

1 On the vulnerability of food webs to multiple
2 stressors

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

5

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

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

8 ³Department of Integrative Biology, University Of Guelph, Guelph, Ontario, Canada N1G
9 2W1

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

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26 **Correspondence:**

27 David Beauchesne

28 david.beauchesne@uqar.ca

29 1-514-553-4975

30

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32

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⁴³ **Notes**

- ⁴⁴ • In it's current form, I believe that the contribution portion is not good enough
⁴⁵ • I wonder whether the qualifications should be more in depth.
⁴⁶ • Right now, the letter is 43 words over the word limit.
⁴⁷ • Also, this text might be better than the current abstract

⁴⁸ **Letter**

⁴⁹ Evaluating the effects of multiple sources of stress in natural environments has become
⁵⁰ an increasingly important issue as the effects of intensifying global change and expanding
⁵¹ human activities result in complex stress exposure regimes. Even though the non-additive
⁵² effects of multiple stressors have been investigated empirically for a few decades now, there
⁵³ remains a general lack of theoretical understanding of their impacts on natural systems.
⁵⁴ In particular, the role of species and their interactions in mediating the effects of multiple
⁵⁵ disturbances through ecological communities networks, although widely acknowledged, has
⁵⁶ yet to be formally explored. We propose the first such formal exploration by exhaustively
⁵⁷ simulating the impacts of all possible pathways of effects on the dynamics of 3-species motifs
⁵⁸ using Lotka-Volterra models. We uncover that interaction types and species position greatly
⁵⁹ influence sensitivity to and amplification of multiple disturbances and that indirect pathways
⁶⁰ of effects are the main cause of non-additive effects. In particular, predators in food chain and
⁶¹ omnivory interactions act as both weak entry points (*i.e.* highly sensitive to disturbances)
⁶² and biotic amplifiers (*i.e.* affected synergistically by disturbances). We then use the simulated
⁶³ sensitivity and amplification scores as heuristics to infer trophic vulnerability of species
⁶⁴ based on topology and realized pathways of effects in the food web of the Northern Gulf of
⁶⁵ St. Lawrence, Canada, prior to a groundfish stock collapse in the 1990s. We find that heavily
⁶⁶ exploited species appear to be the most vulnerable trophically, while fisheries transitioned to
⁶⁷ insensitive or beneficiary species post-collapse. This contribution is significant and timely for
⁶⁸ two main reasons. First, from a theory stand point, this is the first exhaustive exploration
⁶⁹ of mitigation and amplification of multiple disturbances via trophic motifs. Second, we
⁷⁰ provide a clear link between theory and management by illustrating how our framework can
⁷¹ be applied to detect most sensitive species in a real food web exposed to various stressors.
⁷² Our group of co-authors is singularly positioned to write this paper. D. Beauchesne and P.

⁷³ Archambault both have strong backgrounds in environmental assessments in general and
⁷⁴ cumulative impacts in particular. K. Cazelles and D. Gravel are both experts in theoretical
⁷⁵ ecology with strong backgrounds and recognition in the field.

76 **1 Abstract**

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

⁹⁶ 2 Introduction

⁹⁷ Ecosystems worldwide are increasingly affected by a vast array of environmental pressures,
⁹⁸ commonly referred to as stressors (Boonstra *et al.* 2015; Halpern *et al.* 2019). Pressures may
⁹⁹ be driven by natural or human-induced biophysical processes such as ocean acidification and
¹⁰⁰ warming, or directly from anthropogenic activities such as fisheries. These drivers can be
¹⁰¹ defined as any externality that affects environmental processes and disturbs natural systems.
¹⁰² Individually, drivers have been found to impact all levels of biological organization and cause
¹⁰³ dramatic changes to whole ecosystems. Ocean acidification can reduce coral and mollusk
¹⁰⁴ calcification, metabolic, growth and mortality rates, and has been linked to altered carbon
¹⁰⁵ fluxes in ecological networks (Fabry *et al.* 2008; Kroeker *et al.* 2013; Bove *et al.* 2019).
¹⁰⁶ Fisheries have caused the collapse of commercial species, decreased the mean trophic level in
¹⁰⁷ coastal and oceanic environments by targetting large predators and impaired a variety of
¹⁰⁸ essential ecosystem services (Pauly *et al.* 1998; Myers & Worm 2003; Worm *et al.* 2006).
¹⁰⁹ Rarely do drivers occur individually, and the list of potentially interacting drivers affecting an
¹¹⁰ ecosystem at any given point in time or space can be extensive (Halpern *et al.* 2019). Global
¹¹¹ changes and local human activities thus result in increasingly intricate environmental stress
¹¹² exposure regimes, compounding the pathways of effects through which natural systems can
¹¹³ be impacted (Halpern *et al.* 2019). For example, coral reefs contend with a suite of pressures
¹¹⁴ including fishing, warming temperatures, ocean acidification and water quality that may
¹¹⁵ impact species in contrasting ways (McClanahan *et al.* 2014; Harborne *et al.* 2017). Moreover,
¹¹⁶ the concomitance of stressors may perturb ecosystems in a way that cannot be explained
¹¹⁷ by the examination of individual pressures. Dramatic examples of these non-additive effects
¹¹⁸ include up to 100-fold increases of the sensitivity of certain organisms to toxicants (*e.g.*
¹¹⁹ pesticides) when exposed to other environmental stressors (*e.g.* parasites; Liess *et al.* 2016)
¹²⁰ 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 compounds
¹²⁶ the complexity of multiple drivers studies. For example, hypoxia decreases overall habitat
¹²⁷ quality but has species-dependent effects, ranging from well-adapted (*e.g.* northern shrimp
¹²⁸ *Pandalus borealis* and Greenland halibut *Reinhardtius hippoglossoides*; Pillet *et al.* 2016)
¹²⁹ to avoidance behaviour (*e.g.* Atlantic cod *Gadus morhua*; Chabot & Claireaux 2008), and
¹³⁰ mortality (*e.g.* sessile benthic invertebrates; Eby *et al.* 2005; Belley *et al.* 2010). Moreover,
¹³¹ species are also embedded in a complex web of interactions that provides indirect pathways
¹³² of effects through which pressures may permeate entire ecological communities (Wootton
¹³³ 2002; Bascompte 2009; Montoya *et al.* 2009; O’Gorman & Emmerson 2009; O’Gorman *et*
¹³⁴ *al.* 2012). Indirect effects, *i.e.* when two or more direct effects are linked by a single species
¹³⁵ involved in both effects, may be as important of, and propagate faster than, direct effects
¹³⁶ (Wootton 1993, 2002; Menge 1995; Yodzis 2000). Empirical examples of trophic cascades are
¹³⁷ abundant throughout all types of ecosystems globally (Estes *et al.* 2011). In multi-species
¹³⁸ systems, where both direct and indirect effects are operating simultaneously, it is expected
¹³⁹ that the effects of environmental pressures will be amplified or dampened through biotic
¹⁴⁰ interactions (Ives 1995; Wootton 2002; Thompson *et al.* 2018). Community dynamics and
¹⁴¹ how species are embedded in complex networks is therefore likely to affect their sensitivity to
¹⁴² environmental pressures.

