On the vulnerability of food webs to multiple stressors

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Proposal letter

Instructions

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

our framework can be applied to detect most sensitive species in a real food web exposed to various stressors. Our group of co-authors is singularly positioned to write this paper. D. Beauchesne and P. Archambault both have strong backgrounds in environmental assessments in general and cumulative impacts in particular. K. Cazelles and D. Gravel are both 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

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

Species sensitivity to environmental pressures can be highly variable, which further compounds the complexity of mutliple drivers studies. For example, hypoxia decreases overall habitat quality but has species-dependent effects, ranging from well-adapted (*e.g.* northern shrimp *Pandalus borealis* and Greenland halibut *Reinhardtius hippoglossoides*; Pillet *et al.* 2016) to avoidance behaviour (*e.g.* Atlantic cod *Gadus morhua*; Chabot & Claireaux 2008), and mortality (*e.g.* sessile benthic invertebrates; Eby *et al.* 2005; Belley *et al.* 2010). Moreovers, species are also embedded in a complex web of interactions that provides indirect pathways of effects through which pressures may permeate entire ecological communities (Wootton 2002; Bascompte 2009; Montoya *et al.* 2009; O'Gorman & Emmerson 2009; O'Gorman *et al.* 2012). 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). Empirical examples of trophic cascades are abundant throughout all types of ecosystems globally (Estes *et al.* 2011). 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 (Ives 1995; Wootton 2002; Thompson *et al.* 2018). Community dynamics and how species are embedded in complex networks is therefore likely to affect their sensitivity to environmental pressures.

Confronted with the challenge of managing and preserving complex systems, there is an 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

3 Of food web and multiple disturbances

3.1 Conceptulizing 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 ocean warming and ocean acidification may affect physiological processes of benthic invertebrates such as calcification rates. 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 prevalance (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 conversation efforts. For example, results from Stouffer *et al.* (2012) suggest that certain species may 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. This means that strictly using species richness as a conservation measure may ignore the benefits to community persistence provided by the trophic roles of individual species. Using trophic roles as targets may thus be valuable for community conservation (Stouffer *et al.* 2012).

Managers are not only tasked with species conservation, however. For example, the dynamics of coexisting species is particularly important to practitioners whose mandate is to monitor and manage exploited populations using holistic approaches such as ecosystem based fisheries management. In this context, population fluctuations are at least as important as species persistence. As such, studying the dynamics of persistent communities is of particular relevance to management in the context of multiple environmental pressures (Figure 1C).

