

¹ On the vulnerability of food webs to multiple
² stressors

³ *David Beauchesne^{1,2,*}, Kevin Cazelles³, Philippe Archambault², Dominique
⁴ Gravel⁴*

⁵ ¹Institut des sciences de la mer, Université du Québec à Rimouski, Rimouski, QC, Canada

⁶ ²Québec Océan, Département de biologie, Université Laval, Québec, QC, Canada

⁷ ³Department of Integrative Biology, University Of Guelph, Guelph, Ontario, Canada N1G
⁸ 2W1

⁹ ⁴Département de biologie, Université de Sherbrooke, Sherbrooke, QC, Canada

¹⁰

¹¹ **Running title:** Of food webs and multiple stressors

¹²

¹³ **Keywords:** antagonism, synergism, non-additive effects, multiple stressors, cumulative
¹⁴ impacts, holistic, indirect effect,

¹⁵

¹⁶ **Type of article:** Ideas and Perspectives

¹⁷

¹⁸ **Abstract word count:**

¹⁹ **Main text word count:**

²⁰ **Number of references:**

²¹ **Number of figures:**

²² **Number of tables:**

²³ **Number of text boxes:**

²⁴

²⁵ **Correspondence:**

²⁶ David Beauchesne

²⁷ david.beauchesne@uqar.ca

²⁸ 1-514-553-4975

²⁹

³⁰ **Statement of authorship:**

³¹

³² **Data accessibility statement:**

³³ **Proposal letter**

³⁴ **Instructions**

³⁵ *Unsolicited proposals, which will be evaluated by the Ideas and Perspectives or*
³⁶ *Reviews and Syntheses Editors, in consultation with the Editorial Board and*
³⁷ *Editor-in-Chief, prior to a full submission. Proposals should be no more than*
³⁸ *300 words long, describe the nature and novelty of the work, the contribution*
³⁹ *of the proposed article to the discipline, and the qualifications of the author(s)*
⁴⁰ *who will write the manuscript. Proposals should be sent to the Editorial Office*
⁴¹ *(ecolets@cefe.cnrs.fr).*

⁴² **Notes**

- ⁴³ • In it's current form, I believe that the contribution portion is not good enough
⁴⁴ • I wonder whether the qualifications should be more in depth.
⁴⁵ • Right now, the letter is 43 words over the word limit.
⁴⁶ • Also, this text might be better than the current abstract

⁴⁷ **Letter**

⁴⁸ Evaluating the effects of multiple sources of stress in natural environments has become an
⁴⁹ increasingly important issue as the effects of intensifying global change and expanding hu-
⁵⁰ man activities result in complex stress exposure regimes. Even though the non-additive
⁵¹ effects of multiple stressors have been investigated empirically for a few decades now, there
⁵² remains a general lack of theoretical understanding of their impacts on natural systems.
⁵³ In particular, the role of species and their interactions in mediating the effects of multiple
⁵⁴ disturbances through ecological ecommunities networks, although widely acknowledged, has
⁵⁵ yet to be formally explored. We propose the first such formal exploration by exhaustively
⁵⁶ simulating the impacts of all possible pathways of effects on the dynamics of 3-species mo-
⁵⁷ tifs using Lotka-Volterra models. We uncover that interaction types and species position
⁵⁸ greatly influence sensitivity to and amplification of multiple disturbances and that indirect
⁵⁹ pathways of effects are the main cause of non-additive effects. In particular, predators in
⁶⁰ food chain and omnivory interactions act as both weak entry points (*i.e.* highly sensitive to
⁶¹ disturbances) and biotic amplifiers (*i.e.* affected synergistically by disturbances). We then
⁶² use the simulated sensitivity and amplification scores as heuristics to infer trophic vulnera-
⁶³ bility of species based on topology and realized pathways of effects in the food web of the
⁶⁴ Northern Gulf of St. Lawrence, Canada, prior to a groundfish stock collapse in the 1990s.
⁶⁵ We find that heavily exploited species appear to be the most vulnerable trophically, while
⁶⁶ fisheries transitioned to insensitive or beneficiary species post-collapse. This contribution is
⁶⁷ significant and timely for two main reasons. First, from a theory stand point, this is the first
⁶⁸ exhaustive exploration of mitigation and amplification of multiple disturbances via trophic
⁶⁹ motifs. Second, we provide a clear link between theory and management by illustrating how

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

⁷⁵ **1 Abstract**

⁷⁶ Evaluating the effects of multiple sources of stress in natural environments has become an in-
⁷⁷ creasingly important issue as the effects of intensifying global change and expanding human
⁷⁸ activities result in complex stress exposure regimes. Even though the non-additive effects of
⁷⁹ multiple stressors have been investigated empirically for a few decades now, there remains a
⁸⁰ general lack of theoretical understanding of their impacts on natural systems. In particular,
⁸¹ the role of species and their interactions in mediating the effects of multiple disturbances
⁸² through ecological communities, although widely acknowledged, has yet to be formally ex-
⁸³ plored. We propose the first such formal exploration by exhaustively simulating trophic
⁸⁴ impacts through all possible pathways of effects on the dynamics of 3-species motifs using
⁸⁵ Lotka-Volterra models. We uncover that interaction types and species position greatly influ-
⁸⁶ ence sensitivity to and amplification of multiple disturbances and that indirect pathways of
⁸⁷ effects are the main source of non-additive effects. In particular, predators in food chain and
⁸⁸ omnivory interactions act as both weak entry points (*i.e.* highly sensitive to disturbances)
⁸⁹ and biotic amplifiers (*i.e.* affected synergistically by disturbances). We then use the simu-
⁹⁰ lations results as heuristics to infer trophic vulnerability of species based on topology and
⁹¹ realized pathways of effects in the food web of the Northern Gulf of St. Lawrence, Canada,
⁹² prior to a groundfish stock collapse in the 1990s. We find that heavily exploited species
⁹³ appear to be the most vulnerable trophically, while fisheries transitioned to insensitive or
⁹⁴ beneficiary species post-collapse.

95 **2 Introduction**

96 Ecosystems worldwide are increasingly affected by a vast array of environmental pressures,
97 commonly referred to as stressors or drivers (Boonstra *et al.* 2015; Halpern *et al.* 2019).
98 Pressures may be driven by natural or human-induced biophysical processes such as ocean
99 acidification and warming, or directly from anthropogenic activities such as fisheries. These
100 drivers can be defined as any externality that affects environmental processes and disturbs
101 natural systems. Individually, drivers have been found to impact all levels of biological or-
102 ganization and cause dramatic changes to whole ecosystems. Ocean acidification can reduce
103 coral and mollusk calcification, metabolic, growth and mortality rates, and has been linked
104 to altered carbon fluxes in ecological networks (Fabry *et al.* 2008; Kroeker *et al.* 2013; Bove
105 *et al.* 2019). Fisheries have caused the collapse of commercial species, decreased the mean
106 trophic level in coastal and oceanic environments by targetting large predators and impaired
107 a variety of essential ecosystem services (Pauly *et al.* 1998; Myers & Worm 2003; Worm *et*
108 *al.* 2006).

109 Rarely do drivers occur individually, and the list of potentially interacting drivers affecting
110 an ecosystem at any given point in time or space can be extensive (Halpern *et al.* 2019).
111 Global changes and local human activities thus result in increasingly intricate environmental
112 stress exposure regimes, compounding the pathways of effects through which natural systems
113 can be impacted (Halpern *et al.* 2019). For example, coral reefs contend with a suite of
114 pressures including fishing, warming temperatures, ocean acidification and water quality that
115 may impact species in contrasting ways (McClanahan *et al.* 2014; Harborne *et al.* 2017).
116 Moreover, drivers may combine to disturb ecosystems in ways that cannot be captured
117 through the examination of individual pressures. Dramatic examples of these non-additive
118 effects include up to 100-fold increases in the sensitivity of certain organisms to toxicants
119 (*e.g.* pesticides) when exposed to other environmental stressors (*e.g.* parasites; Liess *et al.*
120 2016) and the reversal of the positive effects of acidification on primary producer biomass by

¹²¹ warmer waters in boreal lakes (Christensen *et al.* 2006). Such interactions between drivers
¹²² is extremely alarming not only because of their dreadful impacts, but also because, so far,
¹²³ they remain largely unpredictable (Darling & Côté 2008; Côté *et al.* 2016) and pervasive
¹²⁴ (*e.g.* Crain *et al.* 2008; Piggott *et al.* 2015; Jackson *et al.* 2016).

¹²⁵ Species sensitivity to environmental pressures can be highly variable, which further com-
¹²⁶ pounds the complexity of multiple drivers studies. For example, hypoxia decreases overall
¹²⁷ habitat quality but has species-dependent effects, ranging from well-adapted (*e.g.* north-
¹²⁸ ern shrimp *Pandalus borealis* and Greenland halibut *Reinhardtius hippoglossoides*; Pillet *et*
¹²⁹ *al.* 2016) to avoidance behaviour (*e.g.* Atlantic cod *Gadus morhua*; Chabot & Claireaux
¹³⁰ 2008), and mortality (*e.g.* sessile benthic invertebrates; Eby *et al.* 2005; Belley *et al.*
¹³¹ 2010). Moreover, species are also embedded in a complex web of interactions that provides
¹³² indirect pathways of effects through which pressures may permeate entire ecological com-
¹³³ munities (Wootton 2002; Bascompte 2009; Montoya *et al.* 2009; O’Gorman & Emmerson
¹³⁴ 2009; O’Gorman *et al.* 2012). Indirect effects, *i.e.* when two or more direct effects are
¹³⁵ linked by a single species involved in both effects, may be as important of, and propagate
¹³⁶ faster than, direct effects (Wootton 1993, 2002; Menge 1995; Yodzis 2000). Empirical ex-
¹³⁷ amples of trophic cascades are abundant throughout all types of ecosystems globally (Estes
¹³⁸ *et al.* 2011). In multi-species systems, where both direct and indirect effects are operating
¹³⁹ simultaneously, it is expected that the effects of environmental pressures will be amplified
¹⁴⁰ or dampened through biotic interactions (Ives 1995; Wootton 2002; Thompson *et al.* 2018).
¹⁴¹ Community dynamics and how species are embedded in complex networks is therefore likely
¹⁴² to affect their sensitivity to environmental pressures.

¹⁴³ From a practical standpoint, single-driver and single-species assessments remain overwhelm-
¹⁴⁴ ingly applied (O’Brien *et al.* 2019), while most multiple drivers studies have typically focused
¹⁴⁵ on habitats (*e.g.* Ban *et al.* 2010; Halpern *et al.* 2019). This conveniently circumscribes
¹⁴⁶ assessments to a set of tractable units, but it also ignores systems complexity and aggre-
¹⁴⁷ gates biological processes operating at lower levels of organization (Halpern & Fujita 2013;

¹⁴⁸ Giakoumi *et al.* 2015). Studies have also relied on the use of null models that provide little
¹⁴⁹ insights into the mechanisms underlying ecological responses to the effects of multiple drivers
¹⁵⁰ (Griffen *et al.* 2016; Jackson *et al.* 2016; De Laender 2018; Schäfer & Piggott 2018).

¹⁵¹ Confronted with the challenge of managing and preserving complex systems, there is an
¹⁵² urgent need for the development of frameworks that properly consider the complexities of
¹⁵³ multiple drivers and ecological networks in ways that are informative to management. Such
¹⁵⁴ frameworks should be grounded in theory, scaled for gains in ecological understanding rather
¹⁵⁵ than convenience, and allow for dynamic identification of conservation targets. It should also
¹⁵⁶ be flexible and data-oriented so that it can make use of the expanding corpus of openly
¹⁵⁷ available ecological knowledge and computational abilities.

¹⁵⁸ In this paper, we address these issues by conceptualizing how multiple environmental pres-
¹⁵⁹ sures permeate complex ecological communities. Our objective is to theoretically investigate
¹⁶⁰ the role of species and their interactions (*i.e.* food web topology) in driving species sensi-
¹⁶¹tivity to disturbances and how they may buffer against or amplify the effects of multiple
¹⁶² disturbances. We then scale up to complex systems by exploring species vulnerability
¹⁶³ to multiple disturbances as a consequence of their position in empirical food webs. In do-
¹⁶⁴ ing so, we seek to answer questions of particular significance to management, in particular
¹⁶⁵ for the application of holistic environmental approaches: 1) should species interactions be
¹⁶⁶ considered in impact assessments, 2) should the effects of stressors be evaluated separately
¹⁶⁷ or in combination, and 3) which species are most vulnerable to disturbances based on their
¹⁶⁸ trophic position.

