

On the vulneravility of food webs to multiple stressors

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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.

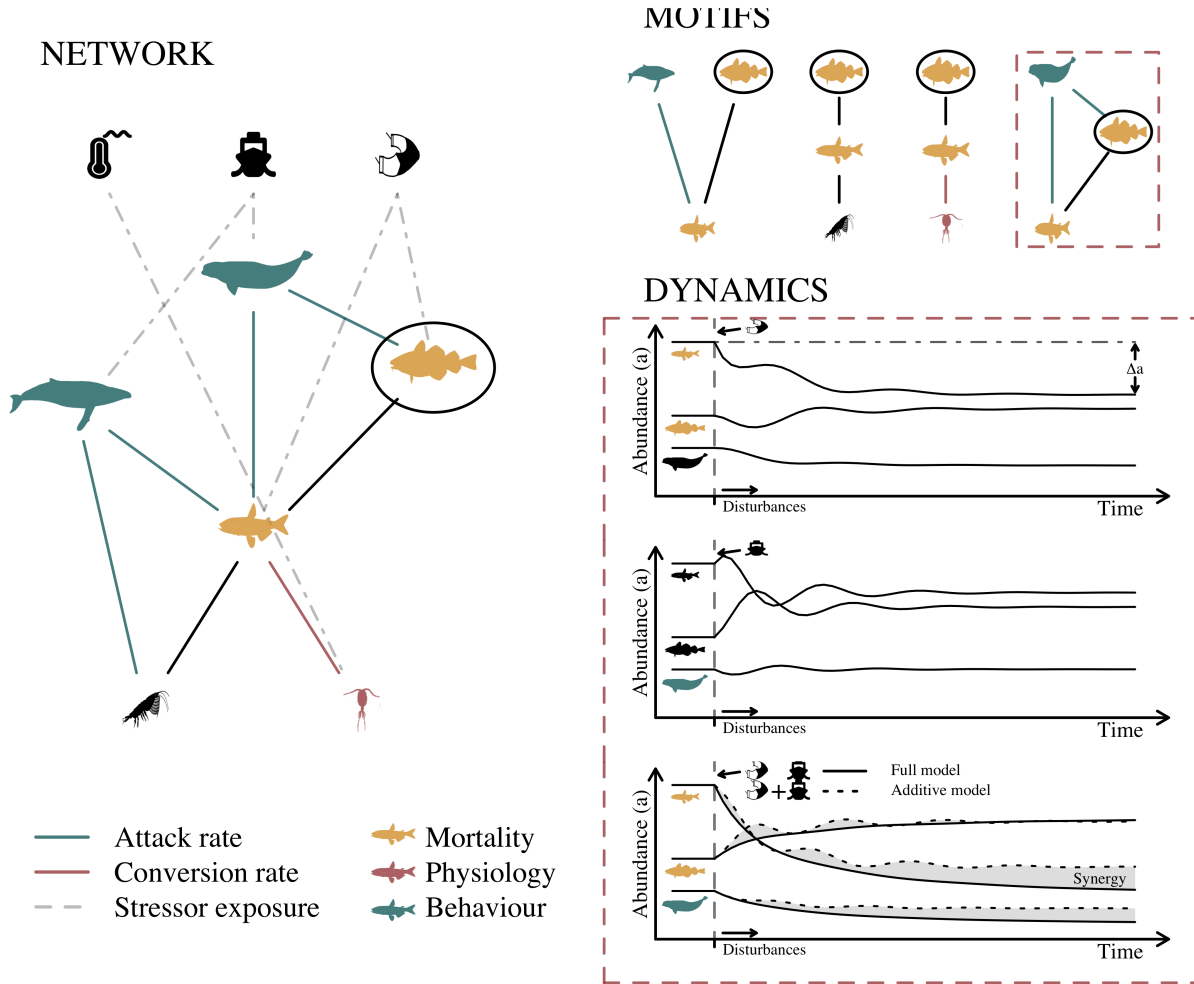


Figure 1: Conceptualization of the effects of multiple sources of environmental stress on the dynamics of a theoretical food web. A) Drivers such as sea surface temperature, marine traffic and fisheries penetrate food webs through various pathways of effects by disturbing ecological processes governing 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, α_{ii} is the density-dependent effect of the resource on itself and α_{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 (α_{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 (α_{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 α_{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 species vulnerability as the combination of trophic sensitivity and trophic amplification, as described in the methodology. Two sets of scores are used 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