Here, we study the equilibrium dynamics, i.e. when species are constrained to coexistence, 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 realized pathways of effects.
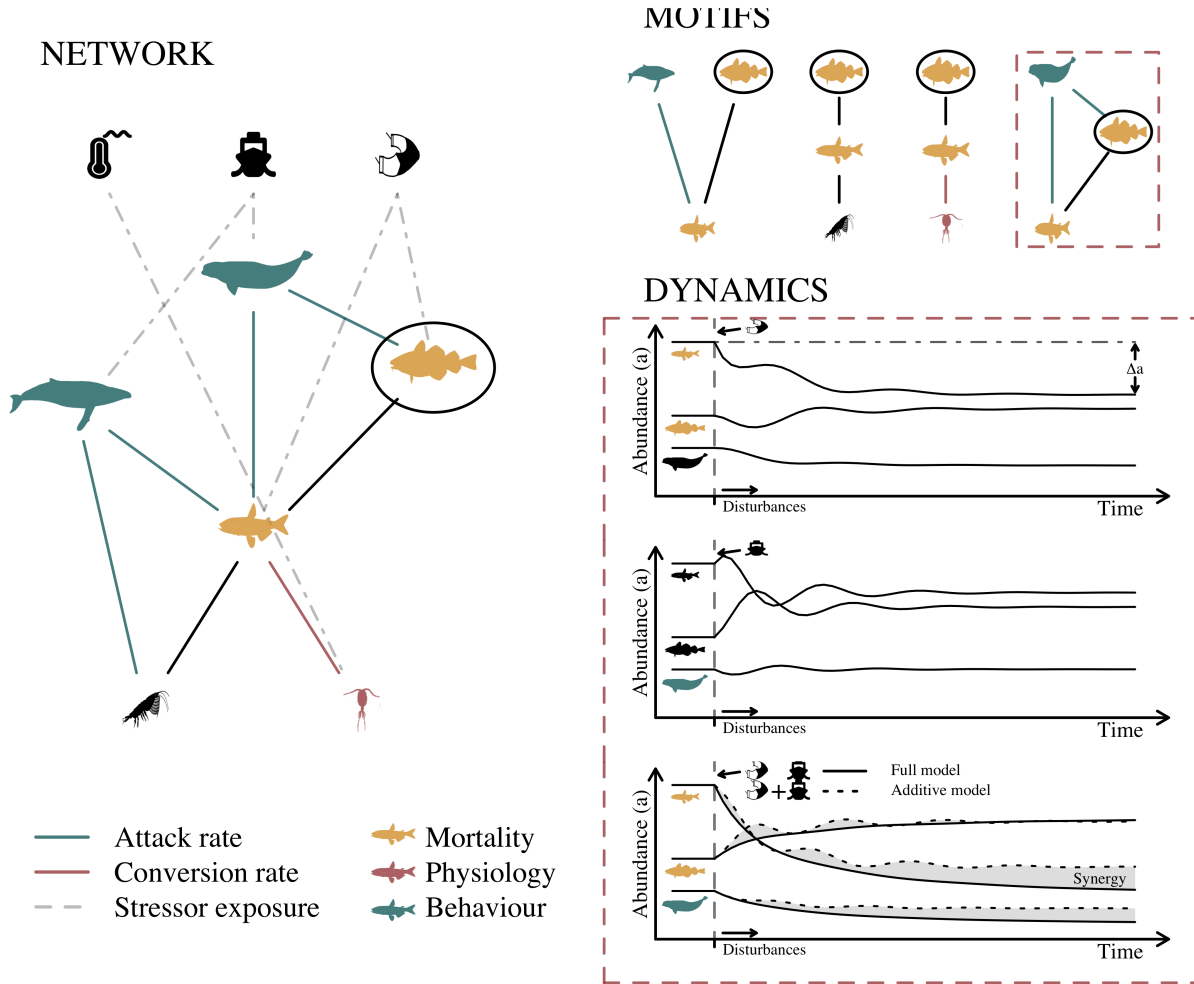
Figure 1: Conceptualization of the effects of multiple sources of environmental stress on the dynamics of a theoretical food web. A) Drivers such as sea surface temperature, marine traffic and fisheries penetrate food webs through various pathways of effects by disturbing ecological processes governing 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 effecs 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

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

where X_i denotes species i, 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

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

where m_j is the mortality rate of species j and e_{ij} is the rate at which resource i biomass is transformed into consumer j 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. Refer to table S1 for the detailed equation systems of all motifs considered.

3.2.2 Models parameterization

Model dynamics was to be constrained by species coexistence, meaning that abundances for all species was to be positive before and after disturbances were simulated. To achieve this, we first arbitrarily set the values of a number of initial model parameters. 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, and conversion rates (e) were fixed to 0.5. We then set an interval of possible values for mortality ($m \in [0.01, 0.5]$) and attack ($\alpha_{ij} \in [0.0001, 0.01]$) in which we extracted 100 sets of initial values. Values were identified using a simulated annealing algorithm optimizing for consumer abundance. Sets of parameters were only retained if initial abundances and abundances resulting from all possible pathways of effect were positive (see next section).

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.

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259 For each motif, all possible mortality, resource growth, conversion and attack rates parameter
260 combinations were simulated. This resulted in a total of 930 unique pathways of effects
261 for all motifs combined (food chain, competitive exploitation and apparent competition:
262 7 parameters, 127 pathways of effects; omnivory: 9 parameters, 511 pathways of effects;
263 partially connected 5 parameters, 31 pathways of effects; disconnected: 3 parameters, 7
264 pathways of effects).

3.3 Motifs vulnerability

3.3.1 Trophic sensitivity

267 For all 13 unique motif positions considered and all unique pathways of effects, we define $s_{i,j}$
268 as:

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

269 where a_i is the initial abundance at position i without disturbance, and $a_{i,j}$ is the abundance
270 at position i with disturbance due to pathway of effect j. Note that, by definition, $s_{i,j}$ is
271 bounded negatively to -1, as abundances cannot fall below 0. We define the sensitivity score
272 of position i for single pathway of effect j $S_{i,j}$ as the mean of $s_{i,j}$ over the 100 sets of initial
273 conditions.

274 The overall position sensitivity S_i was evaluated using the mean of $S_{i,j}$ over the set of all
275 possible pathways of effect $(K^{(i)})$ for a given position i:

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

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

278 positions ($|S_i| = 0$).

3.3.2 Trophic amplification

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

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

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

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

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

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

3.4 Species vulnerability

3.4.1 Scores

We broadly refer to species vulnerability as the combination of trophic sensitivity and trophic amplification, as defined in this study. Two sets of scores are presented at the species level.