₁₆₉ **3 Of food web and multiple disturbances**

₁₇₀ **3.1 Conceptualizing disturbances**

₁₇₁ Drivers can disturb the dynamics of ecological communities by disrupting a variety of bi-
₁₇₂ ological processes (Figure 1A) such as behaviour (*e.g.* Chabot & Claireaux 2008; Hale *et*
₁₇₃ *al.* 2017), reproduction [*e.g.* ref], physiology (*e.g.* Dupont-Prinet *et al.* 2013), mortality
₁₇₄ (*e.g.* Belley *et al.* 2010), and species interactions (*e.g.* Wootton 2002; Guiden *et al.* 2019).

₁₇₅ Multiple processes may be affected by a single driver, while multiple drivers may target a
₁₇₆ single process. For instance, fishing could affect the behaviour and the mortality of cod,
₁₇₇ while ocean warming and ocean acidification may jointly affect physiological processes of
₁₇₈ benthic invertebrates such as calcification rates. The potential number of univariate and
₁₇₉ multivariate pathways of effects through which community dynamics may be affected is ex-
₁₈₀ tensive and increases exponentially with the number of species and the number on links in
₁₈₁ a network.

₁₈₂ A thorough understanding of the impacts of disturbance regimes and community dynamics
₁₈₃ would be necessary to fully capture the effects of multiple drivers, but the complexity of
₁₈₄ empirical food webs in itself is prohibitive to investigations of community dynamics. Studying
₁₈₅ smaller subgraphs - community motifs or modules - has thus emerged as an alternative to
₁₈₆ gather insights into the dynamics and stability of complex ecological communities (Holt
₁₈₇ 1997; Holt & Hochberg 2001). Motifs are collections of n -species that, when put together,
₁₈₈ construct whole food webs (Milo *et al.* 2002; Stouffer *et al.* 2007). They form the backbone
₁₈₉ of food webs and provide a mesoscale characterization of community structure (Bascompte
₁₉₀ & Melián 2005; Stouffer *et al.* 2007). A species can be described as a function of all n -species
₁₉₁ motifs it is involved in in an empirical food web (Figure 1B; Stouffer *et al.* 2012).

₁₉₂ There are 13 distinct 3-species motifs composed of 30 unique positions (Milo *et al.* 2002;
₁₉₃ Stouffer *et al.* 2007, 2012). Four 3-species motifs have received particular attention in

¹⁹⁴ theoretical and empirical studies due to their roles [ref] and prevalence (Camacho *et al.* 2007;
¹⁹⁵ Stouffer & Bascompte 2010) in food webs: tri-trophic food chain, omnivory or intraguild
¹⁹⁶ predation, exploitative competition and apparent competition.

¹⁹⁷ Motif dynamics has been studied extensively to uncover how structural properties of food
¹⁹⁸ webs can benefit community persistence and stability (Allesina & Pascual 2008; Kondoh
¹⁹⁹ 2008; Stouffer & Bascompte 2010, 2011; Monteiro & Faria 2016) and to assess the structural
²⁰⁰ roles of species within food webs (Stouffer *et al.* 2012; Cirtwill & Stouffer 2015). These
²⁰¹ provide meaningful insights for conservation efforts. For example, results from Stouffer *et*
²⁰² *al.* (2012) suggest that certain species may benefit whole community persistence based on
²⁰³ their trophic position, and that the diversity of trophic roles found in empirical food webs
²⁰⁴ does not correlate to species richness. This means that strictly using species richness as
²⁰⁵ a conservation measure may ignore the benefits to community persistence provided by the
²⁰⁶ trophic roles of individual species. Using trophic roles as targets may thus be valuable for
²⁰⁷ community conservation (Stouffer *et al.* 2012).

²⁰⁸ Managers are not only tasked with species conservation, however. For example, the dynamics
²⁰⁹ of coexisting species is particularly important to practitioners whose mandate is to moni-
²¹⁰ tor and manage exploited populations using holistic approaches such as ecosystem based
²¹¹ fisheries management. In this context, population fluctuations are at least as important as
²¹² species persistence. As such, studying the dynamics of persistent communities is of partic-
²¹³ ular relevance to management in the context of multiple environmental pressures (Figure
²¹⁴ 1C).

²¹⁵ Here, we study the equilibrium dynamics, i.e. when species are constrained to coexistence,
²¹⁶ of the most prevalent 3-species motifs in food webs (i.e. food chain, omnivory, exploitative
²¹⁷ competition, and apparent competition) to exhaustively investigate how trophic position and
²¹⁸ interaction type influences the sensitivity to and the amplification of the effects of multiple
²¹⁹ disturbances. We then use the simulations to infer species trophic vulnerability in complex

220 food webs as a function of species position in food web and realized pathways of effects.

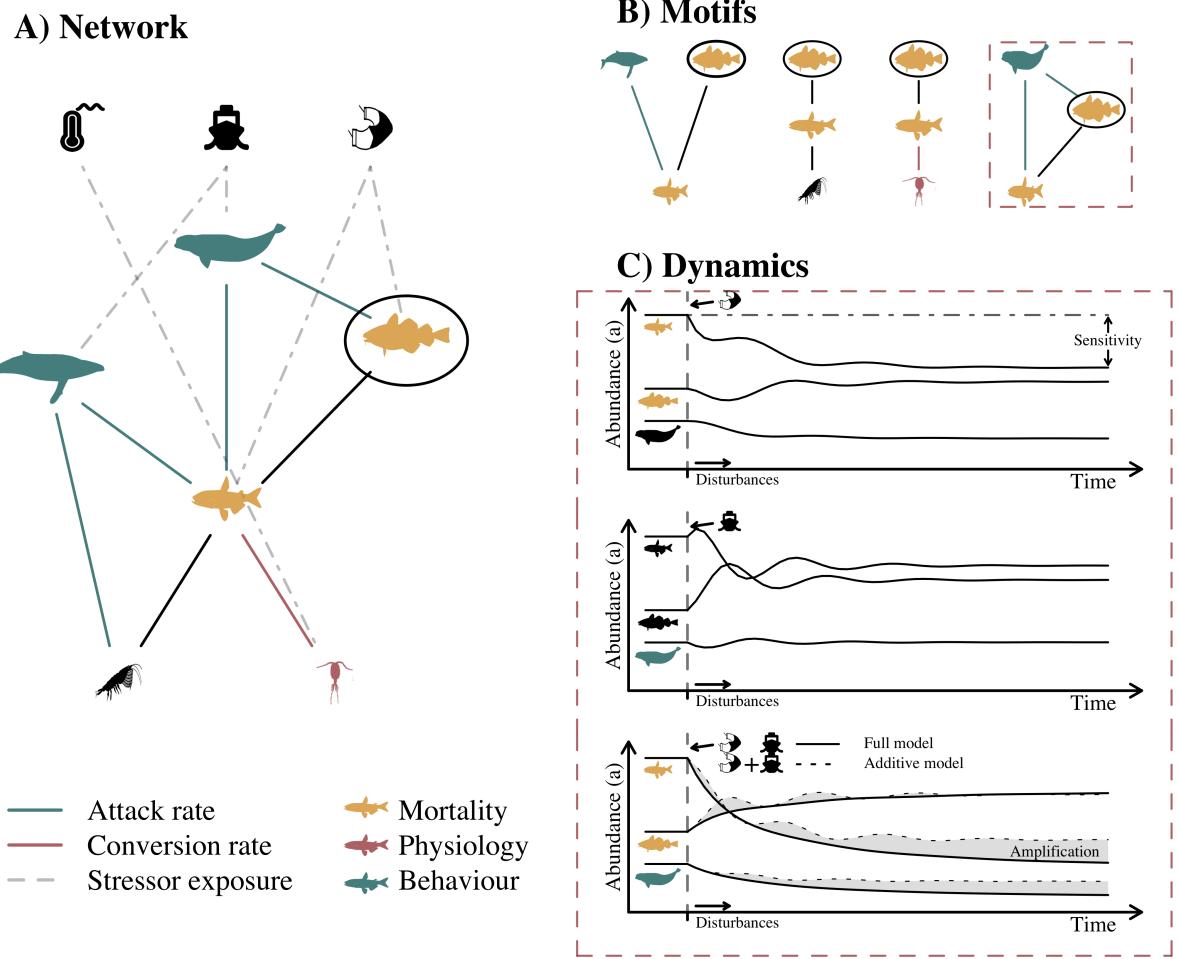


Figure 1: Conceptualization of the effects of multiple sources of environmental stress on the dynamics of a theoretical food web. A) Drivers such as sea surface temperature, marine traffic and fisheries penetrate food webs through various pathways of effects by disturbing ecological processes governing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

221 **3.2 Simulating disturbances**

222 **3.2.1 Models formulation**

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

229 Resources were modeled using logistic growth equations of the form

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

230 where X_i denotes species i , r_i is the intrinsic resource growth rate, α_{ii} is the density-
231 dependent effect of the resource on itself and α_{ij} is the rate at which consumer j affects
232 resource i , *i.e.* the attack rate.

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

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

234 where m_j is the mortality rate of species j and e_{ij} is the rate at which resource i biomass is
235 transformed into consumer j biomass, *i.e.* the conversion rate, and is a scaling parameter of
236 the attack rate which cannot exceed 1.

237 Models were solved at equilibrium to study the effects of disturbances on persistent motif dy-
238 namics. As no equilibrium exists for the exploitative competition motif with Lotka-Volterra
239 models of the selected forms, competitive parameters of the form

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

240 were included to the consumer models to constrain growth and limit competitive exclusion.
241 Refer to table S1 for the detailed equation systems of all motifs considered.

242 **3.2.2 Models parameterization**

243 Model dynamics was constrained by species coexistence, meaning that abundances for all
244 species was to be positive before and after disturbances were simulated. To achieve this,
245 we first arbitrarily set the values of a number of initial model parameters. Intrinsic growth
246 (r) and resource density-dependence (α_{ii}) were fixed to 1 and 0.001, respectively, to bound
247 all resource solutions. Competitive parameters for the exploitative competition motif were
248 also fixed at 0.001, and conversion rates (e) were fixed to 0.5. We then set an interval
249 of possible values for mortality ($m \in [0.01, 0.5]$) and attack rate ($\alpha_{ij} \in [0.0001, 0.01]$) in
250 which we extracted 100 sets of initial values. Values maximising stability (i.e. XXX) were
251 identified using a simulated annealing algorithm optimizing for consumer abundance. Sets
252 of parameters were only retained if initial abundances and abundances resulting from all
253 possible pathways of effect were positive (see next section).

254 **3.2.3 Disturbances**

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

261 For each motif position, all possible mortality, resource growth, conversion and attack rates
262 parameter combinations were simulated. This resulted in a total of 930 unique pathways of
263 effects for all motif positions combined (food chain, competitive exploitation and apparent
264 competition motif positions: 7 parameters, 127 pathways of effects; omnivory motif positions:
265 9 parameters, 511 pathways of effects; partially connected motif positions: 5 parameters, 31
266 pathways of effects; disconnected motif position: 3 parameters, 7 pathways of effects).

267 3.3 Motifs vulnerability

268 3.3.1 Trophic sensitivity

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

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

271 where a_i is the initial abundance at position i without disturbance, and $a_{i,j}$ is the abundance
272 at position i with disturbance due to pathway of effect j . Note that, by definition, $s_{i,j}$ is
273 bounded negatively to -1, as abundances cannot fall below 0. We define the sensitivity score
274 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
275 conditions.

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

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

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

280 positions ($|S_i| = 0$). Thresholds are arbitrary and used for discussion purposes.

281 3.3.2 Trophic amplification

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

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

284 where K_j is a multivariate pathway of effect j and k denote the n unitary pathways included
285 in K_j . The amplification score evaluates the deviance of a multivariate pathway of effect and
286 the sum of the univariate effects composing the pathway of effect, *i.e.* the additive model.
287 Thus, a value of 0 identifies a null of additive effect, a value below 0 identifies an antagonistic
288 effect, and a value over 0 identifies synergistic effects.

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

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

291 We define *biotic amplifiers* as multivariate pathways of effect or motif positions that are more
292 affected than expected from an additive model ($A_{i,j} > 0.0002$, $A_i > 0.0002$). *Biotic buffers*
293 are multivariate pathways of effect or motif positions that are less affected than expected
294 from an additive model ($A_{i,j} < 0.0002$, $A_i < 0.0002$). Thresholds are arbitrary and used for
295 discussion purposes.