287 frequency of times it occupies a position in a food web:

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

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

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

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

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

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

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

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

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

299 ***Explain here that this evaluation is not one of the vulnerability of species from***
300 ***their biological perspective, but rather their vulnerability based on the types of***
301 ***drivers in the system and their trophic position***

4 Results

4.1 Motifs vulnerability

The simulations uncover, as anticipated, that interaction motifs (*i.e.* food chain, omnivory, exploitative and apparent competition) are more sensitive and more likely to amplify the effects of multiples disturbances than control motifs (Figures 2, 4). Species in omnivory and food chain motifs are generally more sensitive and likely to amplify the effects of disturbances than species in competitive interaction motifs (Figures 2, 4).

Biotic sinks are composed almost exclusively of pathways targeting control motif positions (Figure 2) and simulations on control motifs largely result in additive affects (Figure 4). Weak entry points, biotic buffers and biotic amplifiers, meanwhile, are prevalent for all interaction motifs (Figures 2, 4). This is particularly true for species in the omnivory motif and for the top predator in the food chain motif, whose trophic sensitivity and amplification scores are highly variable (Figures 2, 4).

Species position also greatly influences trophic sensitivity to and amplification of disturbances. In general, top predators are weak entry points for all interaction types (Figure 2). In contrast, non-additive effects on top predators depends on interaction type. Pathways of effect on top predators in omnivory and food chain interactions largely result in synergistic or antagonistic effects, and predators are, on average, biotic amplifiers (Figure {amplification}). Predators in competitive interactions, meanwhile, are less affected by non-additive effects and are fringe biotic buffers (Figure {amplification}).

Resources are largely weak entry points for all motifs, yet the effect are typically negative in food chain and omnivory interactions, and positive in competitive interactions (Figure 2). Although resources are, on average, neither biotic buffers or amplifiers, the effects of individual pathways of effects are mostly non-additive (Figure 4). The effects of disturbances through the other interactions are mostly additive. (Figure 4).

327 Meso-predators, which are found only in omnivory and food chain interactions, are weak
328 entry points and benefit from disturbances in general (Figure 2). Meso-predators in omnivory
329 interactions are, on average, fringe biotic buffers, but like all other positions in the omnivory
330 motif, most individual pathways of effect result in either antagonistic or synergistic effects
331 Figure 4).

332 The nature of the pathways of effects also influences trophic sensitivity and amplification.
333 Unsurprisingly, multivariate pathways of effects are generally more impactful to species sen-
334 sitivity and hold a higher proportion of weak entry points than univariate pathways (Figure
335 2). Similarly, targeting multiple biological processes and combining direct and indirect ef-
336 fects will always result in greater sensitivity and amplification (Figure 3). There are however
337 a few generalities worth noting. Mortality and growth rates are driving heightened trophic
338 sensitivities, yet do not individually contribute to non-additive effects (Figure 4). Trophic
339 amplification is rather driven by attack and conversion rates (Figure 4). Most strikingly,
340 indirect effects are more impactful to both trophic sensitivity and amplification (Figure 4),
341 with direct effects largely resulting in additive impacts (Figure 4).