The first set are topological scores of trophic sensitivity and amplification based on the frequency at which species occupy one of the 4 main motif positions we considered, *i.e.* food chain, omnivory, exploitative and apparent competition, in an empirical 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 mean trophic sensitivity and amplification scores at position i, respectively. Note that for species vulnerability, we do not consider the control motifs any further.

The second set are realized scores of trophic sensitivity and amplification based on realized pathways of effects, *i.e.* known or suspected effects of drivers affecting mortality, behaviour or physiology of species in empirical food webs:

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

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

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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

Realized pathways of effect are identified using the following rules:

1. impacts of drivers on the mortality of resources and consumers are considered as disturbances to resource growth rates and to consumer mortality rates (r, m).
2. impacts on the behaviour of resources and consumers are considered as disturbances to consumer attack rates (α_{ij}).
3. impacts on the physiology of resources and consumers are considered as disturbances to consumer conversation rates (e).

3.4.2 Empirical food webs

We evaluated the vulnerability of species in 3 empirical webs from the Southern (SSL) and Northern (NSL) Gulf, and Estuary (ESL) of St. Lawrence in eastern Canada (**???**; **???**; Morissette *et al.* 2003). The Southern and Northern Gulf of St. Lawrence food webs correspond to the mid-1980s, prior to a groundfish stock collapse in the early 1990s, while the St. Lawrence Estuary food web corresponds to the early 2010s. The total number of species and functional groups differs between food webs ($n_{SSL} = 30$; $n_{NSL} = 32$; $n_{ESL} = 41$;), yet there is significant overlap ($n_{all} = 21$). Food webs resolution is biased towards commercial fish for all food webs. In the food webs, interactions are identified as a percent of species or functional group in the diet of another species or functional group. Only diet percent > 0.1 were considered as interactions in our analysis. Note that detailed vulnerability results are only presented and discussed for the Northern Gulf food web. Results for the Estuary and Southern Gulf are available as supplementary material (Figures S1, S2).

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3.4.3 Drivers

Climate change related drivers (*i.e.* acidification, hypoxia, and bottom and surface temperature anomalies) are prevalent in the St. Lawrence System, with the exception of hypoxia in the Southern Gulf (**???**). Marine traffic is widespread, especially in the Northern Gulf and the Estuary, which serve as the main seaway to inland North-America (**???**). Fisheries have changed through time after the collapse of groundfish stocks in the early 1990s. Species affected by fisheries were identified using the catch data provided in the description of the food web models (**???**; **???**; Morissette *et al.* 2003). Geartype used was identified using landing data from logbooks from the Department of Fisheries and Ocean's Canada [dfo2016b].

The impacts of specific drivers on species and functional groups was done following broad rules to simplify the number of assumptions required. Our approach does not seek to establish the vulnerability of a particular species to all types of drivers, but rather to make general inference on species trophic vulnerability based of its trophic position and the supposed effects of drivers on biological processes driving community dynamics. Detailed literature search or expert knowledge could be used to get a better sense of the proximate effects of drivers on species, but this is beyond the scope of our objective.

The first criteria used to evaluate the effect of drivers on species and functional groups was a broad evaluation of direct exposure to individual drivers. Acidification, hypoxia and bottom temperature anomalies are widespread in the deep habitats of the St. Lawrence, while surface temperature anomalies and marine traffic are operating on the surface layer (**???**). As such, species of functional groups in deep or surface habitats were considered as exposed to deep or surface drivers, respectively. The effects of hypoxia and temperature anomalies was then considered as impacting the physiology or behaviour of exposed species with low or high mobility, respectively. Ocean acidification was assumed to affect the physiology of exposed carbonate-secreting organisms (*e.g.* mollusks and crustaceans; Kroeker *et al.* 2013). Marine traffic was considered as primarily impacting whale behaviour (**???**; **???**). The impact

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of fisheries was assumed to target the mortality rates of species with positive catch rates. Catches of certain species or functional groups of seals and seabird through hunting, and whales through bycatch, is reported for the empirical food webs of the St. Lawrence (**???**; **???**; Morissette *et al.* 2003). We thus considered that the mortality rates of seabirds and marine mammals with reported catches was disturbed.

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, 3). 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, 3).

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 3). Weak entry points, biotic buffers and biotic amplifiers, meanwhile, are prevalent for all interaction motifs (Figures 2, 3). 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, 3).

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

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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). Altough resources are, on average, neither biotic buffers or amplifiers, the effects of individual pathways of effects are mostly non-additive (Figure 3). The effects of disturbances through the other interactions are mostly additive. (Figure 3).