296 **3.4 Species vulnerability**

297 **3.4.1 Scores**

298 IMPORTANT COMMENT: For now, I present the topological score, but I am not
299 sure whether it should be presented at all since I ultimately do not really use it in
300 my discussion. Except if we end up presenting it in the paper to make the point
301 that although it would provide a proxy of trophic vulnerability (which we will be
302 using for my last thesis chapter), it does not really capture realized vulnerability
303 when actual drivers are considered. This is not so true for sensitivity, but it
304 certainly is for amplification. See Figure 10 for a biplot of topological vs realized
305 scores.

306 We broadly refer to species vulnerability as the combination of trophic sensitivity and trophic
307 amplification, as defined in this study. Two sets of scores are presented at the species level,
308 using the simulated disturbances for all possible pathways of effects as heuristics to infer
309 species trophic vulnerability.

310 The first set are topological scores of trophic sensitivity and amplification based on the
311 frequency at which species occupy one of the 4 main motif positions we considered, *i.e.* food
312 chain, omnivory, exploitative and apparent competition, in an empirical food web:

$$S_m = \sum_i f_{m,i} S_i,$$

$$A_m = \sum_i f_{m,i} A_i,$$

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

315 mean trophic sensitivity and amplification scores at position i , respectively. Note that for
316 species vulnerability, we do not consider the control motifs any further.

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

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

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

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

323 Realized pathways of effect are identified using the following rules:

324 1. impacts of drivers on the mortality of resources and consumers are considered as dis-
325 turbances to resource growth rates and to consumer mortality rates (r, m).

326 2. impacts on the behaviour of resources and consumers are considered as disturbances
327 to consumer attack rates (α_{ij}).

328 3. impacts on the physiology of resources and consumers are considered as disturbances
329 to consumer conversation rates (e).

330 By using these scores, we essentially assume that the realized vulnerability of a species will
331 be the sum of all individual 3-species pathways of effect through which a species may be
332 impacted.

³³³ **3.4.2 Empirical food webs**

³³⁴ We evaluated the vulnerability of species in 3 empirical webs from the Southern (SSL) and
³³⁵ Northern (NSL) Gulf, and Estuary (ESL) of St. Lawrence in eastern Canada (Morissette
³³⁶ *et al.* 2003; Savenkoff *et al.* 2004; Savenkoff 2012). The Southern and Northern Gulf of
³³⁷ St. Lawrence food webs correspond to the mid-1980s, prior to a groundfish stock collapse in
³³⁸ the early 1990s, while the St. Lawrence Estuary food web corresponds to the early 2010s.
³³⁹ The total number of species and functional groups differs between food webs ($n_{SSL} = 30$;
³⁴⁰ $n_{NSL} = 32$; $n_{ESL} = 41$), yet there is significant overlap ($n_{all} = 21$). Food webs resolution is
³⁴¹ biased towards commercial fish for all food webs. In the food webs, interactions are identified
³⁴² as a percent of species or functional group in the diet of another species or functional group.
³⁴³ Only diet percent > 0.1 were considered as interactions in our analysis. Note that detailed
³⁴⁴ vulnerability results are only presented and discussed for the Northern Gulf food web. Results
³⁴⁵ for the Estuary and Southern Gulf are available as supplementary material (Figures S1, S2).

³⁴⁶ **3.4.3 Drivers**

³⁴⁷ Climate change related drivers (*i.e.* acidification, hypoxia, and bottom and surface temper-
³⁴⁸ ature anomalies) are prevalent in the St. Lawrence System, with the exception of hypoxia
³⁴⁹ in the Southern Gulf (Beauchesne 2019). Marine traffic is widespread, especially in the
³⁵⁰ Northern Gulf and the Estuary, which serve as the main seaway to inland North-America
³⁵¹ (Beauchesne 2019). Fisheries have changed through time after the collapse of groundfish
³⁵² stocks in the early 1990s. Species affected by fisheries were identified using the catch data
³⁵³ provided in the description of the food web models (Morissette *et al.* 2003; Savenkoff *et al.*
³⁵⁴ 2004; Savenkoff 2012). Geartype used was identified using landing data from logbooks from
³⁵⁵ the Department of Fisheries and Ocean's Canada (???).

³⁵⁶ The impacts of specific drivers on species and functional groups was done following broad
³⁵⁷ rules to simplify the number of assumptions required. Our approach does not seek to establish

358 the vulnerability of a particular species to all types of drivers, but rather to make general
359 inference on species trophic vulnerability based of its trophic position and the supposed
360 effects of drivers on biological processes driving community dynamics. Detailed literature
361 search or expert knowledge could be used to get a better sense of the proximate effects of
362 drivers on species, but this is beyond the scope of our objectives.

363 The first criteria used to evaluate the effect of drivers on species and functional groups was a
364 broad evaluation of direct exposure to individual drivers. Acidification, hypoxia and bottom
365 temperature anomalies are widespread in the deep habitats of the St. Lawrence, while surface
366 temperature anomalies and marine traffic are operating on the surface layer (Beauchesne
367 2019). As such, species of functional groups in deep or surface habitats were considered as
368 exposed to deep or surface drivers, respectively. Hypoxia was considered as impacting the
369 physiology or behaviour of species or functional groups with low or high mobility, respectively
370 (????). Temperature anomalies were considered as impacting the physiology of species with
371 low mobility only. Ocean acidification was assumed to affect the physiology of exposed
372 carbonate-secreting organisms (*e.g.* mollusks and crustaceans; Kroeker *et al.* 2013). Marine
373 traffic was considered as primarily impacting whale behaviour (Christiansen *et al.* 2013;
374 Lesage *et al.* 2017). The impact of fisheries was assumed to target the mortality rates of
375 species with positive catch rates. Catches of certain species or functional groups of seals
376 and seabird through hunting, and whales through bycatch, is reported for the empirical food
377 webs of the St. Lawrence (Morissette *et al.* 2003; Savenkoff *et al.* 2004; Savenkoff 2012).
378 We thus considered that the mortality rates of seabirds and marine mammals with reported
379 catches was disturbed.

380 **4 Species vulnerability to multiple disturbances**

381 **4.1 Motifs vulnerability**

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

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

393 Species position greatly influences trophic sensitivity to and amplification of disturbances. In
394 general, top predators are weak entry points for all interaction types (Figure 4). In contrast,
395 non-additive effects on top predators depends on interaction type. Pathways of effect on top
396 predators in omnivory and food chain interactions largely result in synergistic or antagonistic
397 effects, and predators are, on average, biotic amplifiers (Figure ref{position}). Predators in
398 competitive interactions, meanwhile, are less affected by non-additive effects and are fringe
399 biotic buffers (Figure ref{position}).

400 Resources are largely weak entry points for all motifs, yet the effect are typically negative
401 in food chain and omnivory interactions, and positive in competitive interactions (Figures
402 2, 4). Although resources are, on average, neither biotic buffers or amplifiers, the effects of
403 individual pathways of effects are mostly non-additive (Figure 2). The effects of disturbances
404 on other interactions are mostly additive. (Figure 2).

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

410 The nature of the pathways of effects influences trophic sensitivity and amplification. Unsur-
411 prisingly, multivariate pathways of effects are generally more impactful to species sensitivity
412 and hold a higher proportion of weak entry points than univariate pathways (Figure 2).
413 Similarly, targeting multiple biological processes results in greater sensitivity and amplifica-
414 tion (Figure 2). There are however a few generalities worth noting. Mortality and growth
415 rates are driving heightened trophic sensitivities, yet do not individually contribute to non-
416 additive effects (Figure 5). Instead, trophic amplification is largely driven by disturbances
417 on species interactions (*i.e.* attack (α_{ij}) and conversion (e) rates; Figure 5).

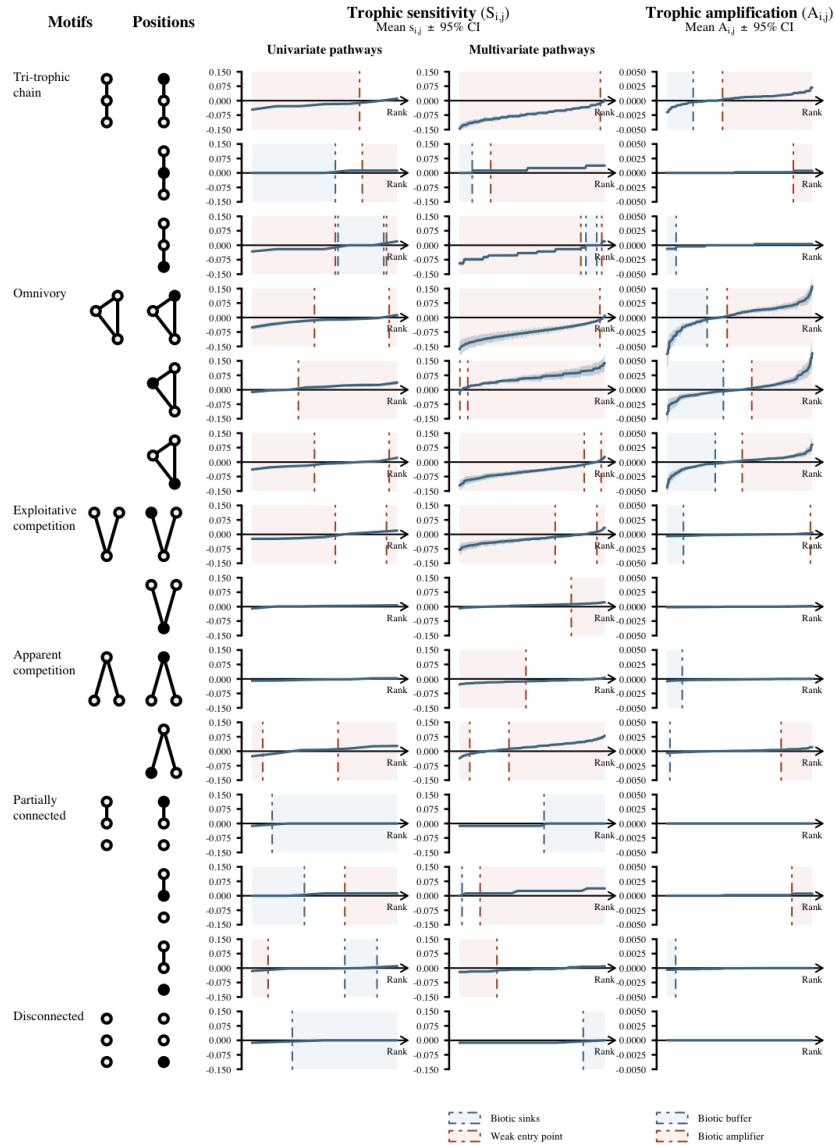


Figure 2: Ranking of trophic sensitivity ($S_{i,j}$) and amplification ($A_{i,j}$) scores for all univariate and multivariate pathways of effects on all 13 unique motif positions in the three-species motifs explored, *i.e.* tri-trophic food chain, omnivory, exploitative competition, apparent competition, partially connected and disconnected. Trophic sensitivity is the variation in species initial abundance at equilibrium and the abundance after disturbances are simulated through univariate or multivariate pathways of effect. Pathways of effects identified as weak entry points (*i.e.* highly sensitive to disturbances) and biotic sinks (*i.e.* insensitive to disturbances) are identified by red and blue regions, respectively. Trophic amplification is 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. Pathways of effect identified as biotic buffers (*i.e.* synergistic effect of disturbances) and biotic buffers (*i.e.* antagonistic effect of disturbances) are identified by the red and blue regions, respectively.