¹⁴³ Confronted with the challenge of managing and preserving complex systems, there is an urgent
¹⁴⁴ need for the development of theoretical frameworks that properly consider the complexities of
¹⁴⁵ multiple drivers and ecological networks in ways that are informative to management. From
¹⁴⁶ a practical standpoint, single-driver and single-species assessments remain overwhelmingly
¹⁴⁷ applied (O’Brien *et al.* 2019), while most multiple drivers studies have typically focused

148 on habitats (*e.g.* Ban *et al.* 2010; Halpern *et al.* 2019). This conveniently circumscribes
149 assessments to a set of tractable units, but it also ignores systems complexity and aggregates
150 biological processes operating at lower levels organization (Halpern & Fujita 2013; Giakoumi
151 *et al.* 2015). Studies have also relied on the use of null models that provide little insights into
152 the mechanisms underlying ecological responses to the effects of multiple drivers (Griffen *et al.*
153 2016; Jackson *et al.* 2016; De Laender 2018; Schäfer & Piggott 2018) Theoretically, species
154 interactions have long been identified as key components to the sensitivity of whole networks
155 to disturbances (*e.g.* Ives 1995; Wootton 2002; O’Gorman & Emmerson 2009; O’Gorman
156 *et al.* 2012), but the effects of multiple disturbances on networks have yet to be formally
157 explored.

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

165 **3 Of food web and multiple disturbances**

166 **3.1 Conceptualizing disturbances**

167 Drivers can disturb the dynamics of ecological communities by disrupting a variety of biological
168 processes (Figure 1A) such as behaviour (*e.g.* Chabot & Claireaux 2008; Hale *et al.* 2017),
169 reproduction [*e.g.* ref], physiology (*e.g.* Dupont-Prinet *et al.* 2013), mortality (*e.g.* Belley
170 *et al.* 2010), and species interactions (*e.g.* Wootton 2002; Guiden *et al.* 2019). Multiple
171 processes may be affected by a single driver, while multiple drivers may target a single process.
172 For instance, fishing could affect the behaviour and the mortality of cod, while ocean warming

¹⁷³ and ocean acidification may jointly affect physiological processes of benthic invertebrates
¹⁷⁴ such as calcification rates. The potential number of univariate and multivariate pathways
¹⁷⁵ of effects through which community dynamics may be affected is extensive and increases
¹⁷⁶ exponentially with the number of species and the number on links in a network.

¹⁷⁷ A thorough understanding of the impacts of disturbance regimes and community dynamics
¹⁷⁸ would be necessary to fully capture the effects of multiple drivers, but the complexity of
¹⁷⁹ empirical food webs in itself is prohibitive to investigations of community dynamics. Studying
¹⁸⁰ smaller subgraphs - community motifs or modules - has thus emerged as an alternative to
¹⁸¹ gather insights into the dynamics and stability of complex ecological communities (Holt 1997;
¹⁸² Holt & Hochberg 2001). Motifs are collections of n -species that, when put together, construct
¹⁸³ whole food webs (Milo *et al.* 2002; Stouffer *et al.* 2007). They form the backbone of food
¹⁸⁴ webs and provide a mesoscale characterization of community structure (Bascompte & Melián
¹⁸⁵ 2005; Stouffer *et al.* 2007). A species can be described as a function of all n -species motifs it
¹⁸⁶ is involved in in an empirical food web (Figure 1B; Stouffer *et al.* 2012).

