

# On the sensitivity of food webs to multiple disturbances

*David Beauchesne<sup>1,2,\*</sup>, Kevin Cazelles<sup>3</sup>, Philippe Archambault<sup>2</sup>, Dominique Gravel<sup>4</sup>*

<sup>1</sup>Institut des sciences de la mer, Université du Québec à Rimouski, Rimouski, QC, Canada

<sup>2</sup>Québec Océan, Département de biologie, Université Laval, Québec, QC, Canada

<sup>3</sup>Department of Integrative Biology, University Of Guelph, Guelph, Ontario, Canada N1G 2W1

<sup>4</sup>Département de biologie, Université de Sherbrooke, Sherbrooke, QC, Canada

**Running title:**

**Keywords:**

**Type of article:** Ideas and Perspectives

**Abstract word count:**

**Main text word count:**

**Number of references:**

**Number of figures:**

**Number of tables:**

**Number of text boxes:**

**Correspondence:**

David Beauchesne

david.beauchesne@uqar.ca

1-514-553-4975

**Statement of authorship:**

**Data accessibility statement:**

## Proposal letter

### Instructions

*Unsolicited proposals, which will be evaluated by the Ideas and Perspectives or Reviews and Syntheses Editors, in consultation with the Editorial Board and Editor-in-Chief, prior to a full submission. Proposals should be no more than 300 words long, describe the nature and novelty of the work, the contribution of the proposed article to the discipline, and the qualifications of the author(s) who will write the manuscript. Proposals should be sent to the Editorial Office (ecolets@cefe.cnrs.fr).*

### Notes

- In it's current form, I believe that the contribution portion is not good enough
- I wonder whether the qualitications 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, 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 realised 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 theoretically as the first exploration of the effects of multiple disturbances on structural properties of food webs, as well as practically by answering questions crucial to management. Our group of co-authors is singularly positioned to write this paper. D. Beauchesne and

69 P. Archambault both have strong backgrounds in environmental assessments in general and  
70 cumulative impacts in particular. K. Cazelles and D. Gravel are both experts in theoretical  
71 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 realised 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

Global changes and human activities result in increasingly intricate environmental stress exposure regimes that can induce complex and unpredictable effects (???; Côté *et al.* 2016; Bowler *et al.* 2019). This cocktail of environmental pressures impedes our ability to evaluate and partition the effects of interacting drivers in cumulative effects assessments (???; ???; Jones 2016). This is in part due to the breadth and interaction potential of environmental pressures operating on natural systems (Côté *et al.* 2016), compounding the pathways of effects through which natural systems can be impacted. Another factor is the potential for non-additive affects, when the effect of multiple interacting drivers is greater (*i.e.* synergism) or lower (*i.e.* antagonism) than the sum of their individual parts, which have been found to be the norm rather than the exception (*e.g.* Darling & Côté 2008; ???; Crain *et al.* 2008; Jackson *et al.* 2016).

Common drivers of environmental stress include climate change, resource exploitation and pollution (???; ???). Drivers have typically been described according to their effects on habitats [*e.g.* (???); (???)]. For instance, fisheries can destroy benthic habitats and extract biomass. Focusing on habitats conveniently circumscribes assessments to a set of tractable units. It also has the drawback of aggregating processes operating at lower levels of ecological organization that we know respond differently to driver exposure (???; ???). For example, hypoxia decreases overall habitat quality but has species-dependent effects, ranging from well-adapted (???) to avoidance behaviour (???), reduced growth (???) and mortality (???; ???; ???). As a consequence, current practice to assess the effects of multiple drivers has offered little insight into underlying ecological mechanisms (Griffen *et al.* 2016; Jackson *et al.* 2016; De Laender 2018; Schäfer & Piggott 2018). Focusing on ecosystem components such as species and communities has thus been deemed necessary to provide a mechanistic understanding of the effects of multiple drivers (???; ???)

At the species and community scales, drivers may be more appropriately described as eco-

logical process modifiers, which we define as natural or anthropogenic processes resulting in a disturbance to ecological processes (Figure 1A). Drivers may disturb a variety of ecological processes such as behaviour (*e.g.* ???; ???), reproduction (*e.g.* ???), physiology (*e.g.* ???), mortality (*e.g.* ???), and species interactions (*e.g.* ???). Multiple processes may be affected by a single driver, while multiple drivers may target a single process. Through this lens, disturbances to cod behaviour and mortality may arise from benthic habitat destruction and from direct extraction, respectively.