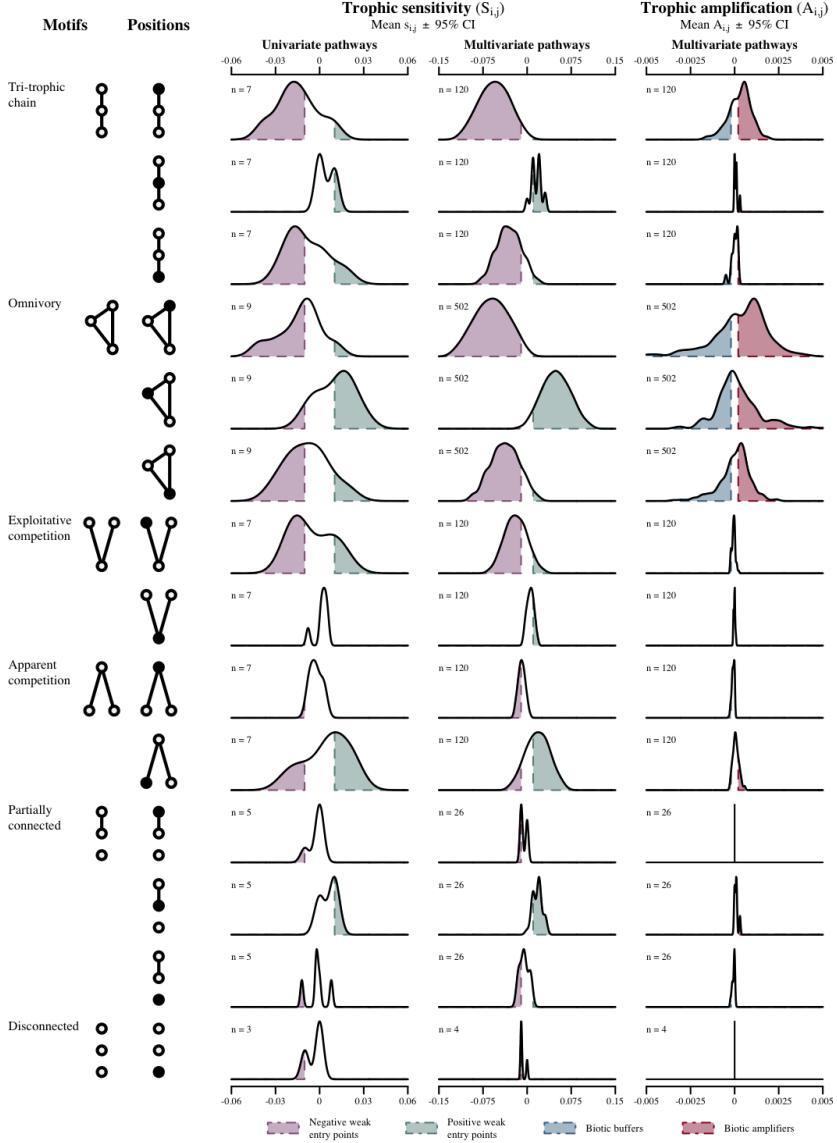


Figure 3: Ranking of trophic sensitivity (S_{ij}) and amplification (A_{ij}) scores for all univariate and multivariate pathways of effects on all 13 unique motif positions in the three-species motifs explored, *i.e.* tri-trophic food chain, omnivory, exploitative competition, apparent competition, partially connected and disconnected. Trophic sensitivity is the variation in species initial abundance at equilibrium and the abundance after disturbances are simulated through univariate or multivariate pathways of effect. Pathways of effects identified as weak entry points (*i.e.* highly sensitive to disturbances) and biotic sinks (*i.e.* insensitive to disturbances) are identified by red and blue regions, respectively. Trophic amplification is 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. Pathways of effect identified as biotic buffers (*i.e.* synergistic effect of disturbances) and biotic buffers (*i.e.* antagonistic effect of disturbances) are identified by the red and blue regions, respectively.

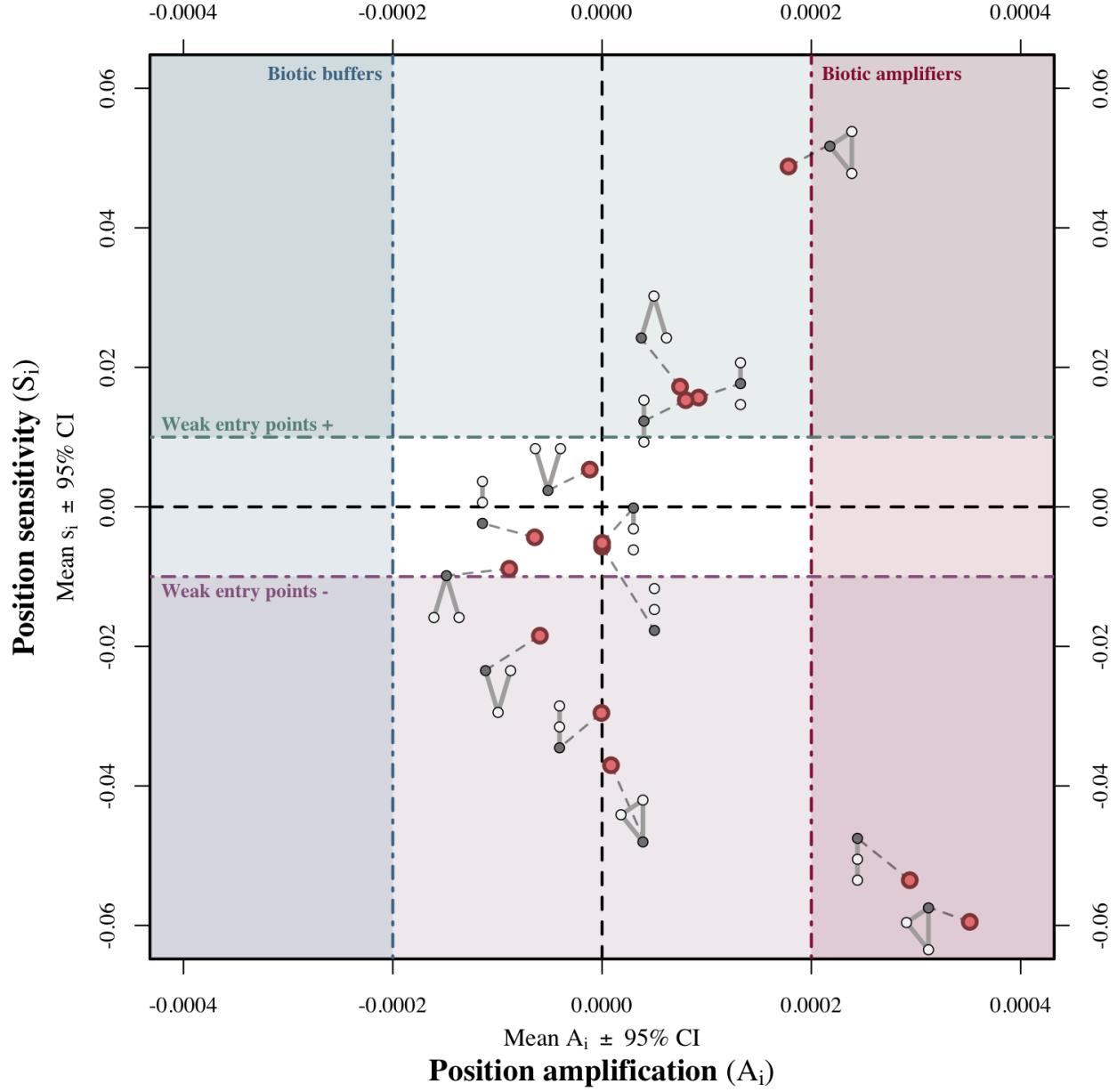


Figure 4: Ranking of 13 motif positions as a function of position sensitivity (S_i) and amplification (A_i) scores in the three-species motifs explored, *i.e.* tri-trophic food chain, omnivory, exploitative competition, apparent competition, partially connected and disconnected. Position sensitivity is mean value of the variation in species initial abundance at equilibrium and the abundance after disturbances are simulated for all univariate and multivariate pathways of effect on a motif position. 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 blue regions. Position amplification is the mean deviance of a multivariate pathway of effect and the sum of the univariate effects composing the pathway of effect, *i.e.* the additive model, for all multivariate pathways of effect on a motif position. Motif positions identified as biotic buffers (*i.e.* synergistic effect of disturbances) and biotic amplifiers (*i.e.* antagonistic effect of disturbances) are identified by the red regions.

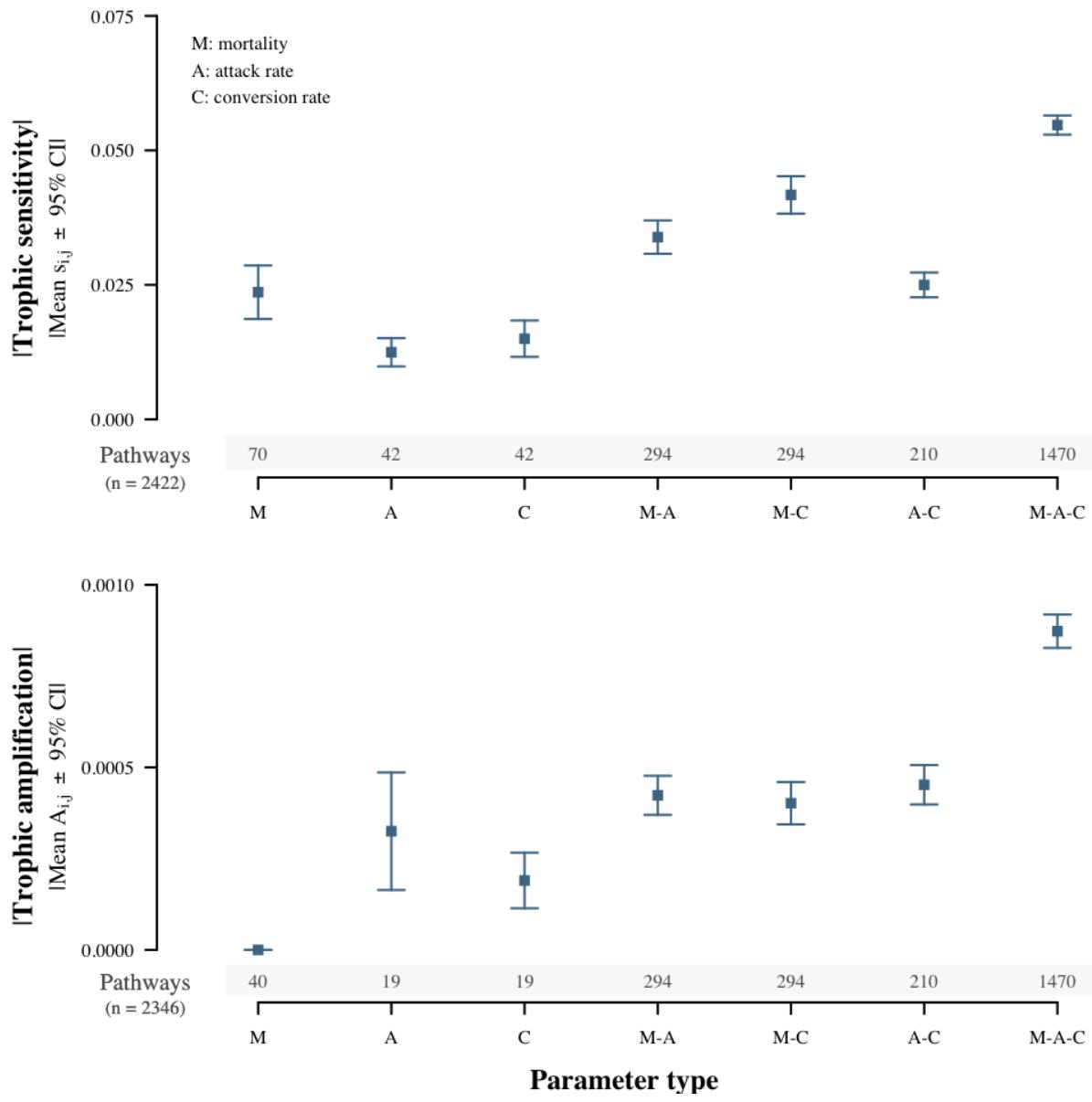


Figure 5: Absolute values of the mean trophic sensitivity ($S_{i,j}$; A) and amplification ($A_{i,j}$; B) as a function of the types of parameter composing a pathway of effect. All pathways of effect targeting a specific parameter type (*i.e.* mortality, attack and conversion rates) were grouped to evaluate their respective and combined effect on trophic sensitivity and amplification.

