbances. In doing so, we seek to answer questions of particular significance to management: 1) should species interactions be considered in impact assessments, 2) should the effects of stressors be evaluated separately or in combination, 3) which species are most vulnerable to disturbances based on their trophic position, and 4) what types of pathways of effect most influences species vulnerability?

## 3 Of food web and multiple disturbances

### 3.1 Conceptualizing disturbances

Drivers can disturb the dynamics of ecological communities by disrupting a variety of biological processes (Figure 1A) such as behaviour (*e.g.* Chabot & Claireaux 2008; Hale *et al.* 2017), reproduction [*e.g.* ref], physiology (*e.g.* Dupont-Prinet *et al.* 2013), mortality (*e.g.* Belley *et al.* 2010), and species interactions (*e.g.* Wootton 2002; Guiden *et al.* 2019). Multiple processes may be affected by a single driver, while multiple drivers may target a single process. For instance, fishing could affect the behaviour and the mortality of cod, while hypoxia and ocean acidification may affect the physiology of benthic invertebrates. The potential number of univariate and multivariate pathways of effects through which community dynamics may be affected is extensive and increases exponentially with the number of species and the number on links in a network.

A thorough understanding of the impacts of disturbance regimes and community dynamics would be necessary to fully capture the effects of multiple drivers, but the complexity of empirical food webs in itself is prohibitive to investigations of community dynamics. Studying smaller subgraphs - community motifs or modules - has thus emerged as an alternative to gather insights into the dynamics and stability of complex ecological communities (Holt 1997; Holt & Hochberg 2001). Motifs are collections of  $n$ -species that, when put together, construct whole food webs (Milo *et al.* 2002; Stouffer *et al.* 2007). They form the backbone of food webs and provide a mesoscale characterization of community structure (Bascompte & Melián 2005; Stouffer *et al.* 2007). A species can be described as a function of all  $n$ -species motifs it is involved in in an empirical food web (Figure 1B; Stouffer *et al.* 2012).

There are 13 distinct 3-species motifs composed of 30 unique positions (Milo *et al.* 2002; Stouffer *et al.* 2007, 2012). Four 3-species motifs have received particular attention in theoretical and empirical studies due to their roles [ref] and prevalence (Camacho *et al.* 2007;



Stouffer & Bascompte 2010) in food webs: tri-trophic food chain, omnivory or intraguild predation, exploitative competition and apparent competition.

Motif dynamics has been studied extensively to uncover how structural properties of food webs can benefit community persistence and stability (Allesina & Pascual 2008; Kondoh 2008; Stouffer & Bascompte 2010, 2011; Monteiro & Faria 2016) and to assess the structural roles of species within food webs (Stouffer *et al.* 2012; Cirtwill & Stouffer 2015). These provide meaningful insights for conservation efforts. For example, results from Stouffer *et al.* (2012) suggest that species benefit whole community persistence based on their trophic position and that the diversity of trophic roles found in empirical food webs does not correlate to species richness. Using roles as targets may thus be valuable for community conservation (Stouffer *et al.* 2012). Additional insights into the structural properties of food webs could be gathered by studying motifs at equilibrium, *i.e.* when system dynamics is constrained by species coexistence (Figure 1C). This is of particular relevance to managers using ecosystem-based approaches to manage and maintain exploited populations.

Here, we study the equilibrium dynamics of the most prevalent 3-species motifs in food webs (*i.e.* food chain, omnivory, exploitative competition, and apparent competition) to exhaustively investigate how trophic position and interaction type influences the sensitivity to and the amplification of the effects of multiple disturbances. We then use the simulations to infer species trophic vulnerability in complex food webs as a function of species position in food web and realised pathways of effects.