Species interactions are particularly relevant in the context of multiple disturbances, as they may serve as the indirect pathways through which pressures permeate entire ecological communities (Wootton 2002; Bascompte 2009; Montoya *et al.* 2009; Thompson *et al.* 2018). Indirect effects, *i.e.* when two or more direct effects are linked by a single species involved in both effects, may be as important of, and propagate faster than, direct effects (Wootton 1993, 2002; Menge 1995; Yodzis 2000). In multi-species systems, where both direct and indirect effects are operating simultaneously, it is expected that the effects of environmental pressures will be amplified or dampened through biotic interactions (???; Wootton 2002; Thompson *et al.* 2018). **Provide examples here, cite ogorman2009; ogorman2012;ghedi2015** Interaction strength and type (*e.g.* omnivory vs apparent competition) have also been linked to enhanced or decreased community persistence (???; ???; Allesina & Pascual 2008). How species are embedded in complex communities is therefore likely to affect their sensitivity to and amplification of single and multiple disturbances.

The complexity of empirical food webs is however 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; 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 (???) 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. **Add some discussion here on archetypes of each motifs, trophic cascades and compensatory dynamics. To cite: cote1995; ogorman2010; ogorman2012;**

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, rather than ensure the persistence of species.

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 investigate and infer the structural role of species and their interactions in mediating the effects of individual and multiple disturbances on food webs. In doing so, we seek to answer questions of particular significance to management: 1) should species interactions be considered in im-

171 pact assessments, 2) should the effects of stressors be evaluated separately or in combination,  
172 and 3) which species are most vulnerable to disturbances based on their trophic position?