Meso-predators, which are found only in omnivory and food chain interactions, are weak entry points and benefit from disturbances in general (Figure 2). Meso-predators in omnivory interactions are, on average, fringe biotic buffers, but like all other positions in the omnivory motif, most individual pathways of effect result in either antagonistic or synergistic effects Figure 3).

The nature of the pathways of effects also influences trophic sensitivity and amplification. Unsurprisingly, multivariate pathways of effects are generally more impactful to species sensitivity and hold a higher proportion of weak entry points than univariate pathways (Figure 2). Similarly, targeting multiple biological processes and combining direct and indirect effects will always result in greater sensitivity and amplification (Figure 4). There are however a few generalities worth noting. Mortality and growth rates are driving heightened trophic sensitivities, yet do not individually contribute to non-additive effects (Figure 3).

Trophic amplification is rather driven by attack and conversion rates (Figure 3). Most strikingly, indirect effects are more impactful to both trophic sensitivity and amplification (Figure 3), with direct effects largely resulting in additive impacts (Figure 3).
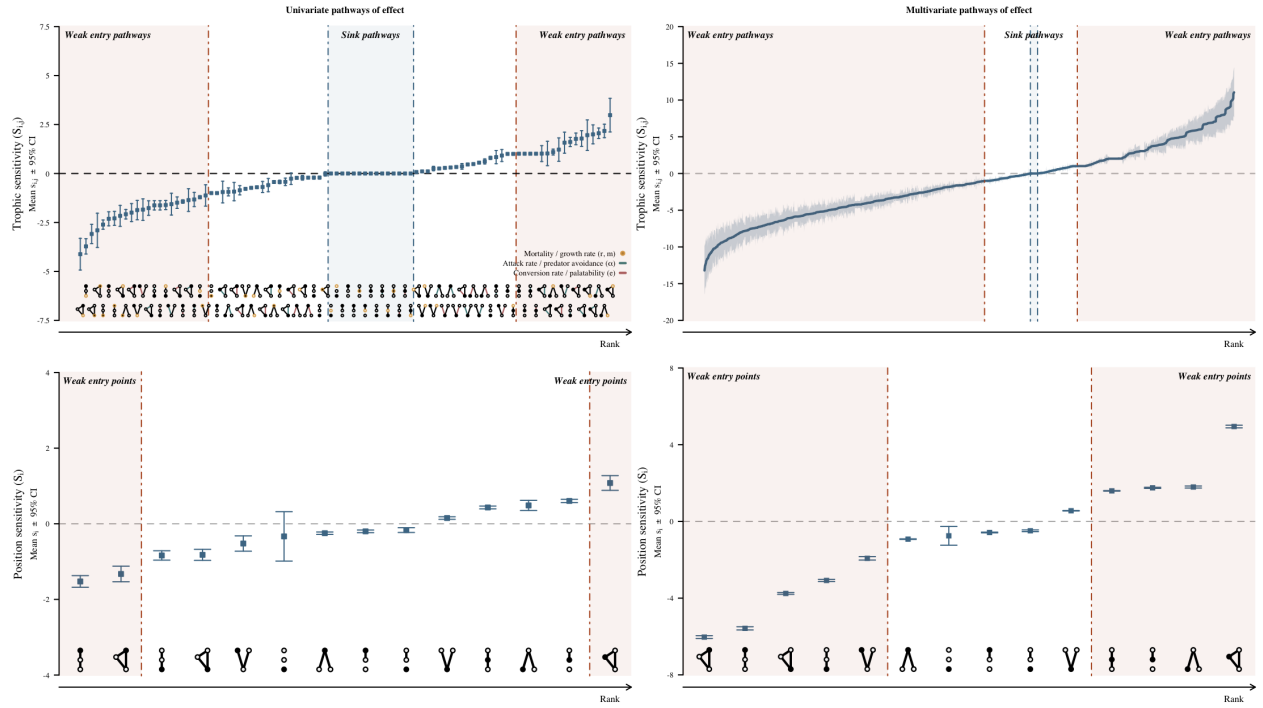
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Figure 2: Ranking of all univariate and multivariate pathways of effect as a function of trophic (A,B) and position (C,D) sensitivity. Pathways and motif positions identified as weak entry points (*i.e.* highly sensitive to disturbances) and biotic sinks (*i.e.* insensitive to disturbances) are identified by the red and blue regions, respectively.