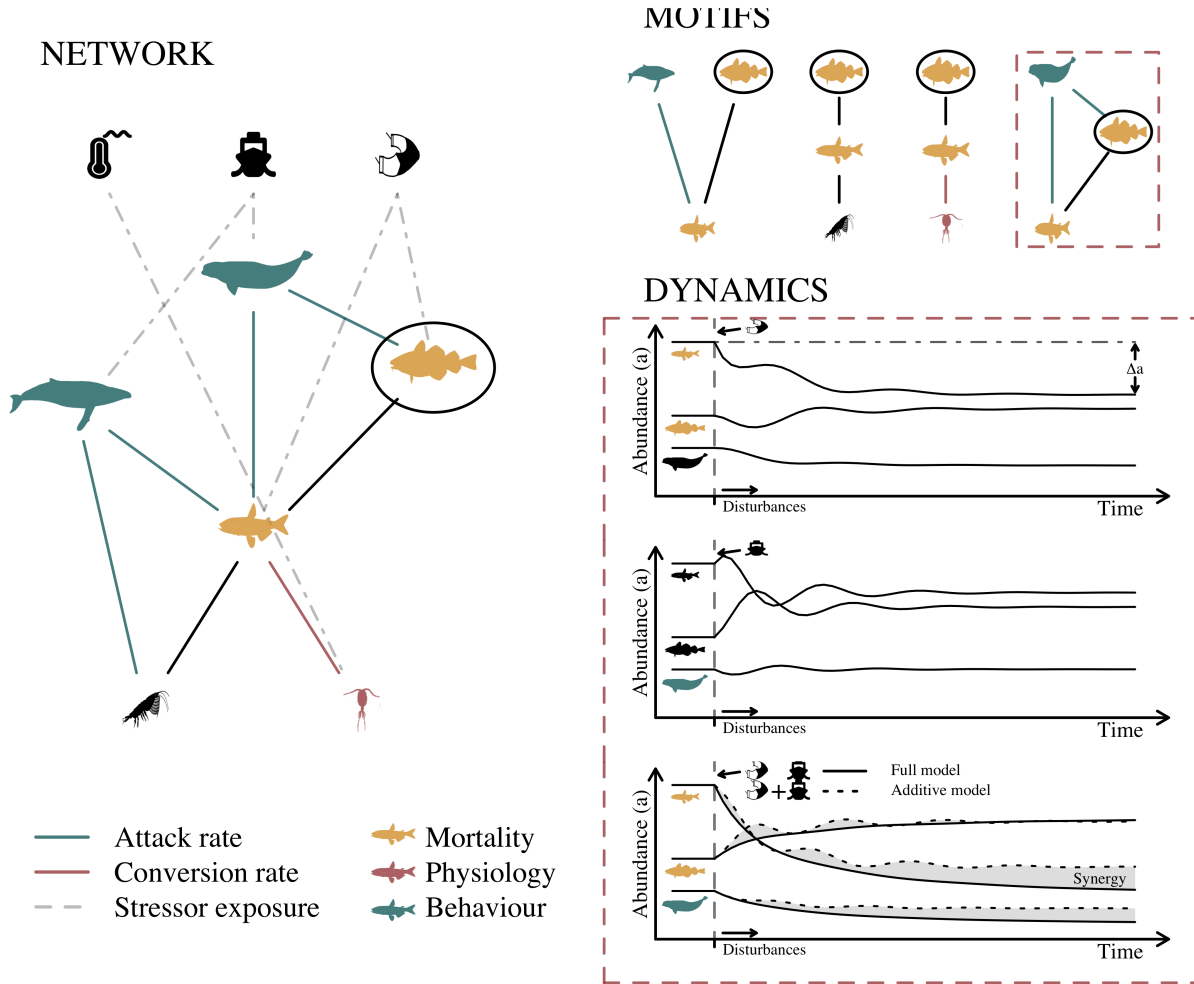


Figure 1: Conceptualization of the effects of multiple sources of environmental stress on the dynamics of a theoretical food web. A) Drivers such as sea surface temperature, marine traffic and fisheries penetrate food webs through various pathways of effects by disturbing ecological processes governing populations and communities. For instance, marine traffic disturbs whale feeding behaviour, which may lead to decreased attack rates on prey species. B) A species position in a food web can be decomposed in a suite of  $n$ -species submodules called motifs that are informative of the role played by a species in the entire food web. Different types of interaction types will lead to different types of community dynamics and a species can be described as a function of the number and types of interactions it is involved in. For instance, the interactions of the meso-predator can be decomposed into 1 exploitative competition, 2 food chains and 1 omnivory motifs. C) The dynamics of motifs can uncover if and how disturbances arising from individual and multiple drivers are propagated and amplified through different types of species interactions. Variations in species abundance due to driver induced disturbances provide an evaluation of motif species sensitivity (C1-3). The difference between the summed effects of individual drivers (*i.e.* additive model; C1-2) and the joint effects of multiple drivers (*i.e.* full model; C3) provides an evaluation of disturbance amplification.

## 3.2 Sumulating disturbances

### 3.2.1 Models formulation

The dynamics of tri-trophic food chain, omnivory, exploitative and apparent competition motifs were modeled using Lotka-Volterra equation systems (Table S1). Two additional motifs were included as controls to test the importance of species interactions in mediating the effects of disturbances, *i.e.* a partially connected motifs with a disconnected species and a predator-prey interaction, and a fully disconnected motif with three fully independent species.

Resources were modeled using logistic growth equations of the form

$$\frac{dX_i}{dt} = X_i(r_i - \alpha_{ii}X_i - \sum \alpha_{ij}X_j)$$

,

where  $X$  are species,  $i$  is the resource,  $j$  are the consumers,  $r_i$  is the intrinsic resource growth rate,  $\alpha_{ii}$  is the density-dependent effect of the resource on itself and  $\alpha_{ij}$  is the rate at which consumer  $j$  affects resource  $i$ , *i.e.* the attack rate.

Consumers were modeled using a Type I functional response of the form

$$\frac{dX_j}{dt} = X_j(-m_j + \sum e_{ij}\alpha_{ij}X_i - \alpha_{jk}X_k)$$

,

where  $m$  is the mortality rate and  $e$  is the rate at which resource biomass is transformed into consumer biomass, *i.e.* the conversion rate, and is a scaling parameter of the attack rate which cannot exceed 1.

Models were solved at equilibrium to study the effects of disturbances on persistent motif dynamics. As no equilibrium exists for the exploitative competition motif with Lotka-Volterra

models of the selected forms, competitive parameters of the form

$$\alpha_{jj}\alpha_{jk}X_jX_k - \alpha_{jj}X_j^2$$

were included to the consumer models to constrain growth and limit competitive exclusion.