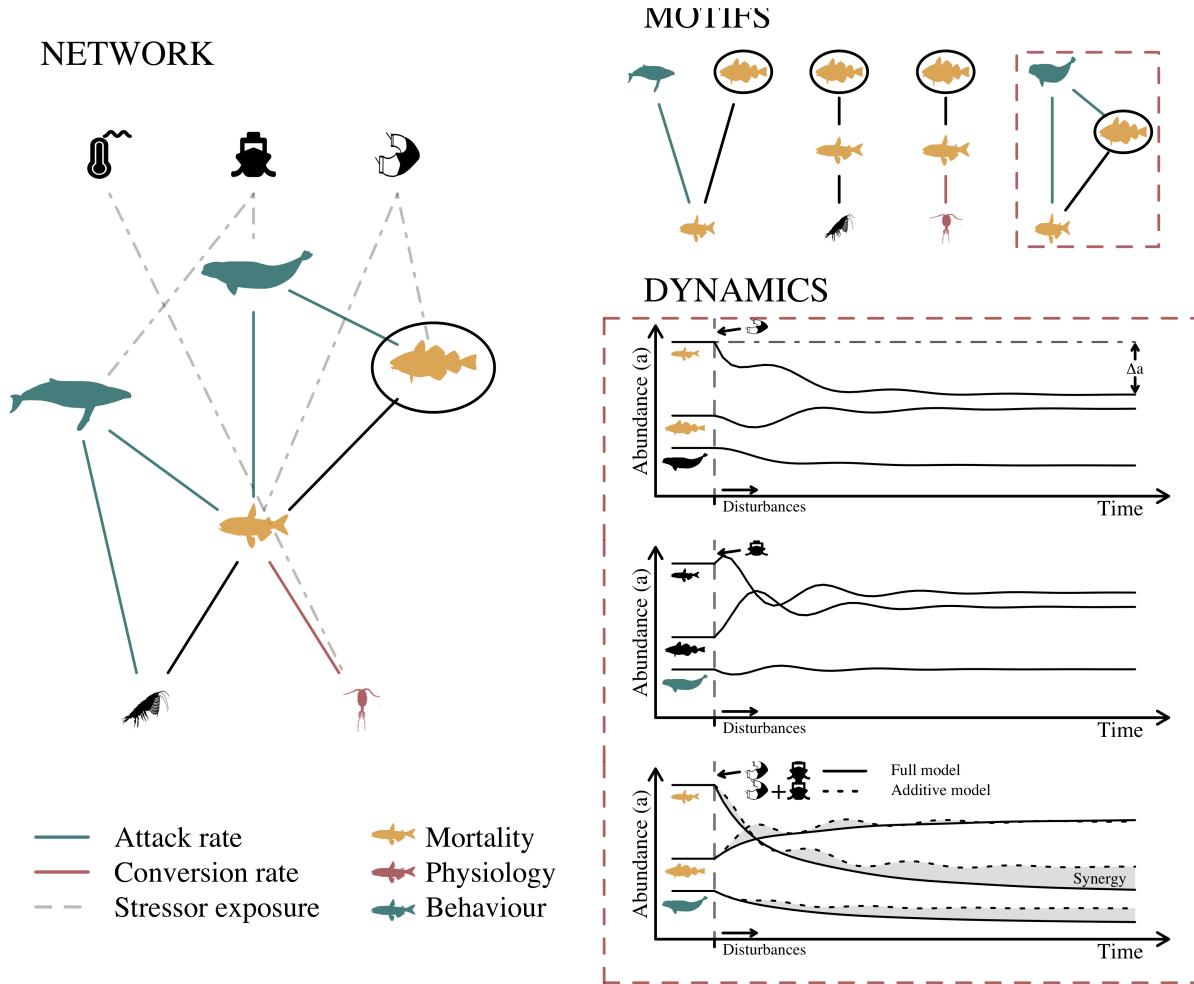


Figure 1: Conceptualization of the effects of multiple sources of environmental stress on the dynamics of a theoretical food web. A) Drivers such as sea surface temperature, marine traffic and fisheries penetrate food webs through various pathways of effects by disturbing ecological processes governing 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 Sumulating disturbances

#### 3.1 Models

The dynamics of the four most abundant 3-species motifs (*i.e.* tri-trophic food chain, omnivory, exploitative and apparent competition) in empirical food webs (Stouffer & Bascompte 2010) were modeled using Lotka-Volterra equation systems (Table S1). Two additional motifs were included to serve as controls to test the importance of considering species interactions when evaluating environmental effects, *i.e.* a partially connected motifs with a disconnected species and a predator-prey interaction, and a fully disconnected motif with three 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 in the consumer models to constrain their growth.

### 3.2 Disturbances

For each motif, a 1% change in initial equilibria equations parameter values was applied to simulate negative disturbances through all possible unique pathways of univariate and multivariate effects. Parameters selected to simulate disturbances were those related to population growth ( $r$  and  $m$ ) and interaction rates ( $e$  and  $\alpha_{ij}$ ), as their effects on population dynamics can readily be attributed to environmental pressure effects. For example, cod mortality will increase through fishing activities, whale attack rates on krill will be altered by behavioural changes induced by marine traffic, and conversion rates of copepods by capelin will be reduced through physiological effects of temperature anomalies on copepods.

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 since those parameters were not to be investigated in our analyses. Conversion rates ( $e$ ) were fixed to 0.5. Finally, a total of 100 sets of mortality ( $m$ ) and attack rates ( $\alpha_{ij}$ ) were evaluated using a simulated annealing algorithm optimizing for consumer abundance.

## 4 Trophic sensitivity

For each 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  $i$  after the simulation of the 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 simulation using all initial conditions:

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

A score of position sensitivity ( $S_i$ ) was evaluated using the mean of the set of all possible pathways of effect ( $K^i$ ) for a give 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 ( $|S_i| = 0$ ).