¹⁸⁷ There are 13 distinct 3-species motifs composed of 30 unique positions (Milo *et al.* 2002;
¹⁸⁸ Stouffer *et al.* 2007, 2012). Four 3-species motifs have received particular attention in
¹⁸⁹ theoretical and empirical studies due to their roles [ref] and prevalence (Camacho *et al.* 2007;
¹⁹⁰ Stouffer & Bascompte 2010) in food webs: tri-trophic food chain, omnivory or intraguild
¹⁹¹ predation, exploitative competition and apparent competition.

¹⁹² Motif dynamics has been studied extensively to uncover how structural properties of food
¹⁹³ webs can benefit community persistence and stability (Allesina & Pascual 2008; Kondoh
¹⁹⁴ 2008; Stouffer & Bascompte 2010, 2011; Monteiro & Faria 2016) and to assess the structural
¹⁹⁵ roles of species within food webs (Stouffer *et al.* 2012; Cirtwill & Stouffer 2015). These
¹⁹⁶ provide meaningful insights for conservation efforts. For example, results from Stouffer *et*
¹⁹⁷ *al.* (2012) suggest that certain species may benefit whole community persistence based on
¹⁹⁸ their trophic position, and that the diversity of trophic roles found in empirical food webs

¹⁹⁹ does not correlate to species richness. This means that strictly using species richness as a
²⁰⁰ conservation measure may ignore the benefits to community persistence provided by the
²⁰¹ trophic roles of individual species. Using trophic roles as targets may thus be valuable for
²⁰² community conservation (Stouffer *et al.* 2012).

²⁰³ Managers are not only tasked with species conservation, however. For example, the dynamics
²⁰⁴ of coexisting species is particularly important to practitioners whose mandate is to monitor
²⁰⁵ and manage exploited populations using holistic approaches such as ecosystem based fisheries
²⁰⁶ management. In this context, population fluctuations are at least as important as species
²⁰⁷ persistence. As such, studying the dynamics of persistent communities is of particular
²⁰⁸ relevance to management in the context of multiple environmental pressures (Figure 1C).

²⁰⁹ Here, we study the equilibrium dynamics, i.e. when species are constrained to coexistence,
²¹⁰ of the most prevalent 3-species motifs in food webs (i.e. food chain, omnivory, exploitative
²¹¹ competition, and apparent competition) to exhaustively investigate how trophic position and
²¹² interaction type influences the sensitivity to and the amplification of the effects of multiple
²¹³ disturbances. We then use the simulations to infer species trophic vulnerability in complex
²¹⁴ food webs as a function of species position in food web and realized pathways of effects.