### 3.2.2 Models parameterization

Initial parameter values for intrinsic growth ( $r$ ) and resource density-dependence ( $\alpha_{ii}$ ) were fixed to 1 and 0.001, respectively, to bound all resource solutions. Competitive parameters for the exploitative competition motif were also fixed at 0.001. Conversion rates ( $e$ ) were fixed to 0.5. A total of 100 sets of mortality ( $m$ ) and attack rates ( $\alpha_{ij}$ ) were evaluated using a simulated annealing algorithm optimizing for consumer abundance.

### 3.2.3 Disturbances

For each motif, a 1% change in initial equilibria equation parameter values was applied to simulate negative disturbances (*e.g.* an increase in mortality). Parameters selected to simulate disturbances were those related to population growth ( $r$  and  $m$ ) and conversion and attack rates ( $e$  and  $\alpha_{ij}$ ). Those parameters were used as they can be linked to disturbance effects on common biological processes affected by disturbances, *i.e.* mortality, physiology and behaviour.

For each motif, all possible mortality, resource growth, conversion and attack rates parameter combinations were simulated. This resulted in a total of 930 unique pathways of effects for all motifs combined (food chain, competitive exploitation and apparent competition: 7 parameters, 127 pathways of effects; omnivory: 9 parameters, 511 pathways of effects; partially connected 5 parameters, 31 pathways of effects; disconnected: 3 parameters, 7 pathways of effects).

### 3.3 Trophic sensitivity

For all 13 unique motif positions considered and all unique pathways of effects, the variation in abundance between the 100 sets of initial conditions and disturbed conditions was used as a proxy of trophic sensitivity ( $s_{i,j}$ ) to disturbances:

$$s_{i,j} = \frac{a_{i,j} - a_i}{a_i}$$

where  $i$  is a motif position,  $j$  is a unique pathway of effect,  $a_i$  is the initial abundance at position  $i$ , and  $a_{i,j}$  is the abundance at position  $i$  due to pathway of effect  $j$ . Sensitivity scores are bounded negatively to -1, as abundances cannot fall below 0. The sensitivity score used for a single pathway of effect ( $S_{i,j}$ ) is the mean of the 100 simulations using all initial conditions:

$$S_{i,j} = \frac{1}{n} \sum_{l=1}^n s_{i,j}$$

Overall position sensitivity ( $S_i$ ) was evaluated using the mean of the set of all possible pathways of effect ( $K^i$ ) for a given position  $i$ :

$$S_i = \frac{1}{|K^i|} \sum_{j \in K^i} S_{i,j}$$

We define *weak entry points* as particularly sensitive pathways of effect ( $|S_{i,j}| > 1$ ) or motif positions ( $|S_i| > 1$ ), while *biotic sinks* are insensitive pathways of effects ( $|S_{i,j}| = 0$ ) or motif positions ( $|S_i| = 0$ ).

### 3.4 Trophic amplification

A score of trophic amplification ( $A_{i,j}$ ) was measured to evaluate non-additive arising through trophic pathways of effects:

$$A_{i,j} = S_{i,K_j} - \sum_{k_j \in K_j} S_{i,j}$$

where  $K_j$  is a multivariate pathway of effect  $j$  and  $k_j$  are unitary pathways of effect composition  $j$ . The amplification score evaluates the deviance of a multivariate pathway of effect and the sum of the univariate effects composing the pathway of effect, *i.e.* the additive model. Thus, a value of 0 identifies a null of additive effect, a value below 0 identifies an antagonistic effect, and a value over 0 identifies synergistic effects.

A score of position amplification ( $A_i$ ) was evaluated using the mean of the set of all possible pathways of effect ( $K^i$ ) for a give position  $i$ :

$$A_i = \frac{1}{|K^i|} \sum_{j \in K^i} A_{i,j}$$

We define biotic amplifiers as multivariate pathways of effect or motif positions that are more affected than expected from an additive model ( $A_{i,j} > 0.0002$ ,  $A_i > 0.0002$ ). Biotic buffers are multivariate pathways of effect or motif positions that are less affected than expected from an additive model ( $A_{i,j} < 0.0002$ ,  $A_i < 0.0002$ ).

### 3.5 Species vulnerability

We define two sets of scores at the species level. The first requires no information on realised pathways of effect and provides a topological evaluation of a species trophic sensitivity and trophic amplification potential based on the frequency of times it occupies a position in a food web:

$$S_m = \sum_i f_{mi} S_i$$

$$A_m = \sum_i f_{mi} A_i$$

where  $S_m$  and  $A_m$  are the sensitivity and amplification scores of species  $m$ , respectively,  $f_{mi}$  is the frequency at which species  $m$  occupies position  $i$  in a food web, and  $S_i$  and  $A_i$  are the sensitivity amplification scores at position  $i$ , respectively.