⁴¹⁸ **Other figures:**

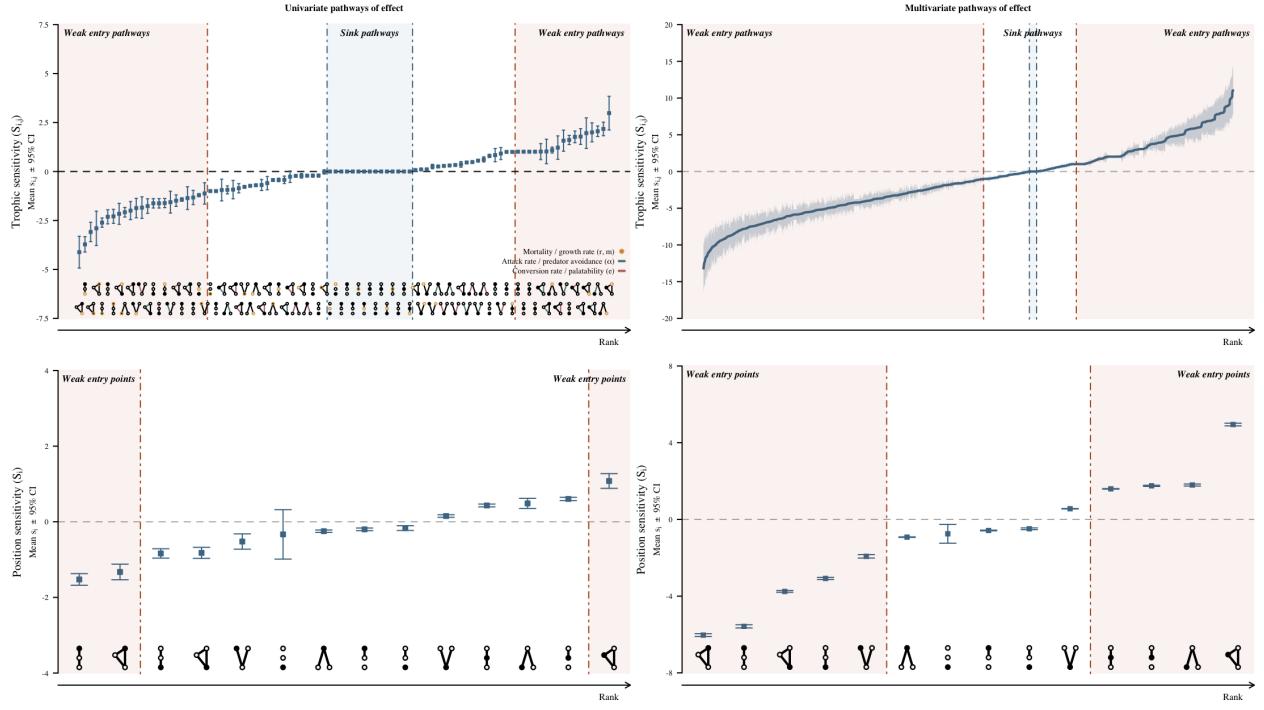


Figure 6: Ranking of all univariate and multivariate pathways of effect as a function of trophic (A,B) and position (C,D) sensitivity. Pathways and motif positions identified as weak entry points (*i.e.* highly sensitive to disturbances) and biotic sinks (*i.e.* insensitive to disturbances) are identified by the red and blue regions, respectively.

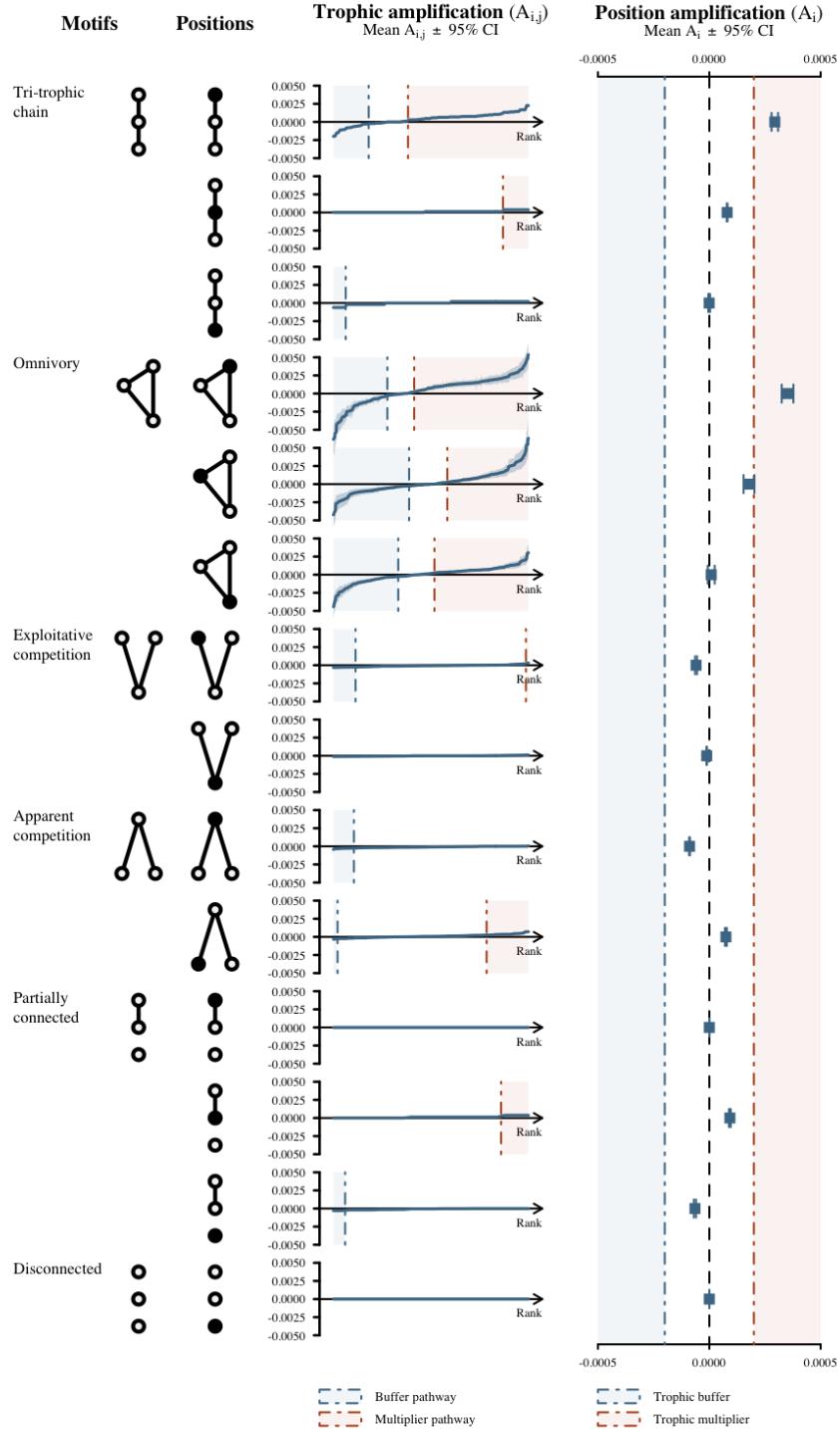


Figure 7: Ranking of all multivariate pathways of effect as a function of trophic and position amplification, for each motif position. Pathways and motif positions identified as biotic buffers (*i.e.* affected synergistically by disturbances) and biotic buffers (*i.e.* affected antagonistically by disturbances) are identified by the red and blue regions, respectively.

⁴¹⁹ 4.2 Species vulnerability

⁴²⁰ Based on their trophic position, the most vulnerable species in the Northern St. Lawrence
⁴²¹ are large predators that are never or rarely resources themselves, such large demersal fish
⁴²² (*i.e.* demersals, atlantic cod and greenland halibut; Figure 8). These species largely appear
⁴²³ to be both weak entry points and biotic amplifiers (Figure 8). Resources are generally less
⁴²⁴ sensitive, depending on their position in food webs. Large crustaceans, for example, are
⁴²⁵ positive weak entry points and biotic amplifiers, which is likely due to their position as both
⁴²⁶ predator and resource in the food web (*e.g.* resource in apparent competition; Figure 8).
⁴²⁷ Other species like redfish and shrimp are in motif positions leading both to positive (*e.g.*
⁴²⁸ meso-predator in omnivory interaction) and negative (*e.g.* resources in omnivory interations)
⁴²⁹ effects in motif-scale simulations (Figure 8). This likely leads to counteracting effects that
⁴³⁰ dampen their overal sensitivity to disturbances. Species sensitivity and amplification scores
⁴³¹ do not co-vary. In fact, few species are biotic buffers, with most acting as biotic amplifiers
⁴³² to some degree (Figure 8).

⁴³³ Species targeted by multiple drivers are not necessarily the most vulnerable based on their
⁴³⁴ trophic position. For example, even though the mortality, physiology and behaviour of
⁴³⁵ shrimp were expected to be impacted by drivers, it is nonetheless insensitive based on its
⁴³⁶ trophic position (Figure 8). In contrast, species impacted by few drivers like cetaceans, or
⁴³⁷ no drivers at all like harbour seals, may nonetheless be highly vulnerable due to their trophic
⁴³⁸ position (Figure 8).

⁴³⁹ Focusing on cod, shrimp and large crustaceans, 3 species with contrasting vulnerabilities in
⁴⁴⁰ the St. Lawrence, we see that different driver combinations and food web topologies lead to
⁴⁴¹ different species vulnerability (Figure 9). Combinations of drivers may increase or dampen
⁴⁴² effects on species sensitivity. For instance, fisheries and climate combine to increase and
⁴⁴³ decrease sensitivity of cod and shrimp, respectively (Figure 9). Driver combinations may
⁴⁴⁴ also lead to effect amplification even though a driver group has no effect. The combined

⁴⁴⁵ effect of fisheries and climate drivers on shrimp leads to drastically increased amplification
⁴⁴⁶ scores even if fisheries in isolation does not lead to non-additive effects (Figure 9).

⁴⁴⁷ Food web topology also impacts a species vulnerability. Based on topology, cod seem more
⁴⁴⁸ vulnerable in the Northern Gulf of St. Lawrence than in the Estuary and Southern Gulf
⁴⁴⁹ (Figure 9). Shrimp and crustaceans, meanwhile, are more sensitive in the Estuary, although
⁴⁵⁰ amplification is more important in the Gulf (Figure 9). Contrasts between food webs may
⁴⁵¹ even lead to flipped species vulnerabilities. Large crustaceans seem to be negative entry
⁴⁵² points and biotic buffers in the Estuary, yet are positive weak entry points and biotic am-
⁴⁵³ plifiers in the Gulf (Figure 9).

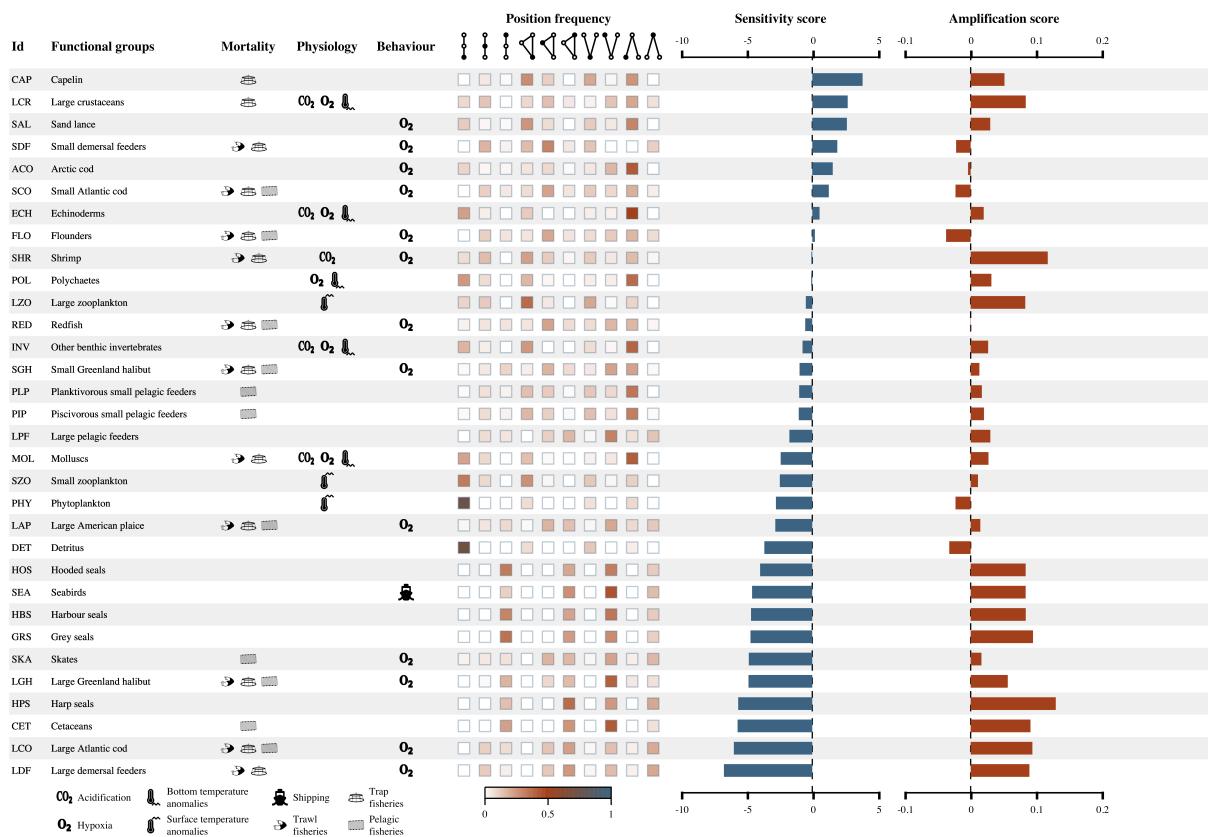


Figure 8: Change in species and functional groups sensitivity and amplification scores as a function of realized pathways of effects for an empirical food web of the Northern Gulf of St. Lawrence in the mid-1980s [?]. The left-hand side of the table presents the species and functional groups, the drivers 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 realized 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 realized pathways of effects for each species and functional group (Figure 2). 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.