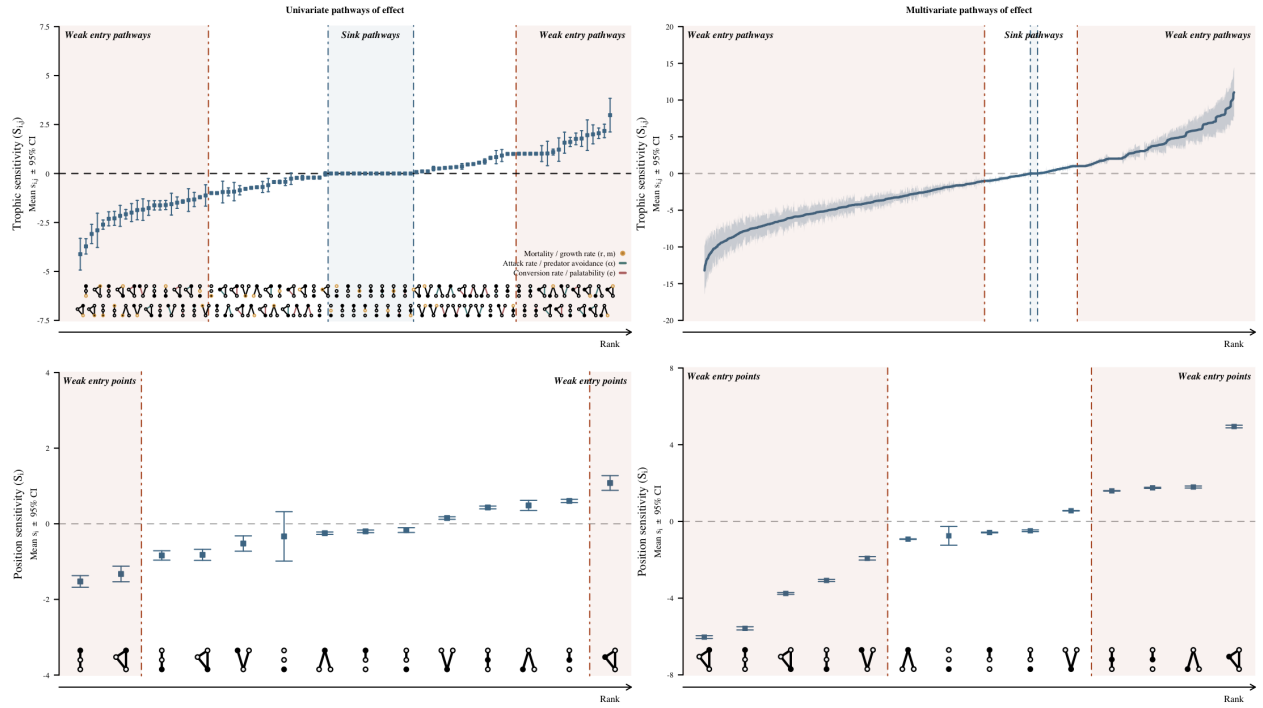


Figure 2: Ranking of all univariate and multivariate pathways of effect as a function of trophic (A,B) and position (C,D) sensitivity. Pathways and motif positions identified as weak entry points (*i.e.* highly sensitive to disturbances) and biotic sinks (*i.e.* insensitive to disturbances) are identified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