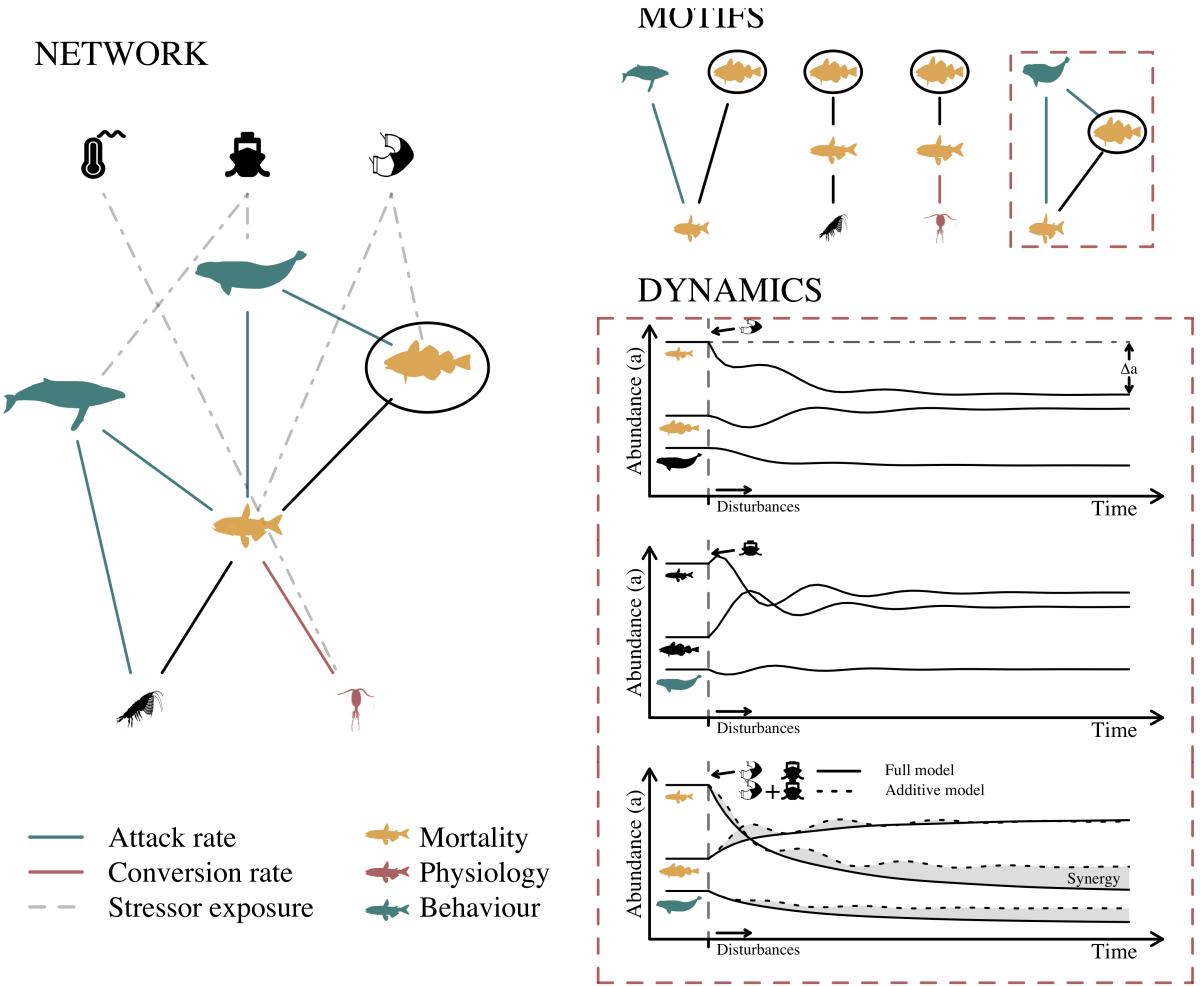


Figure 1: Conceptualization of the effects of multiple sources of environmental stress on the dynamics of a theoretical food web. A) Drivers such as sea surface temperature, marine traffic and fisheries penetrate food webs through various pathways of effects by disturbing ecological processes governing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

215 **3.2 Simulating disturbances**

216 **3.2.1 Models formulation**

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

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

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

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

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

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

230 Models were solved at equilibrium to study the effects of disturbances on persistent motif
231 dynamics. As no equilibrium exists for the exploitative competition motif with Lotka-Volterra
232 models of the selected forms, competitive parameters of the form

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

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

234 Refer to table S1 for the detailed equation systems of all motifs considered.

235 3.2.2 Models parameterization

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

247 3.2.3 Disturbances

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

254 For each motif, all possible mortality, resource growth, conversion and attack rates parameter

255 combinations were simulated. This resulted in a total of 930 unique pathways of effects
 256 for all motifs combined (food chain, competitive exploitation and apparent competition:
 257 7 parameters, 127 pathways of effects; omnivory: 9 parameters, 511 pathways of effects;
 258 partially connected 5 parameters, 31 pathways of effects; disconnected: 3 parameters, 7
 259 pathways of effects).

260 3.3 Motifs vulnerability

261 3.3.1 Trophic sensitivity

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

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

264 where a_i is the initial abundance at position i without disturbance, and $a_{i,j}$ is the abundance
 265 at position i with disturbance due to pathway of effect j . Note that, by definition, $s_{i,j}$ is
 266 bounded negatively to -1, as abundances cannot fall below 0. We define the sensitivity score
 267 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
 268 conditions.

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

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

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

274 **3.3.2 Trophic amplification**

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

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

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

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

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

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

288 **3.4 Species vulnerability**

289 **3.4.1 Scores**

290 IMPORTANT COMMENT: For now, I present the topological score, but I am
291 not sure whether it should be presented at all since I ultimately do not really
292 use it in my discussion. Except if we end up presenting it in the paper to make

293 the point that although it would provide a proxy of trophic vulnerability (which
294 we will be using for my last thesis chapter), it does not really capture realized
295 vulnerability when actual drivers are considered. This is not so true for sensitivity,
296 but it certainly is for amplification. See Figure 9 for a biplot of topological vs
297 realized scores.

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

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

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

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

305 where S_m and A_m are the sensitivity and amplification scores of species m , respectively, $f_{m,i}$
306 is the frequency at which species m occupies position i in a food web, and S_i and A_i are the
307 mean trophic sensitivity and amplification scores at position i , respectively. Note that for
308 species vulnerability, we do not consider the control motifs any further.

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

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

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

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

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

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

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

325 3.4.2 Empirical food webs

326 We evaluated the vulnerability of species in 3 empirical webs from the Southern (SSL) and
 327 Northern (NSL) Gulf, and Estuary (ESL) of St. Lawrence in eastern Canada (Morissette
 328 *et al.* 2003; Savenkoff *et al.* 2004; Savenkoff 2012). The Southern and Northern Gulf of
 329 St. Lawrence food webs correspond to the mid-1980s, prior to a groundfish stock collapse in
 330 the early 1990s, while the St. Lawrence Estuary food web corresponds to the early 2010s.
 331 The total number of species and functional groups differs between food webs ($n_{SSL} = 30$;

³³² $n_{NSL} = 32$; $n_{ESL} = 41$;), yet there is significant overlap ($n_{all} = 21$). Food webs resolution is
³³³ biased towards commercial fish for all food webs. In the food webs, interactions are identified
³³⁴ as a percent of species or functional group in the diet of another species or functional group.
³³⁵ Only diet percent > 0.1 were considered as interactions in our analysis. Note that detailed
³³⁶ vulnerability results are only presented and discussed for the Northern Gulf food web. Results
³³⁷ for the Estuary and Southern Gulf are available as supplementary material (Figures S1, S2).