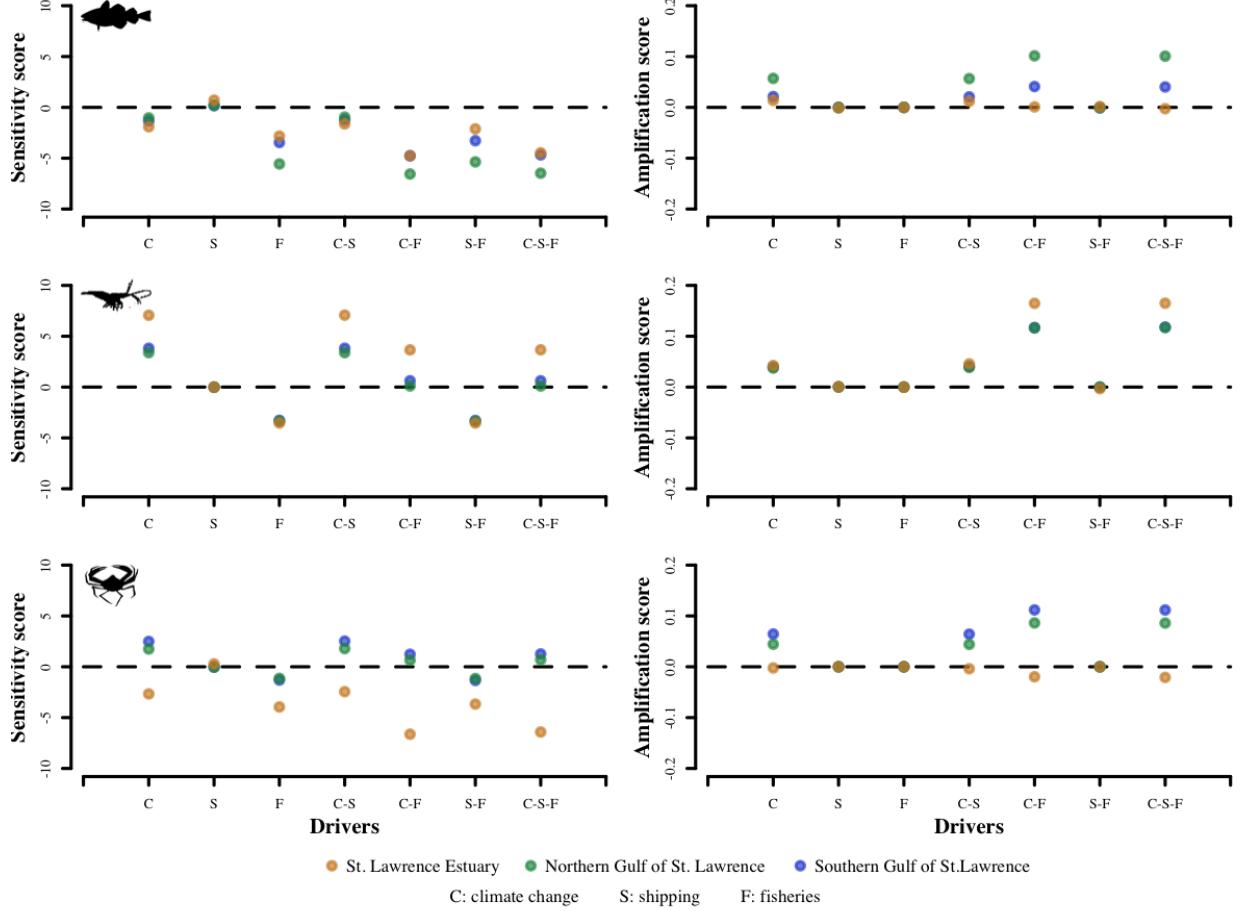


Figure 9: Realized sensitivity (S_m^*) and amplification (A_m^*) scores for Atlantic cod (*Gadus morhua*), shrimp (*Pandalus borealis*) and large crustaceans (*Crustacea*), 3 species or functional groups part of the food webs of the Southern and Northern Gulf of St. Lawrence in the mid-1980s [?] and the St. Lawrence Estuary [?]. Scores are presented when groups of drivers are considered individually and in combination.

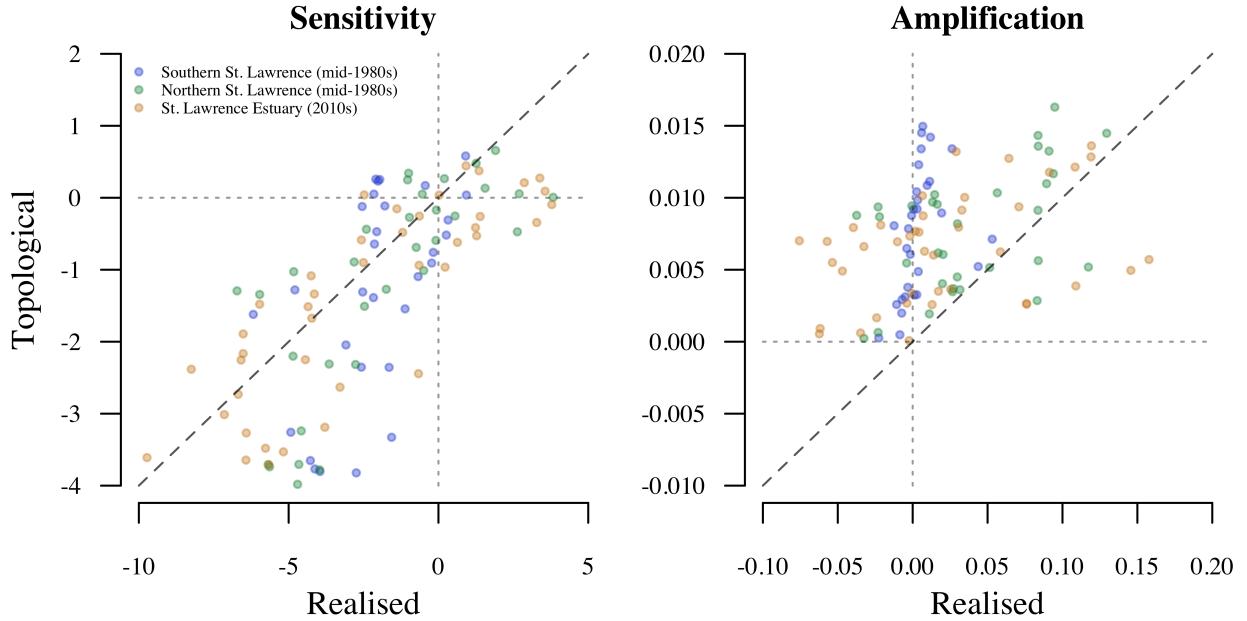


Figure 10: Biplot of the realized and topological species sensitivity (S_m^* , S_m) and amplification (A_m^* , A_m) scores in the food webs of the Southern and Northern Gulf of St. Lawrence in the mid-1980s [?] and the St. Lawrence Estuary [?].

454 5 What it all means

455 Start with a bit more context

456 In this paper, we conceptualized how multiple sources of environmental pressure may perme-
 457 ate entire ecological communities by way of species interactions and hypothesized that the
 458 position of a species in a food web and the types of interactions it is involved in would dictate
 459 its sensitivity to and amplification of pressures. To do so, we simulated disturbances on the
 460 dynamics of the four most common 3-species motifs (*i.e.* tri-trophic food chain, omnivory,
 461 competitive and apparent competition) using Lotka-Volterra models. Disturbances were
 462 simulated numerically through all possible univariate and multivariate pathways of effects
 463 targeting species mortality, growth, attack and conversion rates. Numerical simulations
 464 were then used as heuristics to infer species vulnerability in empirical food webs on the basis
 465 of their trophic position and local sources of stress.

⁴⁶⁶ We found that, indeed, the vulnerability of species to multiple disturbances is largely in-
⁴⁶⁷ fluenced by the types of interactions and the trophic position of a species. In particular,
⁴⁶⁸ predators involved in omnivory and food chain interactions are highly vulnerable to multiple
⁴⁶⁹ disturbances by acting as both weak entry points and biotic amplifiers. This observation
⁴⁷⁰ scales up to empirical food webs, in which predators are the most vulnerable species, and
⁴⁷¹ they need not be directly impacted to be highly vulnerable to environmental pressures.

⁴⁷² Arguably, the simplified model formulations we use are unlikely to fully capture the dynamics
⁴⁷³ of complex ecosystems and the vulnerability of species in food webs. Our approach ignores
⁴⁷⁴ such things as species interaction strength, stressor intensity and spatialtemporal dynamics,
⁴⁷⁵ all of which are known to play crucial roles in community dynamics and their reponses to
⁴⁷⁶ environmental pressures (???). However, in the absence of appropriate knowledge, as is
⁴⁷⁷ the case for the effects of multiple environmental pressures on ecological communities, it is
⁴⁷⁸ reasonable to first explore the simplest possibilities, from which will emerge broad conclu-
⁴⁷⁹ sions and provide new hypotheses to test theoretically or empirically (Wootton 2002). Our
⁴⁸⁰ approach, even if simple, does just that by providing compelling evidence of the importance
⁴⁸¹ of species interactions in impacts assessments and by reinforcing the case for the application
⁴⁸² of holitcis approaches. It also provides the flexibility required to test increasingly complex
⁴⁸³ hypotheses, all while providing mechanistic rather than correlative evidence.

⁴⁸⁴ In conceptualizing the effects of multiple disturbances on food webs, we sought to formulate
⁴⁸⁵ a theory-grounded framework through which the complexities of real-world systems may be
⁴⁸⁶ studied for an improved application of holistic environmental approaches. In the context of
⁴⁸⁷ multiple disturbances in particular, we sought to answer questions of particular relevance to
⁴⁸⁸ management.

489 **1. Should species interactions be considered in impact assessments?**

490 We find, as expected, that species interactions should be explicitly considered in impact
491 assessments, as they drive the vulnerability of species to the effects of disturbances. This
492 supports longstanding evidence that interactions play a crucial role in spreading the effects
493 of individual disturbances through food webs (*e.g.* Menge 1995; Wootton 1993, 2002; Yodzis
494 2000), and unsurprisingly extends this conclusion to multiple disturbances.

495 We further uncover that species vulnerability is modulated by interaction type. Omnivory
496 and food chains are particularly responsive to disturbances, while exploitative and apparent
497 competition are generally less vulnerable.

- 498 • Chain length & trophic cascades
499 • Stouffer motifs (stark contrast when we are interested in stability instead)

500 **2. Should joint stressors assessments be prioritized?**

501 We find that the effects of multiple disturbances should be considered in combination, as
502 non-additive effects arising through species interactions are prevalent. Omnivory interactions
503 and the top predators in food chains in particular are susceptible to non-additive effects, with
504 little indication as to whether an individual pathway of effect will result in antagonistic or
505 synergistic effects.

506 This suggests that food webs with high proportions of omnivory and food chain motifs might
507 be particularly prone to ecological surprises.

508 It also suggests that predicting whether a species will be a biotic buffer or amplifier will
509 likely be system specific and require a thorough understanding of realized pathways of effect,
510 which we also showed through our food web scale inference.

511 We also provide evidence that species interactions rather than population growth or mortality
512 are driving non-additive effects at the community scale. [...]

513 This suggests that the effects of disturbances on populations should not be studied outside
514 of the context of species interactions.

515 This suggests and reinforces that even if one's goal is to evaluate the impacts of a single
516 environmental pressure on a single species, species interactions and multiple drivers should
517 be considered jointly through holistic approaches to properly capture the effects.

518 **3. Which species are most vulnerable to disturbances?**

519 In a nutshell: Predators always negatively affected Meso-predator always positively affected
520 Resources negatively affected in food chain and omnivory, positively affected in competitive
521 interactions.

522 At the motif scale, predators in food chain and omnivory interactions are the most vulnerable
523 species, by acting as both weak entry points and biotic amplifiers. Talk about predators and
524 their vulnerability [...].

525 All species involved in omnivory or food chains are however susceptible to disturbances, with
526 impact on resources mirroring to a lesser degree those on predators, while mesopredators tend
527 to be positively affected by disturbances. This is likely due to trophic cascades (*e.g.* Estes
528 *et al.* 2011)

529 In contrast, exploitative and apparent competition then to be [...]. This is likely due to
530 compensatory effects of [...].