The second set of scores at the species level uses a list of realised pathways of effect:

$$S_m = \sum_{j \in K^{i*}}^{position} S_{i,j}$$

$$A_m = \sum_{j \in K^{i*}}^{position} A_{i,j}$$

where  $S_m$  and  $A_m$  are the sensitivity and amplification scores of species  $m$ , respectively,  $j$  are pathways of effect,  $K^{i*}$  is the set of realised pathways of effects for position  $i$ , and  $S_{i,j}$  and  $A_{i,j}$  are the sensitivity and amplification scores for pathway of effect  $j$  on position  $i$

We evaluate the trophic sensitivity and amplification for the functional groups and species found in an empirical food web for the Northern Gulf of St. Lawrence, in Eastern Canada, prior to a groundfish stock collapse in the early 1990s (Morissette *et al.* 2003).

***Describe how driver effects on biological processes were identified.***

## 4 Results

### 4.1 Motifs

#### Sensitivity

##### *Interactions:*

- Interaction motifs are more sensitive than control motifs to disturbances (Figure 2A).
- Control motifs are, overall, less sensitive to disturbances than control motifs.
- Biotic sinks are composed almost exclusively of pathways targetting control motifs

##### *Motifs:*

- Food chain and omnivory are more sensitive than competitive motifs (Figure 2C-D)
- The average sensitivity of omnivory and food chain motif positions is higher than that of competitive motifs
- Omnivory > Food chain > competitive exploitation > apparent competition

##### *Position:*

- Predators and resources in omnivory and food chains are negative weak entry points, while consumers are positive weak entry points (Figure 2C-D)
- Consumers in omnivory and food chains are positive weak entry points (Figure 2C-D)
- Resources in competitive motifs benefit from disturbances (Figure 2C-D)
- Consumers in competitive motifs are negatively affected by disturbances

##### *Disturbances:*

- Multivariate pathways of effect result in heightened sensitivity (Figure 2B)



- Targetting multiple biological process increases sensitivity (Figure 3A)
- Mortality and conversion rates result in slightly higher sensitivities (Figure 3A)
- Combinations of direct and indirect effect result in greater sensitivity (Figure 3A)
- Indirect effects result in higher sensitivities (Figure 3A)

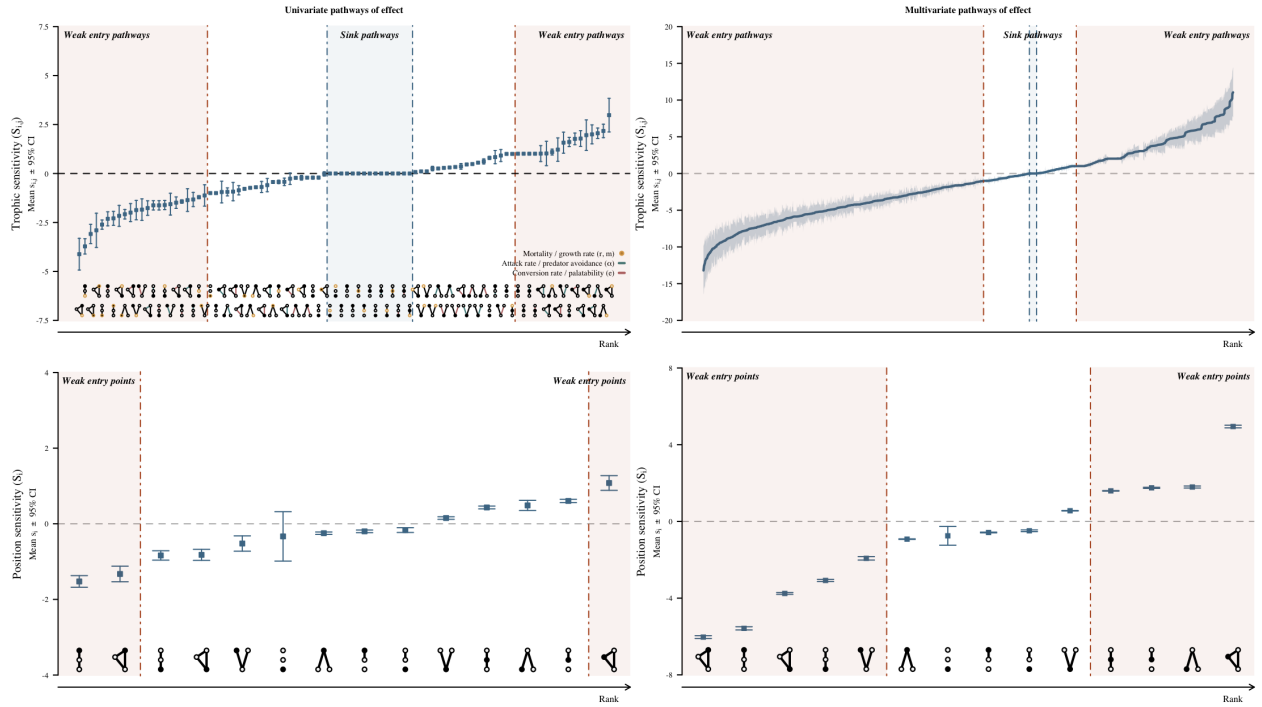


Figure 2: Ranking of all univariate and multivariate pathways of effect as a function of trophic (A,B) and position (C,D) sensitivity. Pathways and motif positions identified as weak entry points (*i.e.* highly sensitive to disturbances) and biotic sinks (*i.e.* insensitive to disturbances) are identified by the red and blue regions, respectively.