Figure 3: 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 antagonisticaly by disturbances) are identified by the red and blue regions, respectively.
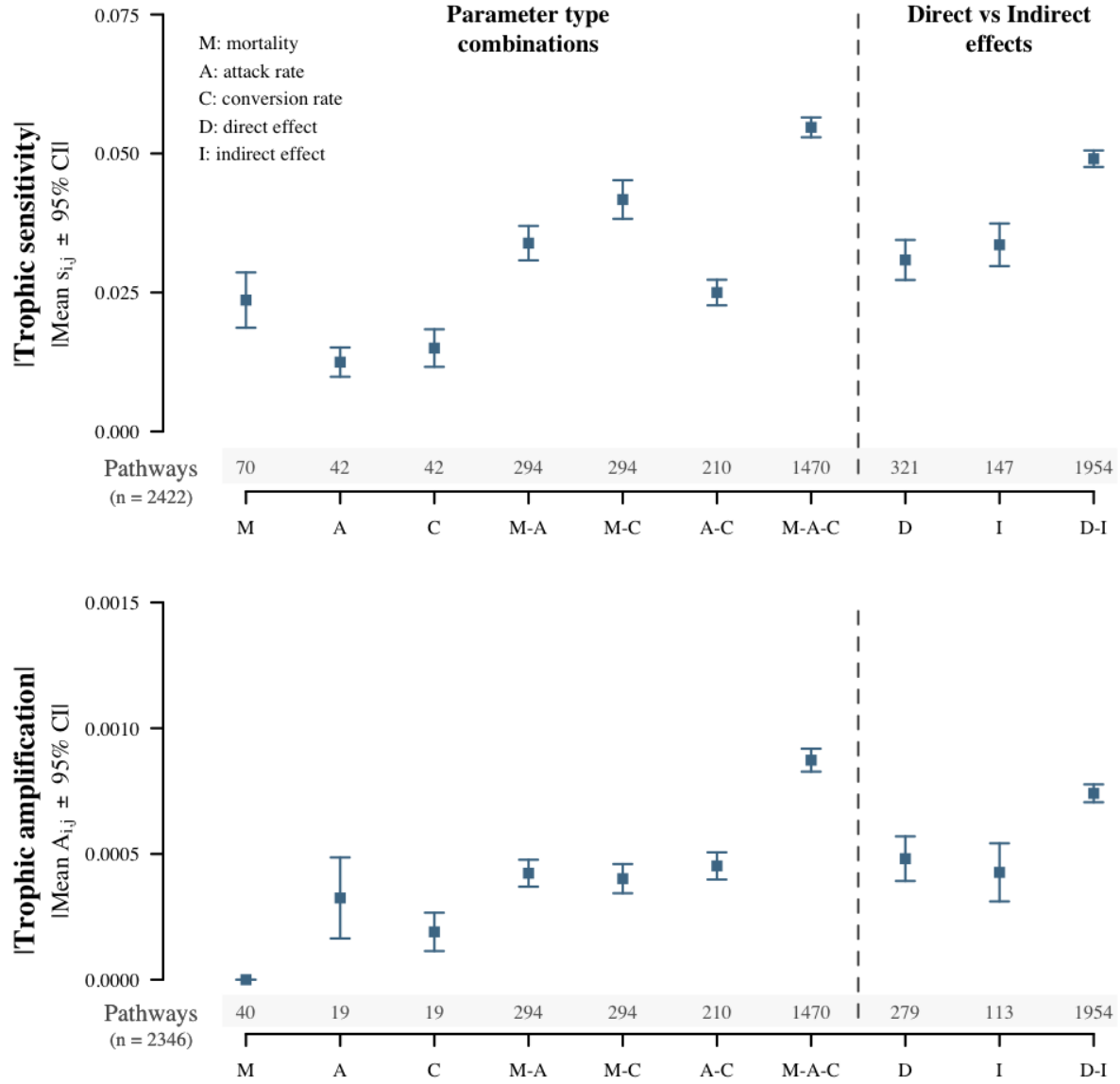
Figure 4: Absolute values of the mean trophic sensitivity (A) and amplification (B) as a function of disturbed parameter type and direct or indirect effects. All pathways of effect targeting a specific parameter type (*i.e.* mortality, attack and conversion rates) were grouped to evaluate their respective 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.