531 These obervations scale up to food webs, where large predators such as Atlantic cod and
532 Greenland halibut, which are rarely resources themselves, are the most vulnerable species.

533 These observation generally fit with the groundfish stock collapse in which stocks of XXX
534 decreased dramatically

535 This led to a shift in fisheries activities towards large crustaceans and shrimp

- 536 • Limits & opportunities:

- 537 – No interaction strength
538 – No driver intensity
539 – Simple model formulations

540 • In the absence of appropriate knowledge, it is reasonable to first explore the simplest
541 possibilities, which will provide novel hypotheses to test theoretically and empirically
542 in follow-up studies (Wootton 2002).

543 • Even if our simulations are simplifications of realworld system, they still provide com-
544 pelling evidence that reinforce the need to explicitly consider the complexity of ecolog-
545 ical systems.

546 • Name new hypotheses to test theoretically and empirically.

547 – a) IDEAS?

548 – b)

549 – ...

550 • This framework is also so flexible that we could easily include other drivers typically
551 found in systems, such as pollution or seal hunting.

552 • Spatial and temporral vulnerability of species.

553 • Other models could be used to explicitly incorporate things like competition,

554 • Positive effects of drivers (*e.g.* nutrients on growth, at least initially)

555 • Management and conservation:

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

- 559 – Single species may be vulnerable (or not) in different contexts, so that the struc-
560 ture of a network should be considered and conservation targets may change as
561 the vulnerability of species changes in time and space as a function of network
562 structure and driver combinations.

563 **6 Supplementary Material**

564 **6.1 Models**

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

Table 1: Systems of Lotka-Volterra equations used to model the effects of multiple disturbances on the six 3-species motifs selected explored.

565 6.2 Supplementary figures

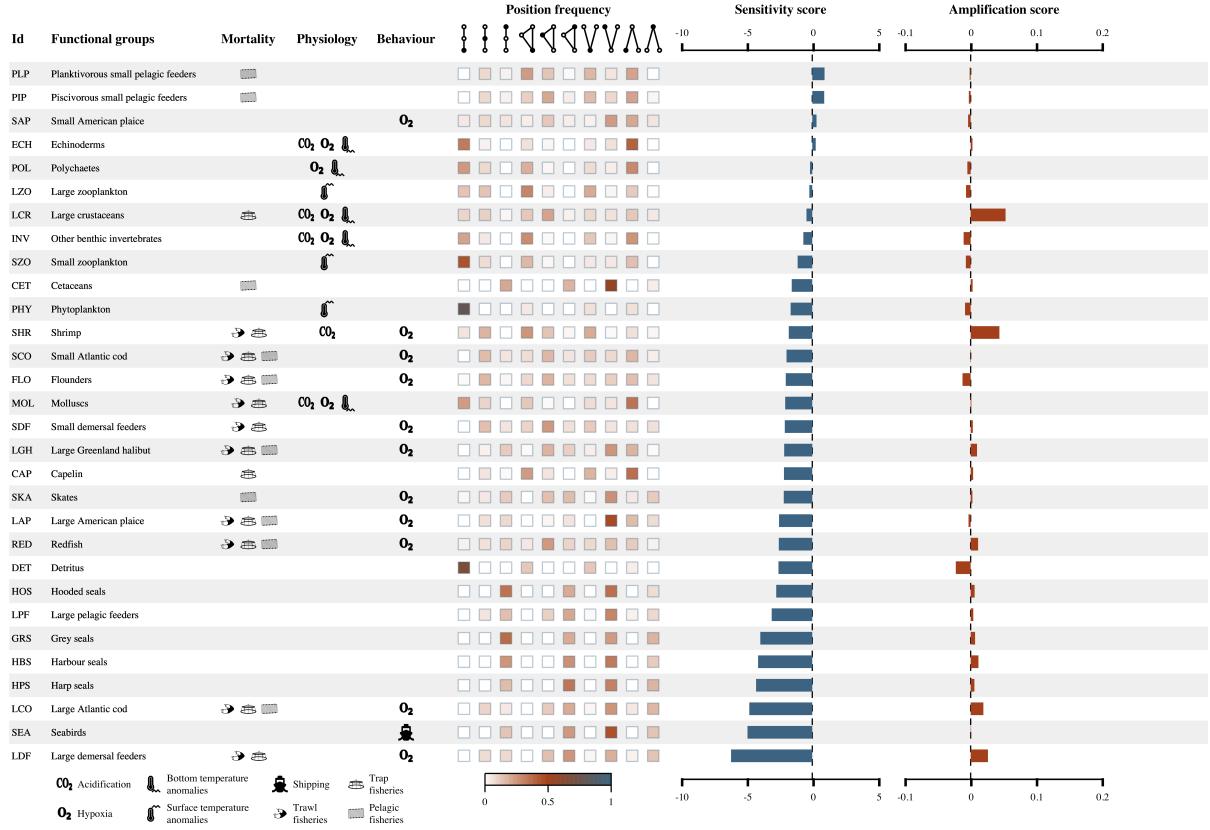


Figure 11: Change in species and functional groups sensitivity and amplification scores as a function of realized pathways of effects for an empirical food web of the Southern Gulf of St. Lawrence in the mid-1980s [?]. The left-hand side of the table presents the species and functional groups, the drivers 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 Southern 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 realized 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 realized pathways of effects for each species and functional group (Figure 2). 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.

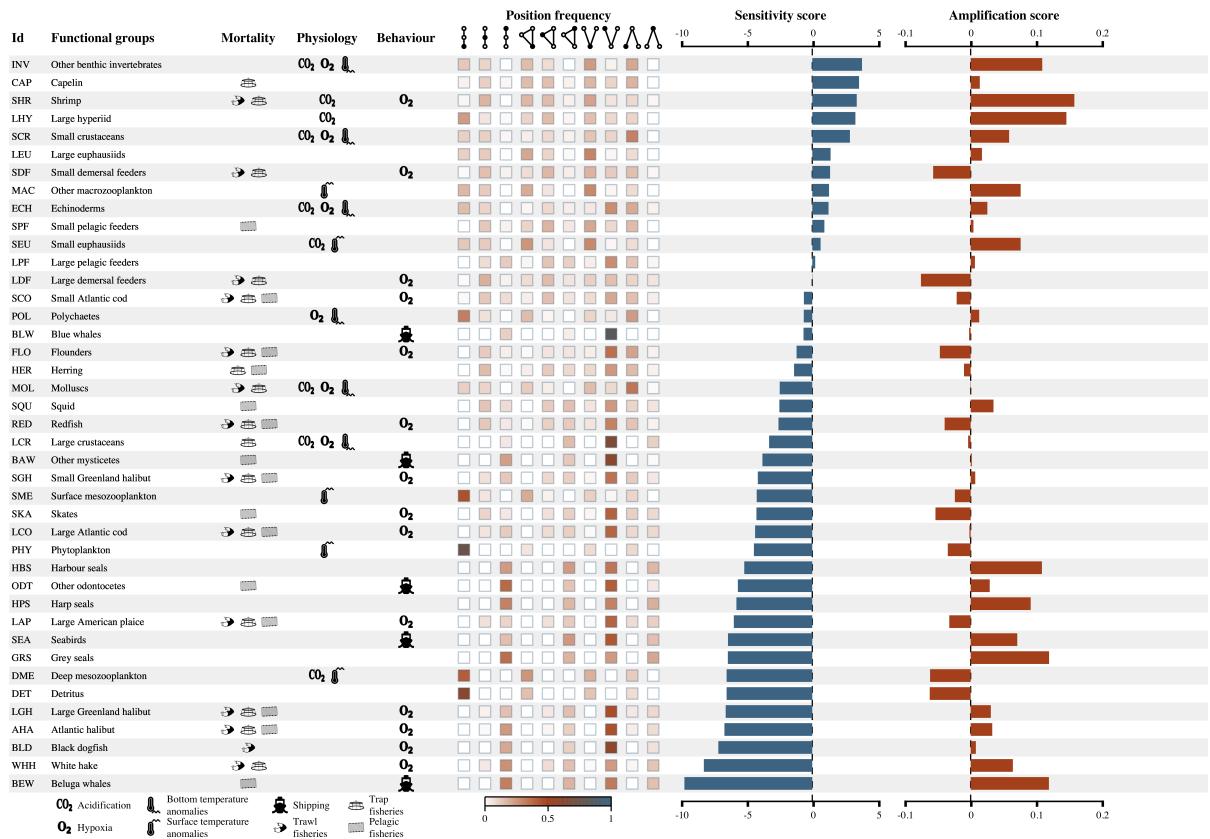


Figure 12: Change in species and functional groups sensitivity and amplification scores as a function of realized pathways of effects for an empirical food web of the St. Lawrence Estuary in the mid-1980s [?]. The left-hand side of the table presents the species and functional groups, the drivers supposed 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 St. Lawrence Estuary 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 realized 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 realized pathways of effects for each species and functional group (Figure 2). 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.

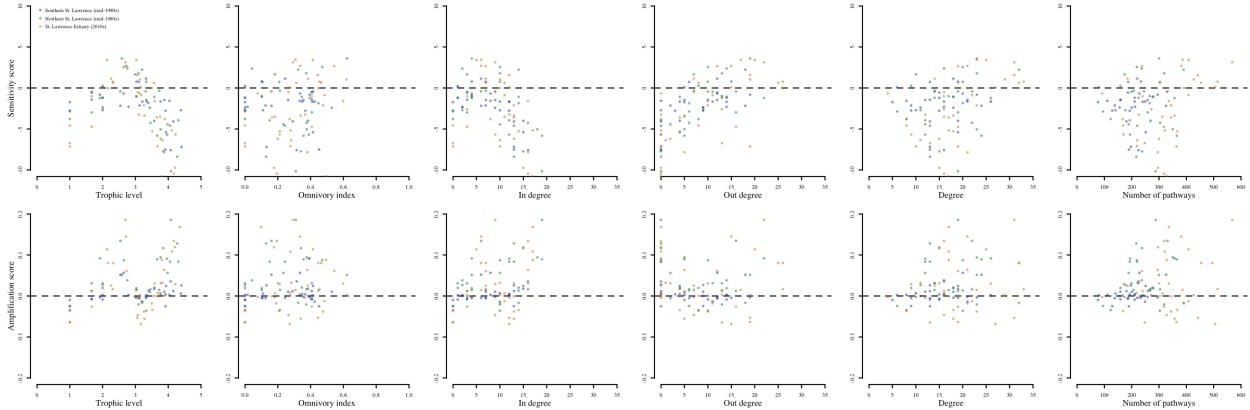


Figure 13: Species sensitivity and amplification scores as a function of network metrics: 1) trophic level, 2) omnivory index, 3) in-degree, 4) out-degree, 5) degree and 6) number of pathways of effect for the food webs of the Southern and Northern Gulf of St. Lawrence in the mid-1980s [?] and the St. Lawrence Estuary in the 2010s [?].

566 7 References

- 567 Allesina, S. & Pascual, M. (2008). Network structure, predatorPrey modules, and stability
568 in large food webs. *Theoretical Ecology*, 1, 55–64.
- 569 Ban, N.C., Alidina, H.M. & Ardrion, J.A. (2010). Cumulative impact mapping: Advances,
570 relevance and limitations to marine management and conservation, using Canada’s Pacific
571 waters as a case study. *Marine Policy*, 34, 876–886.
- 572 Bascompte, J. (2009). Disentangling the Web of Life. *Science*, 325, 416–419.
- 573 Bascompte, J. & Melián, C.J. (2005). Simple Trophic Modules for Complex Food Webs.
574 *Ecology*, 86, 2868–2873.
- 575 Beauchesne, D. (2019). Next Generation Planning - Structuring and Sharing Environmental
576 Drivers Data for the St. Lawrence. *Frontiers in Marine Science*, 1, 1.
- 577 Belley, R., Archambault, P., Sundby, B., Gilbert, F. & Gagnon, J.-M. (2010). Effects of
578 hypoxia on benthic macrofauna and bioturbation in the Estuary and Gulf of St. Lawrence,
579 Canada. *Continental Shelf Research*, 30, 1302–1313.