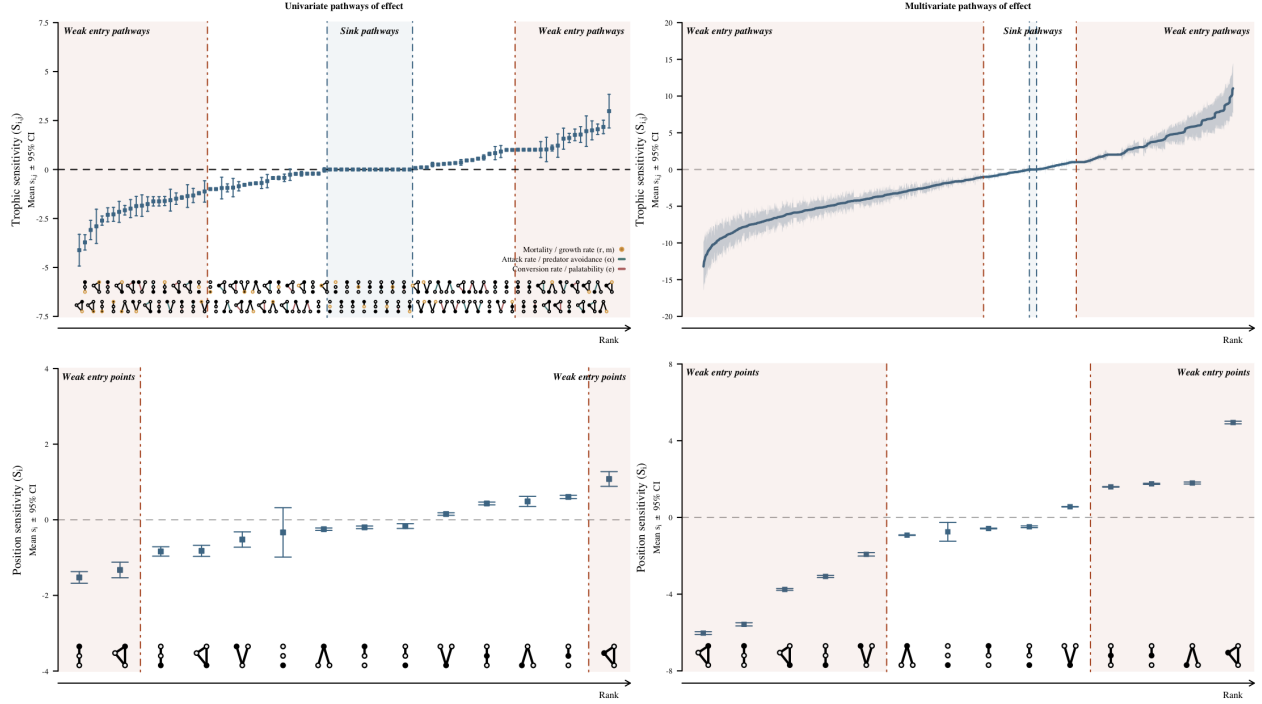


Figure 2

## 5 Trophic amplification

To evaluate whether the effects of disturbances should be investigated in combination, a score of trophic amplification was evaluated to

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

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

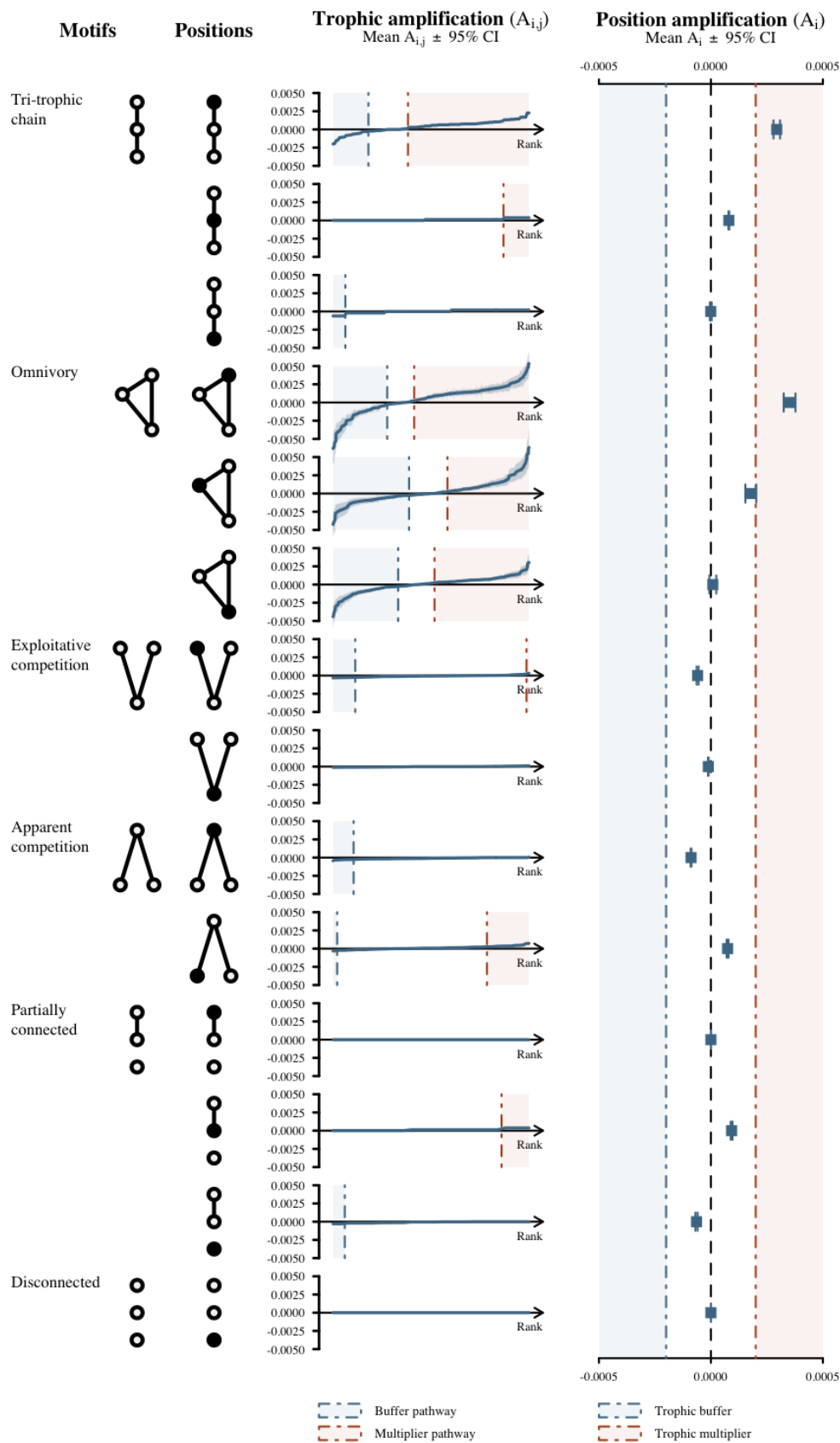
where  $K_j$  is a multivariate pathway of effect  $j$  and  $k_j$  are unitary pathways of effect composition  $j$ . The amplification score evaluates the deviance of a multivariate pathway of effect and the sum of the univariate effects composing the pathway of effect, *i.e.* the additive model. Thus,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