4.2 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).
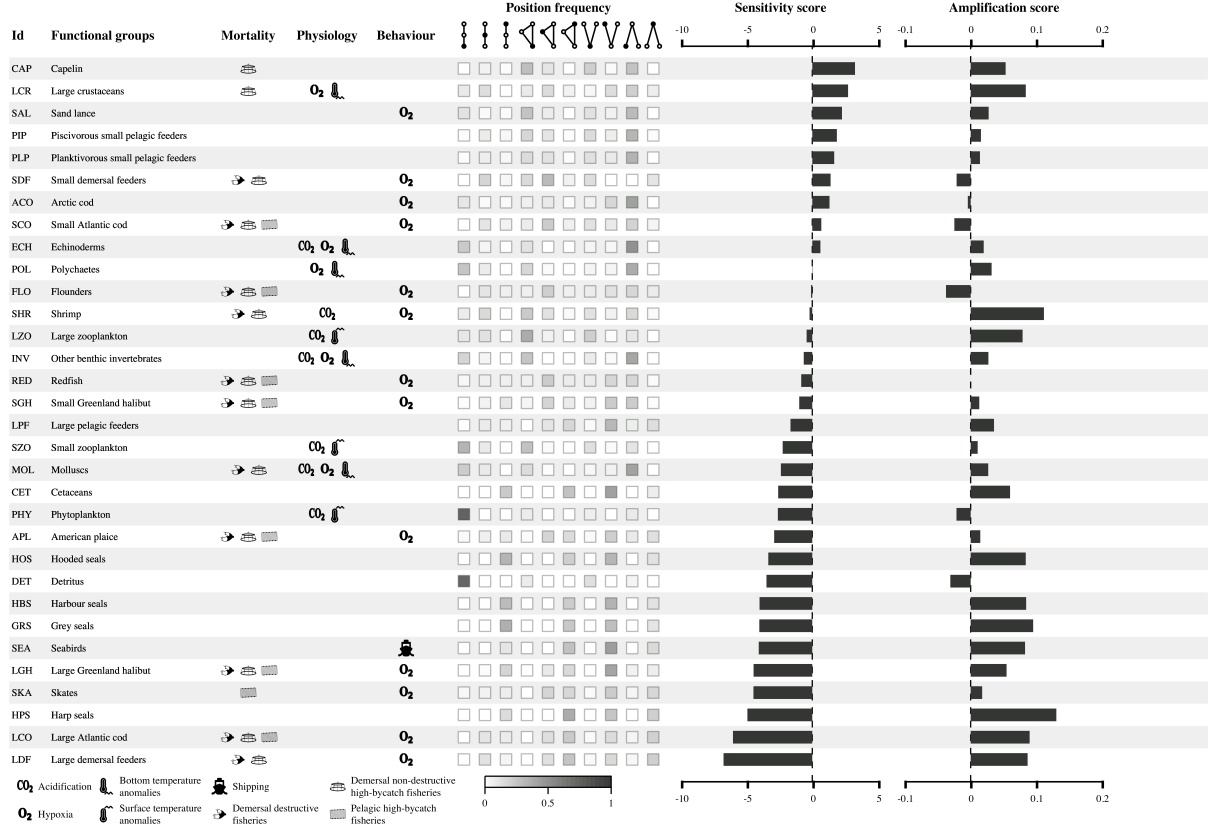
Figure 5: Change in species and functional groups sensitivity and amplification scores as a function of realised pathways of effects for an empirical food web of the Northern Gulf of St. Lawrence in the mid-1980s [**?**]. The left-hand side of the table presents the species and functional groups, the 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, 3). 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.

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5 What it all means

- Amplification increases with interaction complexity

First try: using introductory questions to structure discussion

In conceptualizing the effects of multiple environmental pressures on food webs and the role of species and their interactions in spreading disturbances, we sought to use well-established ecological theory to answer questions of particular relevance to management.

We first find, as expected, that species interactions should be explicitly considered in impact assessments, as they greatly influence trophic vulnerability to the effects of disturbances. This supports longstanding evidence that interactions play a crucial role in spreading the effects of individual disturbances through food webs (*e.g.*@menge1995; Wootton 1993, 2002; Yodzis 2000), and unsurprisingly extends this conclusion to multiple disturbances.

We further uncover the that type of interactions a species is involved in influences its vulnerability to disturbances.

Omnivory and food chain in particular are responsive to disturbances, while exploitative and apparent competition are less vulnerable. [. . .]

We provide evidence that indirect effects are at least as important as direct effects in driving species vulnerability and that they are they seem to be the main source of non-additive effects at the community scale. [. . .]. This means that when studying population dynamics, the effects of multiple drivers cannot be studied outside of the context of species interactions.

Secondly, we find that the effects of multiple disturbances should be considered in combination, as non-additive effects often arise from disturbances to two or more biological processes.

Pathways of effect to omnivory and top predator in food chain interations

Au final, ce que je veux dire c<et que les interactions d'omnivorie et le top prédateur de la chaîne tri-trophique en particulier sont caractérisés par des effects non-additifs. La majorité

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des pathways

Ça va dépendre de chemins d'effects spécifiques, pas de généralité possible sur ces positions!