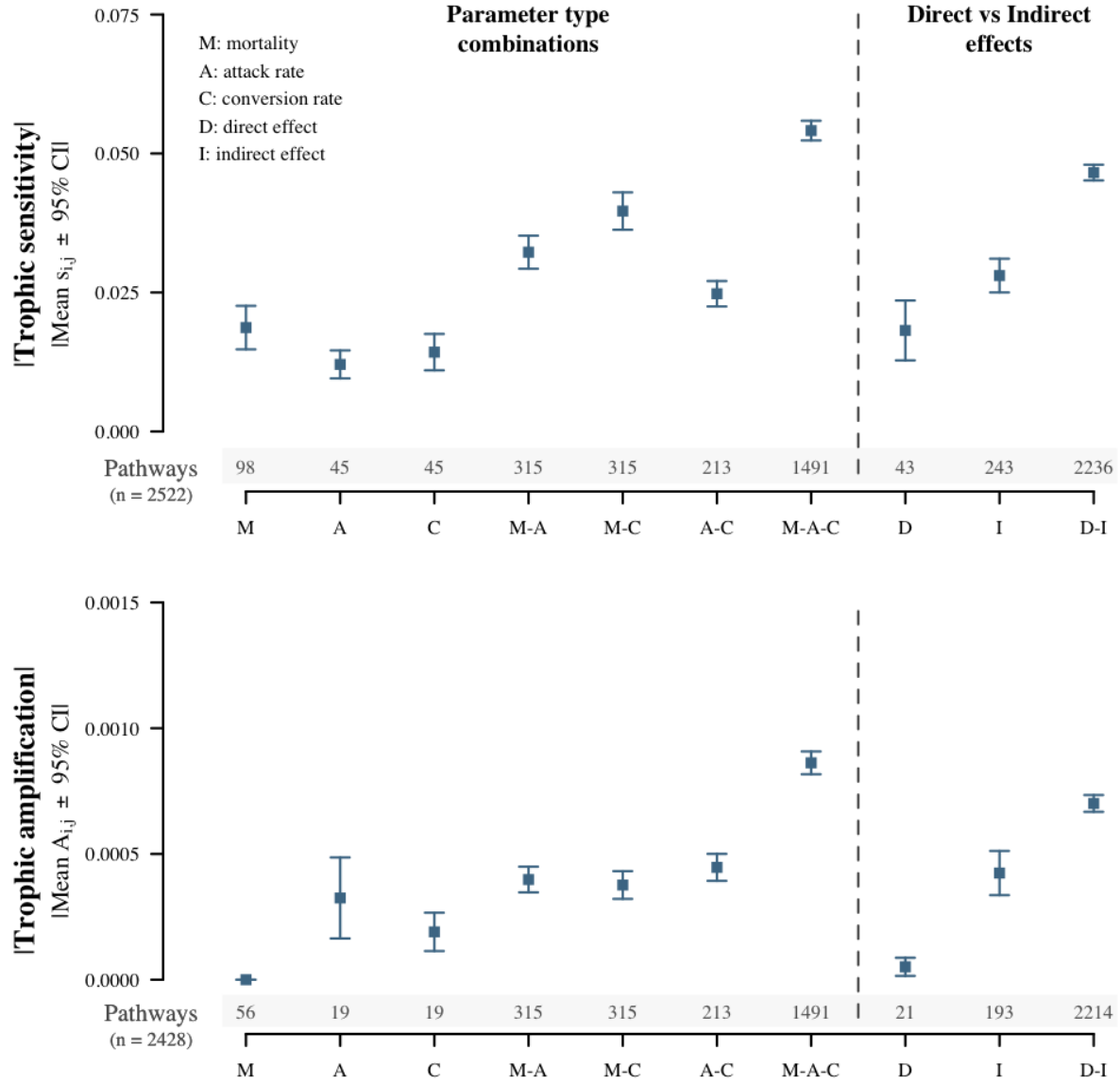


Figure 3: Absolute values of the mean trophic sensitivity (A) and amplification (B) as a function of disturbed parameter type and direct or indirect effects. All pathways of effect targeting a specific parameter type (*i.e.* mortality, attack and conversion rates) were grouped to evaluate their respective and combined effect on trophic sensitivity and amplification. Direct and indirect pathways of effect were similarly grouped. A direct or indirect pathway of effect on a motif position is any pathway that directly or indirectly involves a species, respectively. For example, the conversion rate of a resource by a predator in competitive exploitation is a direct pathway of effect for both the resource and the predator, and an indirect pathway of effect for the second predator involved in the interaction.

#### 4.1.1 Amplification

##### *Interactions:*

- Control motifs do not amplify disturbances (Figure 4).
- Biotic buffers and amplifiers more frequent in interaction motifs (Figure 4).

##### *Motifs:*

- Biotic buffers and amplifiers are prevalent in food chain and, in particular, omnivory motifs (Figure 4).
- Competitive motifs are less affected by non additive effects (Figure 4).