234 antagonistic effect, and a value over 0 identifies synergistic effects.

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

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

237 We define biotic amplifiers as multivariate pathways of effect or motif positions that are more  
238 affected than expected from an additive model ( $A_{i,j} > 0.0005$ ,  $A_i > 0.0005$ ). Biotic buffers  
239 are multivariate pathways of effect or motif positions that are less affected than expected  
240 from an additive model ( $A_{i,j} < 0.0005$ ,  $A_i < 0.0005$ ).

Figure 3  
15

## 6 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 general evaluation of a species sensitivity and amplification potential based on the frequency of times it occupies a position in a food web:

$$S_m = \sum_i f_m i S_i$$

$$A_m = \sum_i f_m i A_i$$

where  $S_m$  and  $A_m$  are the sensitivity and amplification scores of species  $m$ , respectively,  $f_m i$  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  $i$

### 6.1 Empirical food webs

We used empirical food web data from the Estuary and Gulf of St. Lawrence, in eastern Canada, to evaluate the sensitivity and amplification scores of its constituent species. The



255 food webs come from different regions of the St. Lawrence and different time periods, and  
256 contain different yet overlapping functional groups. The Northern (???) and Southern (???)  
257 St. Lawrence food webs were for the mid-1980s, prior to the groundfish stock collapses of  
258 the early 1990s, and contain the same functional groups. The Estuary food web, mean-  
259 while, contains more functional groups and represents the beginning of the 2010s (???). See  
260 supplementary materials for a description of the food webs used for this analysis.