Additionally, there are no specific property of individual pathways of effect that conclusively differentiate biotic buffers and amplifiers.

Pathways of effects

Omnivory interactions and the top predator in the food chain motif in particular are characterized mostly

However, non-additive effects are however highly variable between interaction type and species position. In particular, pathways of effect on omnivory interacations largely lead to both biotic buffers and biotic amplifiers. Aditionnally, we

Predicting non-additive effects there seems pretty damn hard.

what differentiates biotic buffers and biotic amplifiers.

the types of pathways of effects that either

as to specific types of pathways of effects

accumulation of pathways of effects that lead to non-additive effects.

In general, omnivory and food chain interactions tend to

There is however a lot of variability

- Many non-additive effects arise from
- Lot of variability in the nature of the non-additive effect, with no precise indication of what drives a species to be a biotic buffer or a biotic amplifier, suggesting that considering effects of pressures in combination is the only valid way to truly capture the effects of multiple disturbances.
- Multivariate pathways of effect result in heightened sensitivity (Figure 2B)

- Hypersensitivity when multiple pathways are targetted (jackson2016?) ## Good point to use when I talk about sensitivity to multiple pathways of effect
- HARD TO PREDICT FOR OMNIVORY, LOTS OF VARIABILITY
- Non-additive effects

Lastly, we identify species that are particularly vulnerable to disturbances at the motif-scale, and use these generalities as heuristics to infer species trophic vulnerability in complex networks.

Finally, species themselves are more or less sensitivity, with predators in omnivory and food chain both weak entry points and biotic amplifiers. - Trophic cascades, compensatory effects - Estes *et al.* (2011); - Compensatory effect suppression Thompson *et al.* (2018) - The fact that resources and predators are most affected, look at O'Gorman *et al.* (2012)

In particular, predators in food chain and omnivory interactions are both weak entry points and biotic amplifiers.

Predators and resources

-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). −>

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.

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6 The way forward

- Ignoring the importance of species interactions and pressure at bla bla

- Provide novel hypothesis to test experimentally.

- Our results reinforce that holistic approaches are necessary to properly consider the effects of environmental pressures on complex communities. Although this has been hinted at, no other study [. . .]

- Management

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.

Ban, N.C., Alidina, H.M. & Ardron, J.A. (2010). Cumulative impact mapping: Advances, relevance and limitations to marine management and conservation, using Canada's Pacific waters as a case study. *Marine Policy*, 34, 876–886.

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.

Belley, R., Archambault, P., Sundby, B., Gilbert, F. & Gagnon, J.-M. (2010). Effects of hypoxia on benthic macrofauna and bioturbation in the Estuary and Gulf of St. Lawrence, Canada. *Continental Shelf Research*, 30, 1302–1313.

Boonstra, W.J., Ottosen, K.M., Ferreira, A.S.A., Richter, A., Rogers, L.A. & Pedersen, M.W. *et al.* (2015). What are the major global threats and impacts in marine environments? Investigating the contours of a shared perception among marine scientists from the bottom-up. *Marine Policy*, 60, 197–201.

Bove, C.B., Ries, J.B., Davies, S.W., Westfield, I.T., Umbanhowar, J. & Castillo, K.D. (2019). Common Caribbean corals exhibit highly variable responses to future acidification and warming. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20182840.

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.

Chabot, D. & Claireaux, G. (2008). Environmental hypoxia as a metabolic constraint on fish: The case of Atlantic cod, Gadus morhua. *Marine Pollution Bulletin*, 5th International Conference on Marine Pollution and Ecotoxicology, 57, 287–294.

Christensen, M.R., Graham, M.D., Vinebrooke, R.D., Findlay, D.L., Paterson, M.J. & Turner, M.A. (2006). Multiple anthropogenic stressors cause ecological surprises in boreal lakes. *Global Change Biology*, 12, 2316–2322.

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.

Dupont-Prinet, A., Vagner, M., Chabot, D. & Audet, C. (2013). Impact of hypoxia on the metabolism of Greenland halibut (Reinhardtius hippoglossoides). *Canadian Journal of Fisheries and Aquatic Sciences*, 70, 461–469.

Eby, L.A., Crowder, L.B., McClellan, C.M., Peterson, C.H. & Powers, M.J. (2005). Habitat degradation from intermittent hypoxia: Impacts on demersal fishes. *Marine Ecology Progress Series*, 291, 249–262.

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J. & Bond, W.J. *et al.* (2011). Trophic Downgrading of Planet Earth. *Science*, New Series, 333, 301–306.

Fabry, V.J., Seibel, B.A., Feely, R.A. & Orr, J.C. (2008). Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science*, 65, 414–432.