³³⁸ \rightarrow

³³⁹ 3.4.3 Drivers

³⁴⁰ Climate change related drivers (*i.e.* acidification, hypoxia, and bottom and surface tempera-
³⁴¹ ture anomalies) are prevalent in the St. Lawrence System, with the exception of hypoxia in
³⁴² the Southern Gulf (Beauchesne 2019). Marine traffic is widespread, especially in the Northern
³⁴³ Gulf and the Estuary, which serve as the main seaway to inland North-America (Beauchesne
³⁴⁴ 2019). Fisheries have changed through time after the collapse of groundfish stocks in the
³⁴⁵ early 1990s. Species affected by fisheries were identified using the catch data provided in the
³⁴⁶ description of the food web models (Morissette *et al.* 2003; Savenkoff *et al.* 2004; Savenkoff
³⁴⁷ 2012). Gear type used was identified using landing data from logbooks from the Department
³⁴⁸ of Fisheries and Ocean's Canada [dfo2016b].

³⁴⁹ The impacts of specific drivers on species and functional groups was done following broad
³⁵⁰ rules to simplify the number of assumptions required. Our approach does not seek to establish
³⁵¹ the vulnerability of a particular species to all types of drivers, but rather to make general
³⁵² inference on species trophic vulnerability based on its trophic position and the supposed
³⁵³ effects of drivers on biological processes driving community dynamics. Detailed literature
³⁵⁴ search or expert knowledge could be used to get a better sense of the proximate effects of
³⁵⁵ drivers on species, but this is beyond the scope of our objectives.

³⁵⁶ The first criteria used to evaluate the effect of drivers on species and functional groups was a

357 broad evaluation of direct exposure to individual drivers. Acidification, hypoxia and bottom
358 temperature anomalies are widespread in the deep habitats of the St. Lawrence, while surface
359 temperature anomalies and marine traffic are operating on the surface layer (Beauchesne
360 2019). As such, species of functional groups in deep or surface habitats were considered as
361 exposed to deep or surface drivers, respectively. Hypoxia was considered as impacting the
362 physiology or behaviour of species or functional groups with low or high mobility, respectively
363 (???). Temperature anomalies were considered as impacting the physiology of species with
364 low mobility only. Ocean acidification was assumed to affect the physiology of exposed
365 carbonate-secreting organisms (*e.g.* mollusks and crustaceans; Kroeker *et al.* 2013). Marine
366 traffic was considered as primarily impacting whale behaviour (Christiansen *et al.* 2013;
367 Lesage *et al.* 2017). The impact of fisheries was assumed to target the mortality rates of
368 species with positive catch rates. Catches of certain species or functional groups of seals and
369 seabird through hunting, and whales through bycatch, is reported for the empirical food webs
370 of the St. Lawrence (Morissette *et al.* 2003; Savenkoff *et al.* 2004; Savenkoff 2012). We thus
371 considered that the mortality rates of seabirds and marine mammals with reported catches
372 was disturbed.

373 4 Food web vulnerability to multiple disturbances

374 4.1 Motifs vulnerability

375 The simulations uncover, as anticipated, that interaction motifs (*i.e.* food chain, omnivory,
376 exploitative and apparent competition) are more sensitive and more likely to amplify the
377 effects of multiples disturbances than control motifs (Figures 2, 3). Species in omnivory and
378 food chain motifs are generally more sensitive and likely to amplify the effects of disturbances
379 than species in competitive interaction motifs (Figure 2, 3).

380 Biotic sinks are composed almost exclusively of pathways targeting control motif positions
381 and simulations on control motifs largely result in additive affects (Figure 2). Weak entry

³⁸² points, biotic buffers and biotic amplifiers, meanwhile, are prevalent for all interaction motifs
³⁸³ (Figure 2). This is particularly true for species in the omnivory motif and for the top predator
³⁸⁴ in the food chain motif, whose trophic sensitivity and amplification scores are highly variable
³⁸⁵ (Figure 2).

³⁸⁶ Species position also greatly influences trophic sensitivity to and amplification of disturbances.
³⁸⁷ In general, top predators are weak entry points for all interaction types (Figure 3). In contrast,
³⁸⁸ non-additive effects on top predators depends on interaction type. Pathways of effect on top
³⁸⁹ predators in omnivory and food chain interactions largely result in synergistic or antagonistic
³⁹⁰ effects, and predators are, on average, biotic amplifiers (Figure ref{position}). Predators in
³⁹¹ competitive interactions, meanwhile, are less affected by non-additive effects and are fringe
³⁹² biotic buffers (Figure ref{position}).

³⁹³ Resources are largely weak entry points for all motifs, yet the effect are typically negative
³⁹⁴ in food chain and omnivory interactions, and positive in competitive interactions (Figures
³⁹⁵ 2, 3). Altough resources are, on average, neither biotic buffers or amplifiers, the effects of
³⁹⁶ individual pathways of effects are mostly non-additive (Figure 2). The effects of disturbances
³⁹⁷ on other interactions are mostly additive. (Figure 2).

³⁹⁸ Meso-predators, which are found only in omnivory and food chain interactions, are weak
³⁹⁹ entry points and generally benefit from disturbances (Figure 2). Meso-predators in omnivory
⁴⁰⁰ interactions are, on average, fringe biotic buffers, but like all other positions in the omnivory
⁴⁰¹ motif, most individual pathways of effect result in either antagonistic or synergistic effects
⁴⁰² (Figure 3).