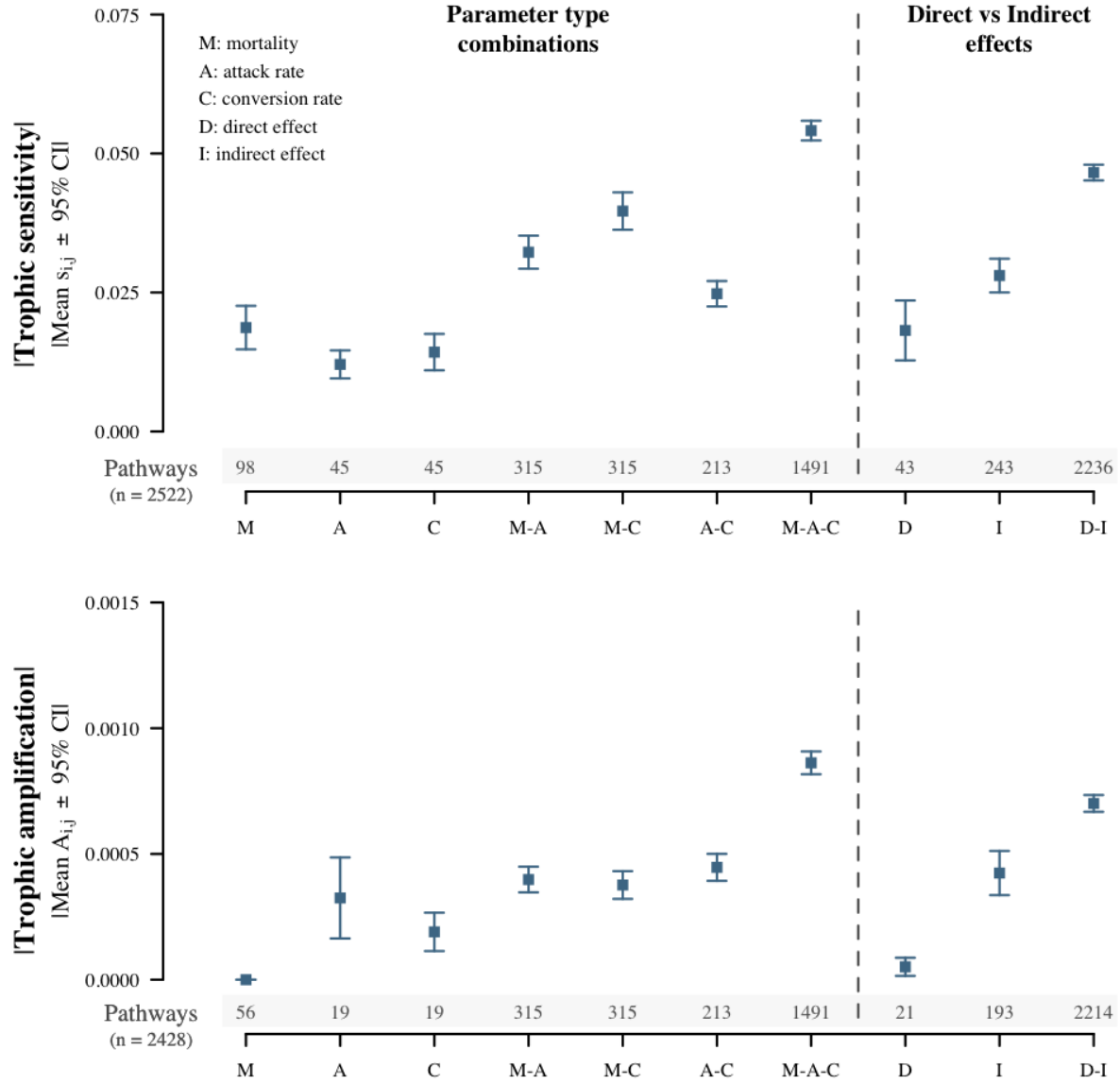


Figure 3: Absolute values of the mean trophic sensitivity (A) and amplification (B) as a function of disturbed parameter type and direct or indirect effects. All pathways of effect targeting a specific parameter type (*i.e.* mortality, attack and conversion rates) were grouped to evaluate their respective 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.