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Giakoumi, S., Halpern, B.S., Michel, L.N., Gobert, S., Sini, M. & Boudouresque, C.-F. *et al.* (2015). Towards a framework for assessment and management of cumulative human impacts on marine food webs. *Conservation Biology*, 29, 1228–1234.

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 Progress Series*, 543, 273–281.

Guiden, P.W., Bartel, S.L., Byer, N.W., Shipley, A.A. & Orrock, J.L. (2019). Predator-Prey Interactions in the Anthropocene: Reconciling Multiple Aspects of Novelty. *Trends in Ecology & Evolution*, 34, 616–627.

Hale, R., Piggott, J.J. & Swearer, S.E. (2017). Describing and understanding behavioral responses to multiple stressors and multiple stimuli. *Ecology and Evolution*, 7, 38–47.

Halpern, B.S., Frazier, M., Afflerbach, J., Lowndes, J.S., Micheli, F. & O'Hara, C. *et al.* (2019). Recent pace of change in human impact on the world's ocean. *Scientific Reports*, 9, 11609.

Halpern, B.S. & Fujita, R. (2013). Assumptions, challenges, and future directions in cumulative impact analysis. *Ecosphere*, 4, art131.

Harborne, A.R., Rogers, A., Bozec, Y.-M. & Mumby, P.J. (2017). Multiple Stressors and the Functioning of Coral Reefs. *Annual Review of Marine Science*, 9, 445–468.

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

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

Ives, A.R. (1995). Measuring Resilience in Stochastic Systems. *Ecological Monographs*, 65,

217–233.

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

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

Kroeker, K.J., Kordas, R.L., Crim, R., Hendriks, I.E., Ramajo, L. & Singh, G.S. *et al.* (2013). Impacts of ocean acidification on marine organisms: Quantifying sensitivities and interaction with warming. *Global Change Biology*, 19, 1884–1896.

Liess, M., Foit, K., Knillmann, S., Schäfer, R.B. & Liess, H.-D. (2016). Predicting the synergy of multiple stress effects. *Scientific Reports*, 6, 32965.

McClanahan, T.R., Graham, N.A. & Darling, E.S. (2014). Coral reefs in a crystal ball: Predicting the future from the vulnerability of corals and reef fishes to multiple stressors. *Current Opinion in Environmental Sustainability*, Environmental change issues, 7, 59–64.

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

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

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

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

Morissette, L., Despatie, S.-P., Savenkoff, C., Hammill, M.O., Bourdages, H. & Chabot, D. (2003). Data gathering and input parameters to construct ecosystem models for the northern

Gulf of St. Lawrence(Mid-1980 s). *Can. Tech. Rep. Fish. Aquat. Sci./Rapp. Tech. Can. Sci. Halieut. Aquat.*, 100.

Myers, R.A. & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, 423, 280.

O'Brien, A.L., Dafforn, K.A., Chariton, A.A., Johnston, E.L. & Mayer-Pinto, M. (2019). After decades of stressor research in urban estuarine ecosystems the focus is still on single stressors: A systematic literature review and meta-analysis. *Science of The Total Environment.*

O'Gorman, E.J. & Emmerson, M.C. (2009). Perturbations to trophic interactions and the stability of complex food webs. *Proceedings of the National Academy of Sciences*, 106, 13393–13398.

O'Gorman, E.J., Fitch, J.E. & Crowe, T.P. (2012). Multiple anthropogenic stressors and the structural properties of food webs. *Ecology*, 93, 441–448.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. (1998). Fishing Down Marine Food Webs. *Science*, 279, 860–863.

Piggott, J.J., Townsend, C.R. & Matthaei, C.D. (2015). Reconceptualizing synergism and antagonism among multiple stressors. *Ecology and Evolution*, 5, 1538–1547.

Pillet, M., Dupont-Prinet, A., Chabot, D., Tremblay, R. & Audet, C. (2016). Effects of exposure to hypoxia on metabolic pathways in northern shrimp (Pandalus borealis) and Greenland halibut (Reinhardtius hippoglossoides). *Journal of Experimental Marine Biology and Ecology*, 483, 88–96.

Schäfer, R.B. & Piggott, J.J. (2018). Advancing understanding and prediction in multiple stressor research through a mechanistic basis for null models. *Global Change Biology*, 24, 1817–1826.

Stouffer, D.B. & Bascompte, J. (2010). Understanding food-web persistence from local to

global scales. *Ecology Letters*, 13, 154–161.

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

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

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

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

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

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

Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C. & Halpern, B.S. *et al.* (2006). Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science*, 314, 787–790.

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