##### *Position:*

- Predators in omnivory and food chain motifs are particularly susceptible to be biotic amplifiers (Figure 4).
- There are no clear biotic buffers (Figure 4).

##### *Disturbances:*

- Mortality parameters have additive effects (Figure 3B)
- Disturbances to interaction parameters (\*i.e. attack and conversion rates) cause most important non-additive effects (Figure 3B)
- Affecting combinations of biological processes results in most important non-additive effects (Figure 3B)
- Direct effects are mostly additive, while non-additive affects result from indirect or combinations of indirect and direct effects.(Figure 3B)

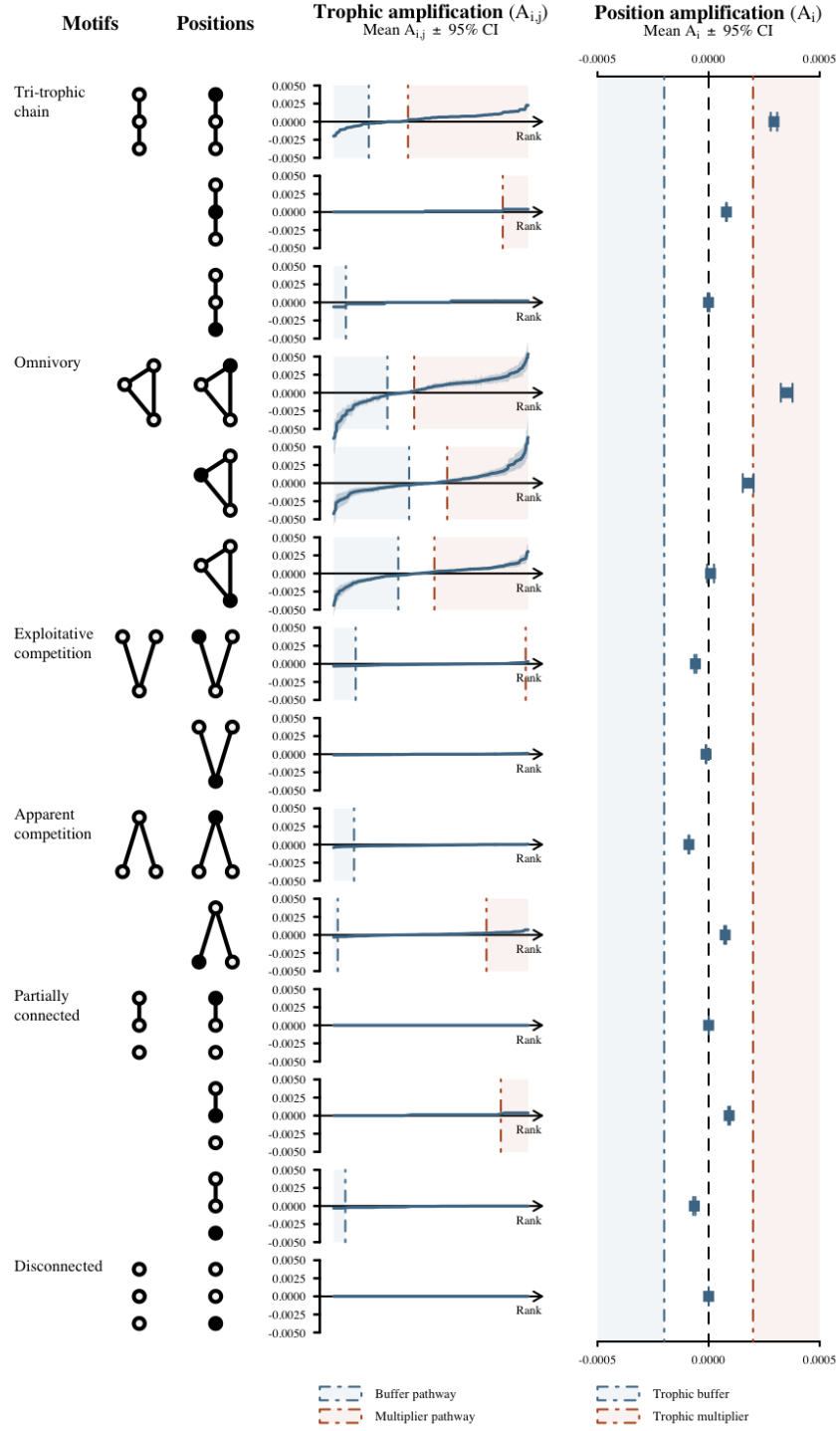


Figure 4: Ranking of all multivariate pathways of effect as a function of trophic and position amplification, for each motif position. Pathways and motif positions identified as biotic buffers (*i.e.* affected synergistically by disturbances) and biotic buffers (*i.e.* affected antagonistically by disturbances) are identified by the red and blue regions, respectively.

## 4.2 Empirical networks

### *Species position in food web matters:*

- Top predators in the system are most vulnerable due to their trophic position.
- Species trophic vulnerability is not necessarily explained by direct exposure to multiple drivers.
- Species with few direct impacts (\textit{e.g.} harp seals) may be highly sensitive due to their trophic position.