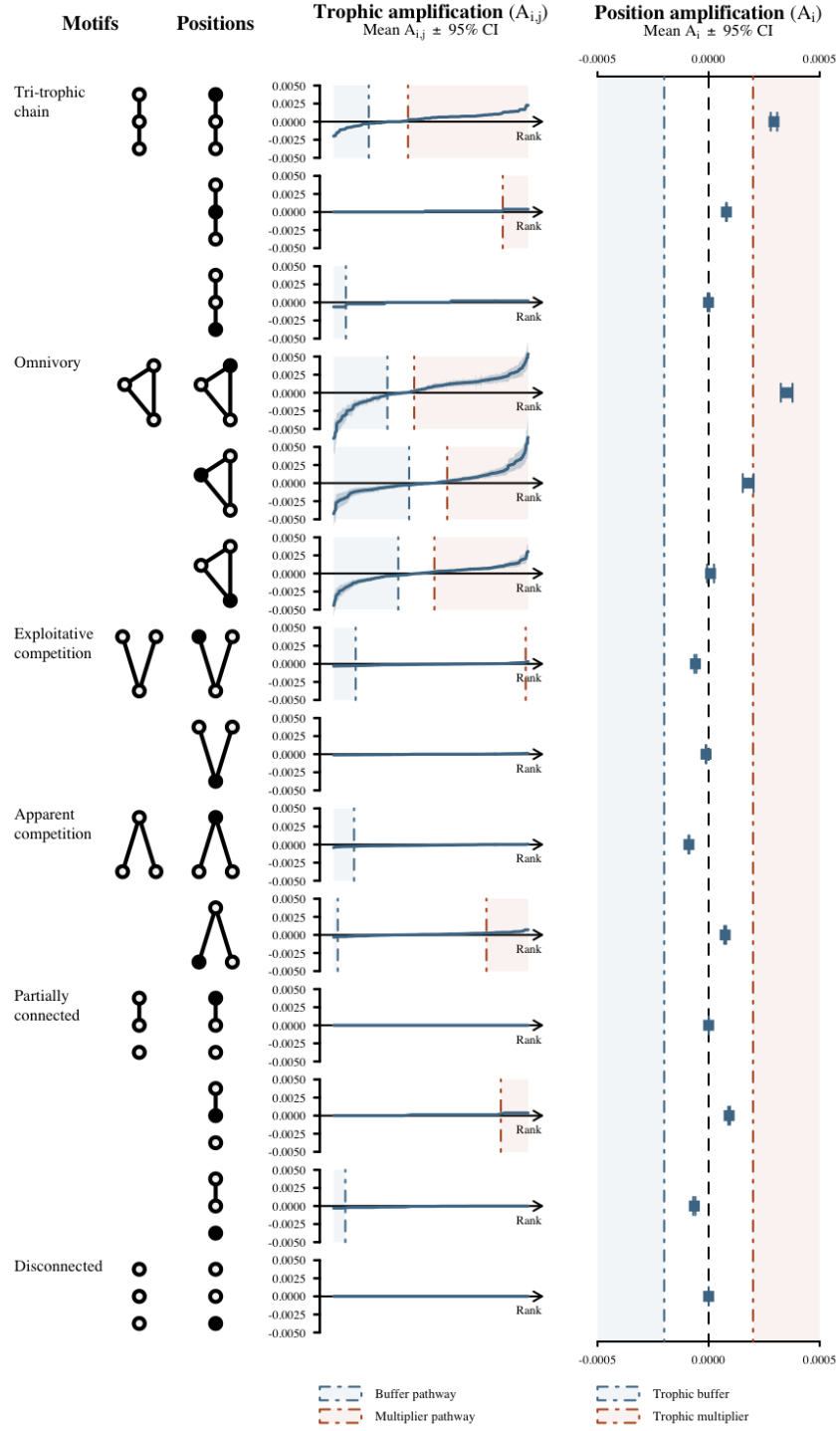


Figure 4: Ranking of all multivariate pathways of effect as a function of trophic and position amplification, for each motif position. Pathways and motif positions identified as biotic buffers (*i.e.* affected synergistically by disturbances) and biotic buffers (*i.e.* affected antagonistically by disturbances)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

4.2 Network-scale vulnerability

Using the most common environmental pressures in the Northern Gulf of St. Lawrence with the topology of a food web from the mid-1980s to identify realised pathways of effect between all 3-species combinations, and their simulated scores as heuristics, we ranked species and functional groups as a function of their overall trophic sensitivity and amplification.

We find that sensitivity and amplification scores do not co-vary (Figure 5). We also find that species targeted by multiple drivers are not necessarily the most vulnerable based on their trophic position. For example, even though the mortality, physiology and behaviour of shrimp were expected to be impacted by drivers, it is nonetheless insensitive based on its trophic position (Figure 5). Similarly, species impacted by few drivers like sea birds, or no drivers at all like seals, may nonetheless be highly vulnerable due to its trophic position (Figure 5).

Large demersal predators, sea birds and seals are mostly weak entry points and biotic amplifiers (Figure 5). Prey species and large crustaceans appear to benefit from disturbances and may act as positive weak entry points in the St. Lawrence (Figure 5). Invertebrates in general and species like shrimp and redfish appear largely insensitive to disturbances (Figure 5).