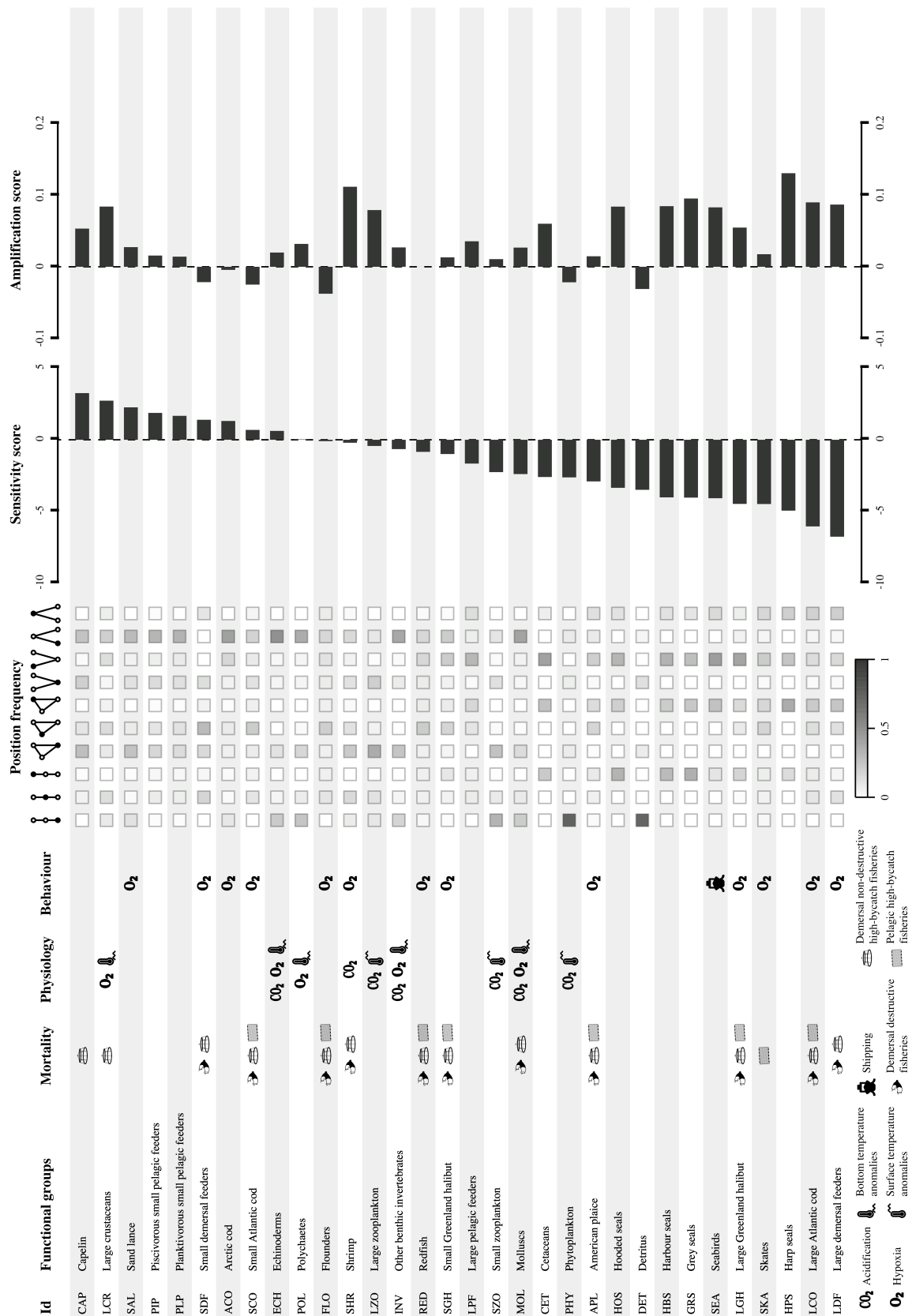


Figure 4

## 7 Supplementary Material

### 7.1 Models

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

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

## 8 References

- Allesina, S. & Pascual, M. (2008). Network structure, predatorPrey modules, and stability in large food webs. *Theoretical Ecology*, 1, 55–64.
- Bascompte, J. (2009). Disentangling the Web of Life. *Science*, 325, 416–419.
- Bascompte, J. & Melián, C.J. (2005). Simple Trophic Modules for Complex Food Webs. *Ecology*, 86, 2868–2873.
- Bowler, D., Bjorkmann, A., Dornelas, M., Myers-Smith, I., Navarro, L. & Niamir, A. *et al.* (2019). The geography of the Anthropocene differs between the land and the sea. *bioRxiv*.
- Camacho, J., Stouffer, D.B. & Amaral, L.A.N. (2007). Quantitative analysis of the local structure of food webs. *Journal of Theoretical Biology*, 246, 260–268.
- Cirtwill, A.R. & Stouffer, D.B. (2015). Concomitant predation on parasites is highly variable but constrains the ways in which parasites contribute to food web structure. *The Journal of Animal Ecology*, 84, 734–744.
- Côté, I.M., Darling, E.S. & Brown, C.J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20152592.
- Crain, C.M., Kroeker, K. & Halpern, B.S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters*, 11, 1304–1315.
- Darling, E.S. & Côté, I.M. (2008). Quantifying the evidence for ecological synergies. *Ecology Letters*, 11, 1278–1286.
- De Laender, F. (2018). Community-and ecosystem-level effects of multiple environmental change drivers: Beyond null model testing. *Global change biology*, 24, 5021–5030.
- Griffen, B.D., Belgrad, B.A., Cannizzo, Z.J., Knotts, E.R. & Hancock, E.R. (2016). Re-thinking our approach to multiple stressor studies in marine environments. *Marine Ecology*