⁴⁰³ The nature of the pathways of effects also influences trophic sensitivity and amplification.
⁴⁰⁴ Unsurprisingly, multivariate pathways of effects are generally more impactful to species
⁴⁰⁵ sensitivity and hold a higher proportion of weak entry points than univariate pathways
⁴⁰⁶ (Figure 2). Similarly, targeting multiple biological processes results in greater sensitivity and
⁴⁰⁷ amplification (Figure 2). There are however a few generalities worth noting. Mortality and

408 growth rates are driving heightened trophic sensitivities, yet do not individually contribute to
409 non-additive effects (Figure 4). Instead, trophic amplification is largely driven by disturbances
410 on species species interactions (*i.e.* attack (α_{ij}) and conversion (e) rates; Figure 4).

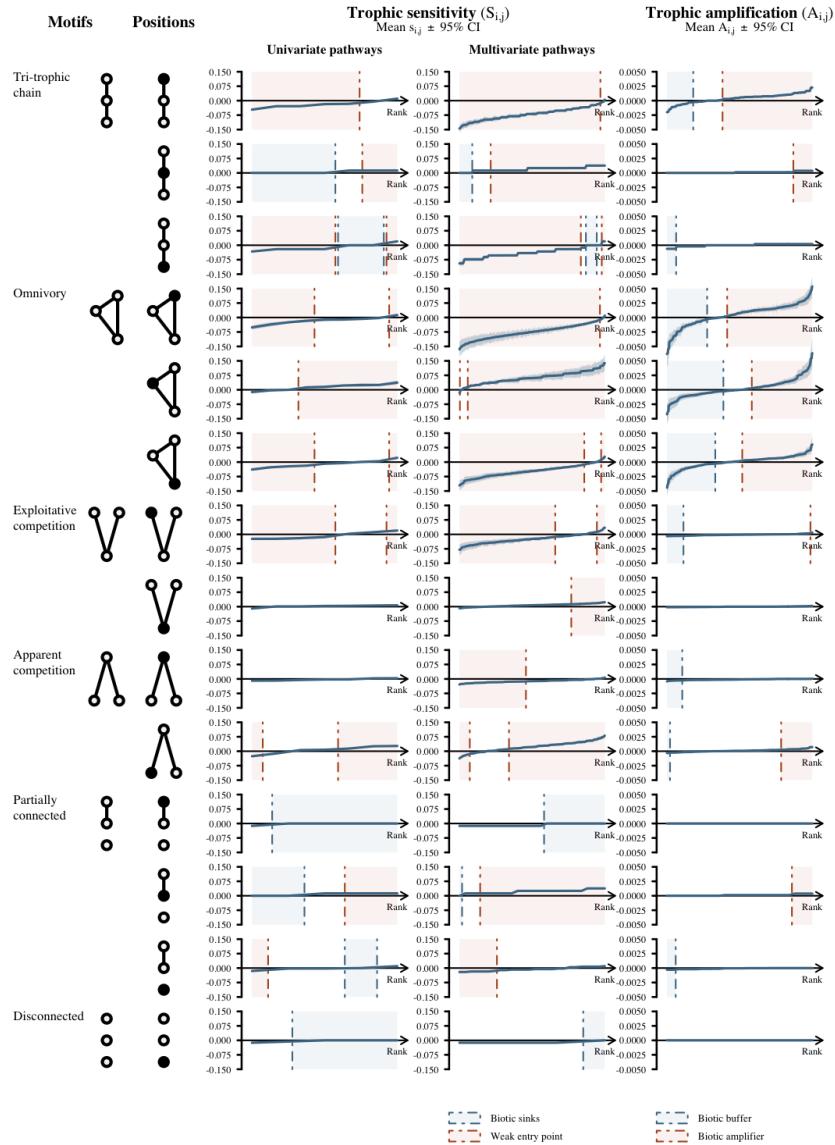


Figure 2: Ranking of trophic sensitivity ($S_{i,j}$) and amplification ($A_{i,j}$) scores for all univariate and multivariate pathways of effects on all 13 unique motif positions in the three-species motifs explored, *i.e.* tri-trophic food chain, omnivory, exploitative competition, apparent competition, 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.