### *Sensitivity does not equal amplification:*

- Amplification and sensitivity have different trends.

### *Groundfish stock collapse: a trophic hint?:*

- Exploited species before the groundfish stock collapse of the 1990s (\textit{e.g.} demersal feeders, Atlantic cod, Greenland halibut) are all negative weak entry points and biotic amplifiers.
- Exploited species after the collapse are either positive weak entry points and biotic amplifiers (\textit{e.g.} large crustaceans) or biotic sinks (\textit{e.g.} shrimp).

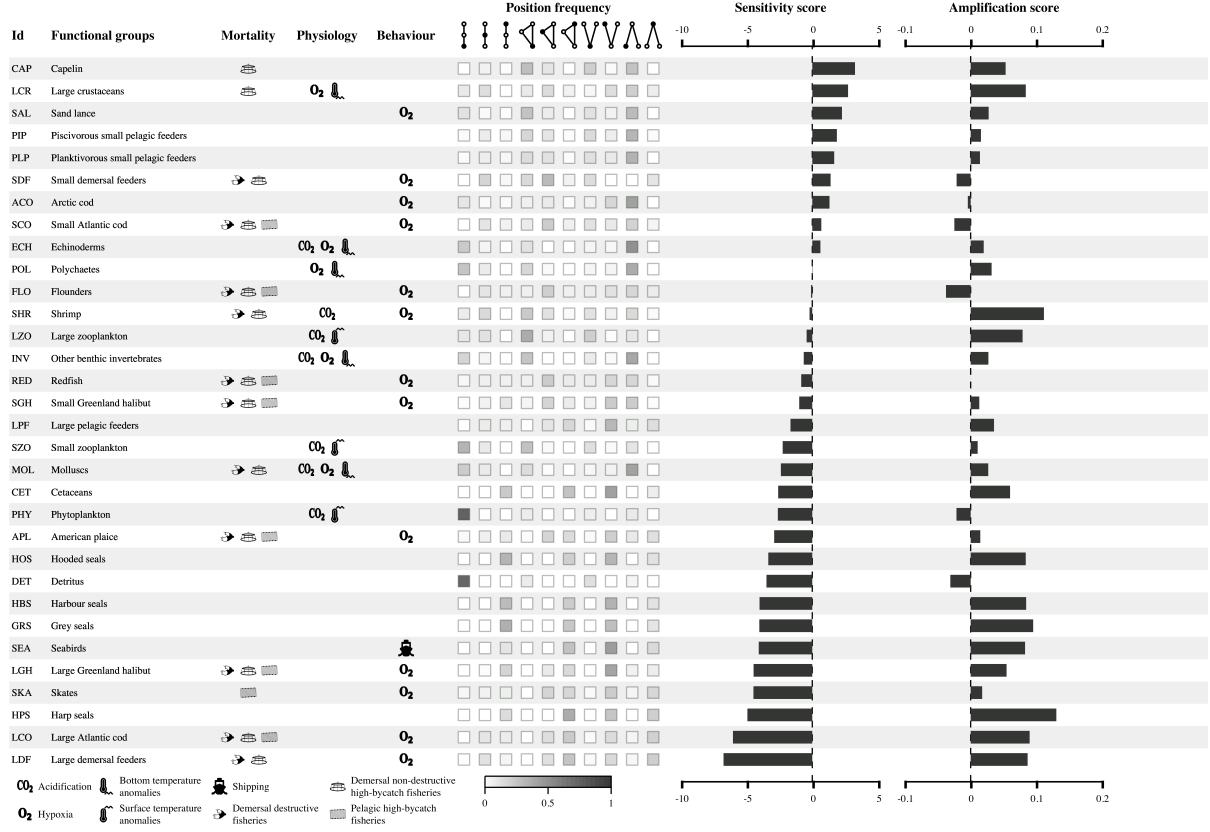


Figure 5: Change in species and functional groups sensitivity and amplification scores as a function of realised pathways of effects for an empirical food web of the Northern Gulf of St. Lawrence in the mid-1980s [?]. The left-hand side of the table presents the species and functional groups, the drivers supposed to be affecting population level mortality, physiology and behaviour, and the frequency at which they are found in each unique position of the food chain, omnivory, exploitative and apparent competition motifs. Important drivers in the Northern Gulf of St. Lawrence are fisheries (*i.e.* demersal destructive, demersal non-destructive high-bycatch and pelagic high-bycatch), climate change (*i.e.* ocean acidification, hypoxia and bottom and surface temperature anomalies), and shipping [?]. Species position and driver effects on biological processes were used to identify realised pathways of effects between all 3-species combinations in the food web. The right-hand side of the table presents the species sensitivity and amplification scores, which corresponds to the sum of the simulated effects of all realised pathways of effects for each species and functional group (Figures 2, 4). Negative and positive sensitivity scores mean that overall pathways affecting a species have negative or positive effects, respectively. The species with the most negative and positive scores are weak entry points (*i.e.* highly sensitive to disturbances), while species with null scores are biotic sinks (*i.e.* insensitive to disturbances). Similarly, negative and positive amplification scores mean that overall pathways affecting a species result in antagonistic or synergistic effects, respectively. Species with negative or positive scores are thus biotic buffers and biotic amplifiers, respectively.