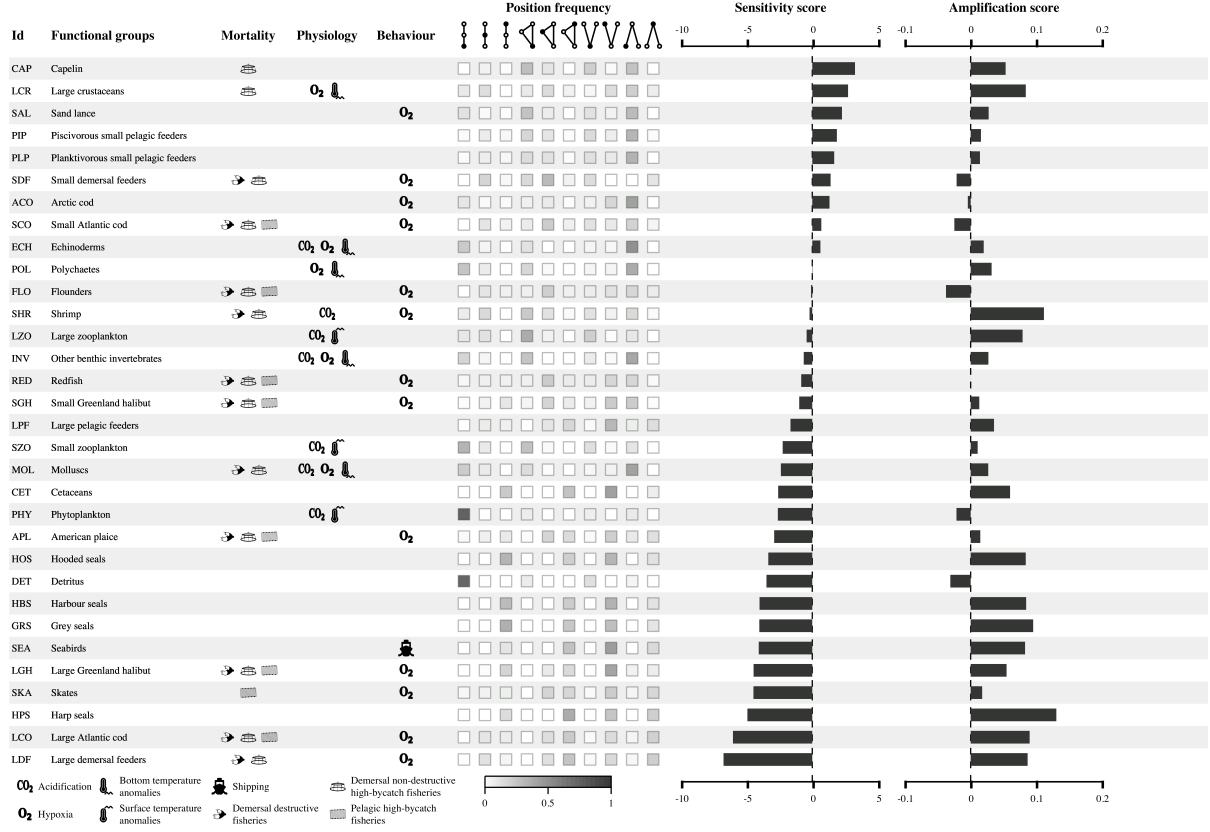


Figure 5: Change in species and functional groups sensitivity and amplification scores as a function of realised pathways of effects for an empirical food web of the Northern Gulf of St. Lawrence in the mid-1980s [?]. The left-hand side of the table presents the species and functional groups, the drivers 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.

³⁵⁹ **5** What it all means

³⁶⁰ **6** The way forward

7 Supplementary Material

7.1 Models

Motifs	Equation systems	Initial parameters values
Tri-trophic food chain	$\begin{aligned}\frac{dX_i}{dt} &= X_i(r_i - \alpha_{ii}X_i - \alpha_{ij}X_j) \\ \frac{dX_j}{dt} &= X_j(e_{ij}\alpha_{ij}X_i - \alpha_{jk}X_k - m_j) \\ \frac{dX_k}{dt} &= X_k(e_{jk}\alpha_{jk}X_j - m_k)\end{aligned}$	$r_i = 1$ $\alpha_{ii} = 0.001$ $\alpha_{ij}, \alpha_{jk} \in [0.0001, 0.01]$ $e_{ij}, e_{jk} = 0.5$ $m_j, m_k \in [0.01, 0.5]$
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

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