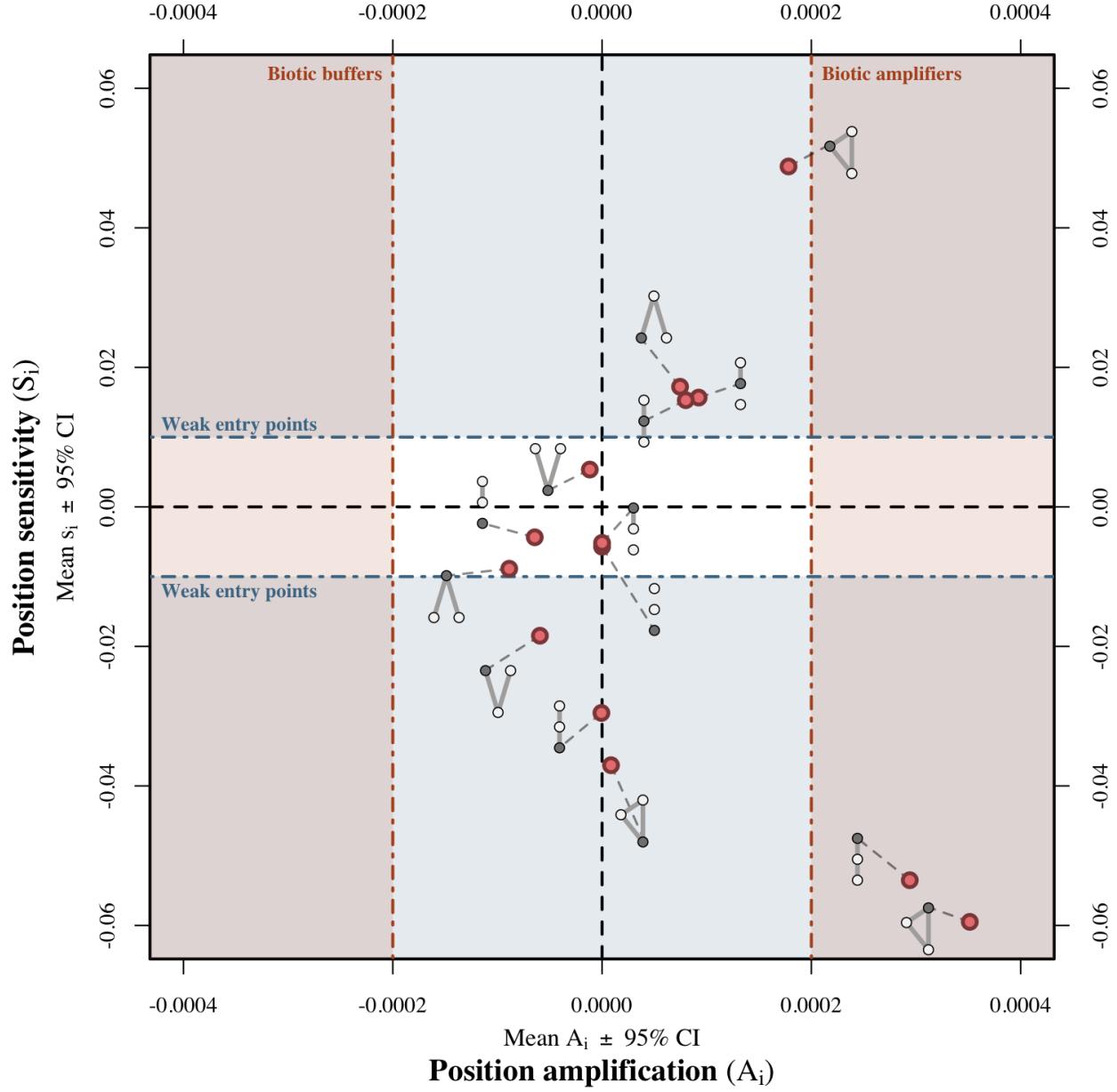


Figure 3: Ranking of 13 motif positions as a function of position sensitivity (S_i) and amplification (A_i) scores in the three-species motifs explored, *i.e.* tri-trophic food chain, omnivory, exploitative competition, apparent competition, partially connected and disconnected. Position sensitivity 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 buffers (*i.e.* antagonistic effect of disturbances) are identified by the red regions.