<sup>357</sup> **5** What it all means

<sup>358</sup> **6** The way forward

## 7 Supplementary Material

### 7.1 Models

Motifs	Equation systems	Initial parameters values
Tri-trophic food chain	$\begin{aligned}\frac{dX_i}{dt} &= X_i(r_i - \alpha_{ii}X_i - \alpha_{ij}X_j) \\ \frac{dX_j}{dt} &= X_j(e_{ij}\alpha_{ij}X_i - \alpha_{jk}X_k - m_j) \\ \frac{dX_k}{dt} &= X_k(e_{jk}\alpha_{jk}X_j - m_k)\end{aligned}$	$\begin{aligned}r_i &= 1 \\ \alpha_{ii} &= 0.001 \\ \alpha_{ij}, \alpha_{jk} &\in [0.0001, 0.01] \\ e_{ij}, e_{jk} &= 0.5 \\ m_j, m_k &\in [0.01, 0.5]\end{aligned}$
Omnivory	$\begin{aligned}\frac{dX_i}{dt} &= X_i(r_i - \alpha_{ii} - \alpha_{ij}X_j - \alpha_{ik}X_k) \\ \frac{dX_j}{dt} &= X_j(e_{ij}\alpha_{ij}X_i - \alpha_{jk}X_k - m_j) \\ \frac{dX_k}{dt} &= X_k(e_{ik}\alpha_{ik}X_i + e_{jk}\alpha_{jk}X_j - m_k)\end{aligned}$	$\begin{aligned}r_i &= 1 \\ \alpha_{ii} &= 0.001 \\ \alpha_{ij}, \alpha_{ik}, \alpha_{jk} &\in [0.0001, 0.01] \\ e_{ij}, e_{ik}, e_{jk} &= 0.5 \\ m_j, m_k &\in [0.01, 0.5]\end{aligned}$
Exploitative competition	$\begin{aligned}\frac{dX_i}{dt} &= X_i(r_i - \alpha_{ii} - \alpha_{ij}X_j - \alpha_{ik}X_k) \\ \frac{dX_j}{dt} &= X_j(e_{ij}\alpha_{ij}X_i - \alpha_{jj}\alpha_{jk}X_k - \alpha_{jj}X_j - m_j) \\ \frac{dX_k}{dt} &= X_k(e_{ik}\alpha_{ik}X_i - \alpha_{kk}\alpha_{kj}X_j - \alpha_{kk}X_k - m_k)\end{aligned}$	$\begin{aligned}r_i &= 1 \\ \alpha_{ii}, \alpha_{jj}, \alpha_{kk}, \alpha_{jk}, \alpha_{kj} &= 0.001 \\ \alpha_{ij}, \alpha_{ik} &\in [0.0001, 0.01] \\ e_{ij}, e_{ik} &= 0.5 \\ m_j, m_k &\in [0.01, 0.5]\end{aligned}$
Apparent competition	$\begin{aligned}\frac{dX_i}{dt} &= X_i(r_i - \alpha_{ii}X_i - \alpha_{ik}X_k) \\ \frac{dX_j}{dt} &= X_j(r_j - \alpha_{jj}X_j - \alpha_{jk}X_k) \\ \frac{dX_k}{dt} &= X_k(e_{ik}\alpha_{ik}X_i + e_{jk}\alpha_{jk}X_j - m_k)\end{aligned}$	$\begin{aligned}r_i, r_j &= 1 \\ \alpha_{ii}, \alpha_{jj} &= 0.001 \\ \alpha_{ik}, \alpha_{jk} &\in [0.0001, 0.01] \\ e_{ik}, e_{jk} &= 0.5 \\ m_k &\in [0.01, 0.5]\end{aligned}$
Partially disconnected	$\begin{aligned}\frac{dX_i}{dt} &= X_i(r_i - \alpha_{ii}X_i - \alpha_{ik}X_k) \\ \frac{dX_j}{dt} &= X_j(r_j - \alpha_{jj}X_j) \\ \frac{dX_k}{dt} &= X_k(e_{ik}\alpha_{ik}X_i - m_k)\end{aligned}$	$\begin{aligned}r_i, r_j &= 1 \\ \alpha_{ii}, \alpha_{jj} &= 0.001 \\ \alpha_{ik} &\in [0.0001, 0.01] \\ e_{ik} &= 0.5 \\ m_k &\in [0.01, 0.5]\end{aligned}$
Disconnected	$\begin{aligned}\frac{dX_i}{dt} &= X_i(r_i - \alpha_{ii}X_i) \\ \frac{dX_j}{dt} &= X_j(r_j - \alpha_{jj}X_j) \\ \frac{dX_k}{dt} &= X_k(r_k - \alpha_{kk}X_k)\end{aligned}$	$\begin{aligned}r_i, r_j, r_k &= 1 \\ \alpha_{ii}, \alpha_{jj}, \alpha_{kk} &= 0.001\end{aligned}$

Table 1: Systems of Lotka-Volterra equations used to model the effect of multiple disturbances



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