287 *Progress Series*, 543, 273–281.

288 Holt, R.D. (1997). Community modules. In: *Multitrophic Interactions in Terrestrial Ecosys-*  
289 *tems, 36th Symposium of the British Ecological Society* (eds. Grange, A.C. & Brown, V.K.).  
290 Blackwell Science, Oxford, pp. 333–349.

291 Holt, R.D. & Hochberg, M.E. (2001). Indirect interactions, community modules and bio-  
292 logical control: A theoretical perspective. *Evaluating indirect ecological effects of biological*  
293 *control*, 13–37.

294 Jackson, M.C., Loewen, C.J.G., Vinebrooke, R.D. & Chimimba, C.T. (2016). Net effects  
295 of multiple stressors in freshwater ecosystems: A meta-analysis. *Global Change Biology*, 22,  
296 180–189.

297 Jones, F.C. (2016). Cumulative effects assessment: Theoretical underpinnings and big prob-  
298 lems. *Environmental Reviews*, 24, 187–204.

299 Kondoh, M. (2008). Building trophic modules into a persistent food web. *Proceedings of the*  
300 *National Academy of Sciences*, 105, 16631–16635.

301 Menge, B.A. (1995). Indirect Effects in Marine Rocky Intertidal Interaction Webs: Patterns  
302 and Importance. *Ecological Monographs*, 65, 21–74.

303 Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D. & Alon, U. (2002). Network  
304 Motifs: Simple Building Blocks of Complex Networks. *Science*, 298, 824–827.

305 Monteiro, A.B. & Faria, L.D.B. (2016). The interplay between population stability and food-  
306 web topology predicts the occurrence of motifs in complex food-webs. *Journal of theoretical*  
307 *biology*, 409, 165–171.

308 Montoya, J., Woodward, G., Emmerson, M.C. & Solé, R.V. (2009). Press perturbations and  
309 indirect effects in real food webs. *Ecology*, 90, 2426–2433.

310 Schäfer, R.B. & Piggott, J.J. (2018). Advancing understanding and prediction in multiple  
311 stressor research through a mechanistic basis for null models. *Global Change Biology*, 24,

312 1817–1826.

313 Stouffer, D.B. & Bascompte, J. (2010). Understanding food-web persistence from local to  
314 global scales. *Ecology Letters*, 13, 154–161.

315 Stouffer, D.B. & Bascompte, J. (2011). Compartmentalization increases food-web persis-  
316 tence. *Proceedings of the National Academy of Sciences*, 108, 3648–3652.

317 Stouffer, D.B., Camacho, J., Jiang, W. & Nunes Amaral, L.A. (2007). Evidence for the  
318 existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society*  
319 *B: Biological Sciences*, 274, 1931–1940.

320 Stouffer, D.B., Sales-Pardo, M., Sirer, M.I. & Bascompte, J. (2012). Evolutionary Conser-  
321 vation of Species’ Roles in Food Webs. *Science*, 335, 1489–1492.

322 Thompson, P.L., MacLennan, M.M. & Vinebrooke, R.D. (2018). Species interactions cause  
323 non-additive effects of multiple environmental stressors on communities. *Ecosphere*, 9,  
324 e02518.

325 Wootton, J.T. (1993). Indirect Effects and Habitat Use in an Intertidal Community: Inter-  
326 action Chains and Interaction Modifications. *The American Naturalist*, 141, 71–89.

327 Wootton, J.T. (2002). Indirect effects in complex ecosystems: Recent progress and future  
328 challenges. *Journal of Sea Research*, Structuring Factors of Shallow Marine Coastal Com-  
329 munities, Part I, 48, 157–172.

330 Yodzis, P. (2000). Diffuse Effects in Food Webs. *Ecology*, 81, 261–266.