- 580 Boonstra, W.J., Ottosen, K.M., Ferreira, A.S.A., Richter, A., Rogers, L.A. & Pedersen,
581 M.W. *et al.* (2015). What are the major global threats and impacts in marine environments?
582 Investigating the contours of a shared perception among marine scientists from the bottom-
583 up. *Marine Policy*, 60, 197–201.
- 584 Bove, C.B., Ries, J.B., Davies, S.W., Westfield, I.T., Umpanhowar, J. & Castillo, K.D.
585 (2019). Common Caribbean corals exhibit highly variable responses to future acidification
586 and warming. *Proceedings of the Royal Society B: Biological Sciences*, 286, 20182840.
- 587 Camacho, J., Stouffer, D.B. & Amaral, L.A.N. (2007). Quantitative analysis of the local
588 structure of food webs. *Journal of Theoretical Biology*, 246, 260–268.
- 589 Chabot, D. & Claireaux, G. (2008). Environmental hypoxia as a metabolic constraint on
590 fish: The case of Atlantic cod, *Gadus morhua*. *Marine Pollution Bulletin*, 5th International
591 Conference on Marine Pollution and Ecotoxicology, 57, 287–294.
- 592 Christensen, M.R., Graham, M.D., Vinebrooke, R.D., Findlay, D.L., Paterson, M.J. &
593 Turner, M.A. (2006). Multiple anthropogenic stressors cause ecological surprises in boreal
594 lakes. *Global Change Biology*, 12, 2316–2322.
- 595 Christiansen, F., Rasmussen, M. & Lusseau, D. (2013). Whale watching disrupts feeding
596 activities of minke whales on a feeding ground. *Marine Ecology Progress Series*, 478, 239–
597 251.
- 598 Cirtwill, A.R. & Stouffer, D.B. (2015). Concomitant predation on parasites is highly variable
599 but constrains the ways in which parasites contribute to food web structure. *The Journal
600 of Animal Ecology*, 84, 734–744.
- 601 Côté, I.M., Darling, E.S. & Brown, C.J. (2016). Interactions among ecosystem stressors and
602 their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*,
603 283, 20152592.
- 604 Crain, C.M., Kroeker, K. & Halpern, B.S. (2008). Interactive and cumulative effects of

- 605 multiple human stressors in marine systems. *Ecology Letters*, 11, 1304–1315.
- 606 Darling, E.S. & Côté, I.M. (2008). Quantifying the evidence for ecological synergies. *Ecology*
607 *Letters*, 11, 1278–1286.
- 608 De Laender, F. (2018). Community-and ecosystem-level effects of multiple environmental
609 change drivers: Beyond null model testing. *Global change biology*, 24, 5021–5030.
- 610 Dupont-Prinet, A., Vagner, M., Chabot, D. & Audet, C. (2013). Impact of hypoxia on
611 the metabolism of Greenland halibut (*Reinhardtius hippoglossoides*). *Canadian Journal of*
612 *Fisheries and Aquatic Sciences*, 70, 461–469.
- 613 Eby, L.A., Crowder, L.B., McClellan, C.M., Peterson, C.H. & Powers, M.J. (2005). Habitat
614 degradation from intermittent hypoxia: Impacts on demersal fishes. *Marine Ecology Progress Series*
615 *Series*, 291, 249–262.
- 616 Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J. & Bond, W.J. *et al.*
617 (2011). Trophic Downgrading of Planet Earth. *Science*, New Series, 333, 301–306.
- 618 Fabry, V.J., Seibel, B.A., Feely, R.A. & Orr, J.C. (2008). Impacts of ocean acidification on
619 marine fauna and ecosystem processes. *ICES Journal of Marine Science*, 65, 414–432.
- 620 Giakoumi, S., Halpern, B.S., Michel, L.N., Gobert, S., Sini, M. & Boudouresque, C.-F. *et al.*
621 (2015). Towards a framework for assessment and management of cumulative human impacts
622 on marine food webs. *Conservation Biology*, 29, 1228–1234.
- 623 Griffen, B.D., Belgrad, B.A., Cannizzo, Z.J., Knotts, E.R. & Hancock, E.R. (2016). Re-
624 thinking our approach to multiple stressor studies in marine environments. *Marine Ecology*
625 *Progress Series*, 543, 273–281.
- 626 Guiden, P.W., Bartel, S.L., Byer, N.W., Shipley, A.A. & Orrock, J.L. (2019). Predator-
627 Prey Interactions in the Anthropocene: Reconciling Multiple Aspects of Novelty. *Trends in*
628 *Ecology & Evolution*, 34, 616–627.
- 629 Hale, R., Piggott, J.J. & Swearer, S.E. (2017). Describing and understanding behavioral

- 630 responses to multiple stressors and multiple stimuli. *Ecology and Evolution*, 7, 38–47.
- 631 Halpern, B.S., Frazier, M., Afflerbach, J., Lowndes, J.S., Micheli, F. & O'Hara, C. *et al.*
- 632 (2019). Recent pace of change in human impact on the world's ocean. *Scientific Reports*, 9,
- 633 11609.
- 634 Halpern, B.S. & Fujita, R. (2013). Assumptions, challenges, and future directions in cumu-
- 635 lative impact analysis. *Ecosphere*, 4, art131.
- 636 Harborne, A.R., Rogers, A., Bozec, Y.-M. & Mumby, P.J. (2017). Multiple Stressors and
- 637 the Functioning of Coral Reefs. *Annual Review of Marine Science*, 9, 445–468.
- 638 Holt, R.D. (1997). Community modules. In: *Multitrophic Interactions in Terrestrial Ecosys-*
- 639 *tems, 36th Symposium of the British Ecological Society* (eds. Grange, A.C. & Brown, V.K.).
- 640 Blackwell Science, Oxford, pp. 333–349.
- 641 Holt, R.D. & Hochberg, M.E. (2001). Indirect interactions, community modules and bio-
- 642 logical control: A theoretical perspective. *Evaluating indirect ecological effects of biological*
- 643 *control*, 13–37.
- 644 Ives, A.R. (1995). Measuring Resilience in Stochastic Systems. *Ecological Monographs*, 65,
- 645 217–233.
- 646 Jackson, M.C., Loewen, C.J.G., Vinebrooke, R.D. & Chimimba, C.T. (2016). Net effects
- 647 of multiple stressors in freshwater ecosystems: A meta-analysis. *Global Change Biology*, 22,
- 648 180–189.
- 649 Kondoh, M. (2008). Building trophic modules into a persistent food web. *Proceedings of the*
- 650 *National Academy of Sciences*, 105, 16631–16635.
- 651 Kroeker, K.J., Kordas, R.L., Crim, R., Hendriks, I.E., Ramajo, L. & Singh, G.S. *et al.*
- 652 (2013). Impacts of ocean acidification on marine organisms: Quantifying sensitivities and
- 653 interaction with warming. *Global Change Biology*, 19, 1884–1896.
- 654 Lesage, V., Omrane, A., Doniol-Valcroze, T. & Mosnier, A. (2017). Increased proximity of

- 655 vessels reduces feeding opportunities of blue whales in the St. Lawrence Estuary, Canada.
- 656 *Endangered Species Research*, 32, 351–361.
- 657 Liess, M., Foit, K., Knillmann, S., Schäfer, R.B. & Liess, H.-D. (2016). Predicting the
658 synergy of multiple stress effects. *Scientific Reports*, 6, 32965.
- 659 McClanahan, T.R., Graham, N.A. & Darling, E.S. (2014). Coral reefs in a crystal ball:
660 Predicting the future from the vulnerability of corals and reef fishes to multiple stressors.
- 661 *Current Opinion in Environmental Sustainability*, Environmental change issues, 7, 59–64.
- 662 Menge, B.A. (1995). Indirect Effects in Marine Rocky Intertidal Interaction Webs: Patterns
663 and Importance. *Ecological Monographs*, 65, 21–74.
- 664 Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D. & Alon, U. (2002). Network
665 Motifs: Simple Building Blocks of Complex Networks. *Science*, 298, 824–827.
- 666 Monteiro, A.B. & Faria, L.D.B. (2016). The interplay between population stability and food-
667 web topology predicts the occurrence of motifs in complex food-webs. *Journal of theoretical
668 biology*, 409, 165–171.
- 669 Montoya, J., Woodward, G., Emmerson, M.C. & Solé, R.V. (2009). Press perturbations and
670 indirect effects in real food webs. *Ecology*, 90, 2426–2433.
- 671 Morissette, L., Despatie, S.-P., Savenkoff, C., Hammill, M.O., Bourdages, H. & Chabot, D.
672 (2003). Data gathering and input parameters to construct ecosystem models for the northern
673 Gulf of St. Lawrence(Mid-1980 s). *Can. Tech. Rep. Fish. Aquat. Sci./Rapp. Tech. Can.
674 Sci. Halieut. Aquat.*, 100.
- 675 Myers, R.A. & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities.
676 *Nature*, 423, 280.
- 677 O'Brien, A.L., Dafforn, K.A., Chariton, A.A., Johnston, E.L. & Mayer-Pinto, M. (2019).
678 After decades of stressor research in urban estuarine ecosystems the focus is still on single
679 stressors: A systematic literature review and meta-analysis. *Science of The Total Environ-*

680 *ment.*

- 681 O’Gorman, E.J. & Emmerson, M.C. (2009). Perturbations to trophic interactions and the
682 stability of complex food webs. *Proceedings of the National Academy of Sciences*, 106,
683 13393–13398.
- 684 O’Gorman, E.J., Fitch, J.E. & Crowe, T.P. (2012). Multiple anthropogenic stressors and
685 the structural properties of food webs. *Ecology*, 93, 441–448.
- 686 Pauly, D., Christensen, V., Dalsgaard, J., Froese, R. & Torres, F. (1998). Fishing Down
687 Marine Food Webs. *Science*, 279, 860–863.
- 688 Piggott, J.J., Townsend, C.R. & Mattheai, C.D. (2015). Reconceptualizing synergism and
689 antagonism among multiple stressors. *Ecology and Evolution*, 5, 1538–1547.
- 690 Pillet, M., Dupont-Prinet, A., Chabot, D., Tremblay, R. & Audet, C. (2016). Effects of
691 exposure to hypoxia on metabolic pathways in northern shrimp (*Pandalus borealis*) and
692 Greenland halibut (*Reinhardtius hippoglossoides*). *Journal of Experimental Marine Biology*
693 and *Ecology*, 483, 88–96.
- 694 Savenkoff, C. (2012). *Input data and parameter estimates for ecosystem models of the lower*
695 *St. Lawrence Estuary (20082010)*. Canadian Technical Report of Fisheries and Aquatic
696 Sciences 2999, Department of Fisheries and Oceans, Mont-Joli, Québec, Canada.
- 697 Savenkoff, C., Bourdages, H., Swain, D.P., Despatie, S.-P., Hanson, J.M. & Méthot, R. *et*
698 *al.* (2004). *Input data and parameter estimates for ecosystem models of the southern Gulf*
699 *of St. Lawrence (mid-1980s and mid-1990s)*. Canadian Technical Report of Fisheries and
700 Aquatic Sciences 2529, Department of Fisheries and Oceans, Mont-Joli, Québec, Canada.
- 701 Schäfer, R.B. & Piggott, J.J. (2018). Advancing understanding and prediction in multiple
702 stressor research through a mechanistic basis for null models. *Global Change Biology*, 24,
703 1817–1826.
- 704 Stouffer, D.B. & Bascompte, J. (2010). Understanding food-web persistence from local to

- 705 global scales. *Ecology Letters*, 13, 154–161.
- 706 Stouffer, D.B. & Bascompte, J. (2011). Compartmentalization increases food-web persis-
707 tence. *Proceedings of the National Academy of Sciences*, 108, 3648–3652.
- 708 Stouffer, D.B., Camacho, J., Jiang, W. & Nunes Amaral, L.A. (2007). Evidence for the
709 existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society
710 B: Biological Sciences*, 274, 1931–1940.
- 711 Stouffer, D.B., Sales-Pardo, M., Sirer, M.I. & Bascompte, J. (2012). Evolutionary Conser-
712 vation of Species' Roles in Food Webs. *Science*, 335, 1489–1492.
- 713 Thompson, P.L., MacLennan, M.M. & Vinebrooke, R.D. (2018). Species interactions cause
714 non-additive effects of multiple environmental stressors on communities. *Ecosphere*, 9,
715 e02518.
- 716 Wootton, J.T. (1993). Indirect Effects and Habitat Use in an Intertidal Community: Inter-
717 action Chains and Interaction Modifications. *The American Naturalist*, 141, 71–89.
- 718 Wootton, J.T. (2002). Indirect effects in complex ecosystems: Recent progress and future
719 challenges. *Journal of Sea Research*, Structuring Factors of Shallow Marine Coastal Com-
720 munities, Part I, 48, 157–172.
- 721 Worm, B., Barbier, E.B., Beaumont, N., Duffy, J.E., Folke, C. & Halpern, B.S. *et al.* (2006).
722 Impacts of Biodiversity Loss on Ocean Ecosystem Services. *Science*, 314, 787–790.
- 723 Yodzis, P. (2000). Diffuse Effects in Food Webs. *Ecology*, 81, 261–266.