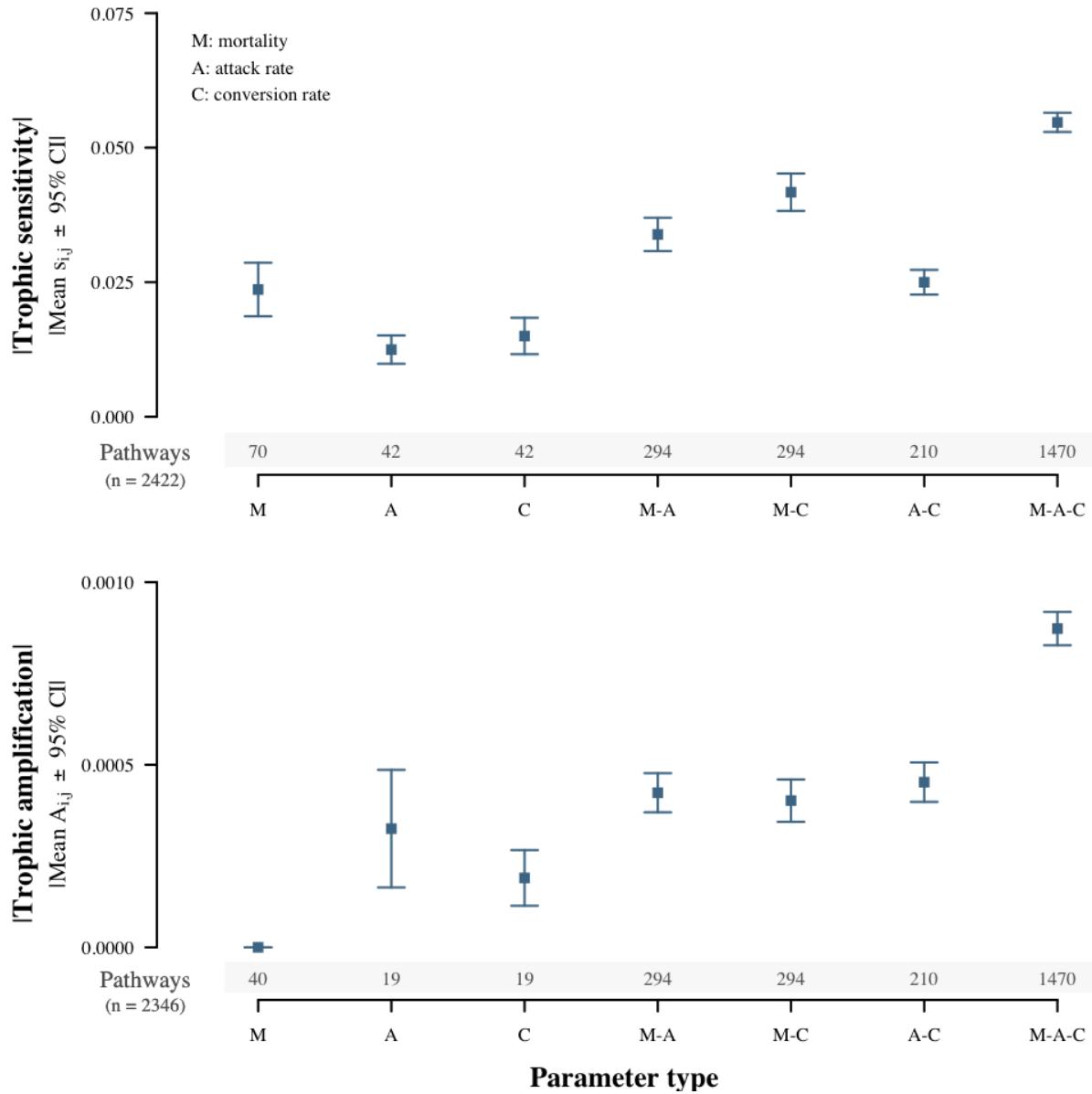


Figure 4: Absolute values of the mean trophic sensitivity ($S_{i,j}$; A) and amplification ($A_{i,j}$; B) as a function of the types of parameter composing a pathway of effect. All pathways of effect targeting a specific parameter type (*i.e.* mortality, attack and conversion rates) were grouped to evaluate their respective and combined effect on trophic sensitivity and amplification.

411 ***Other figures:***

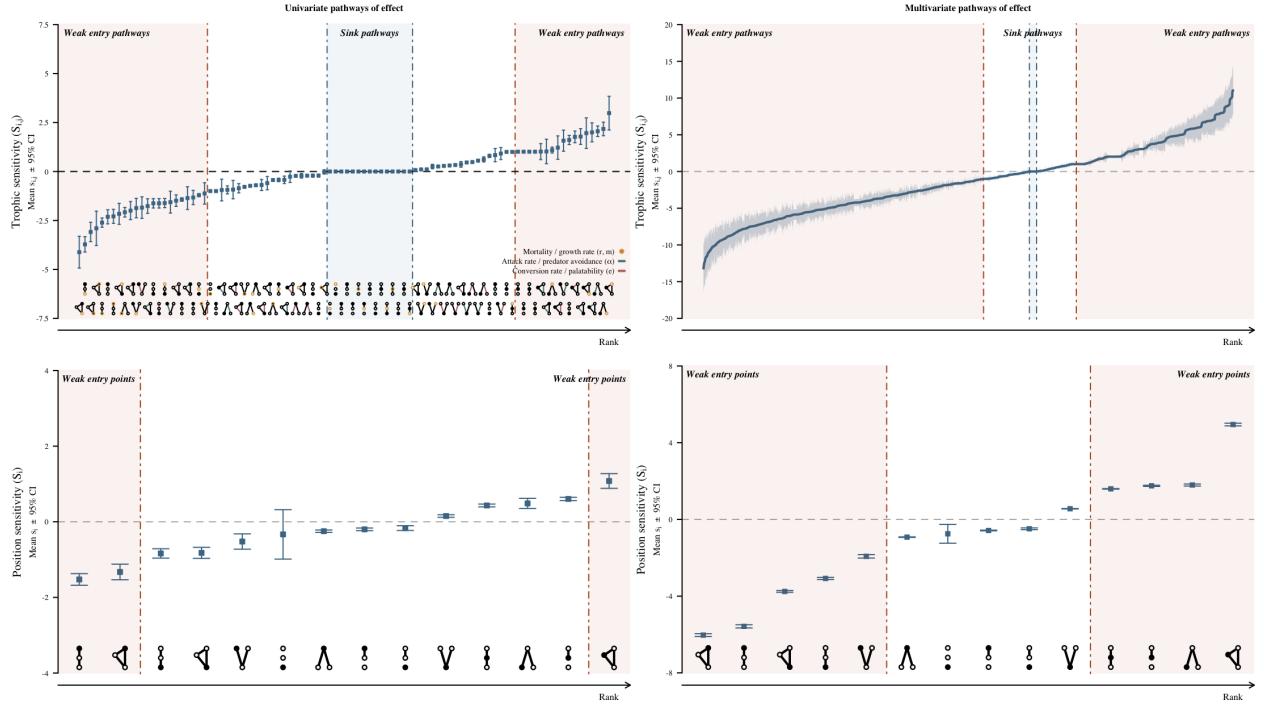


Figure 5: Ranking of all univariate and multivariate pathways of effect as a function of trophic (A,B) and position (C,D) sensitivity. Pathways and motif positions identified as weak entry points (*i.e.* highly sensitive to disturbances) and biotic sinks (*i.e.* insensitive to disturbances) are identified by the red and blue regions, respectively.

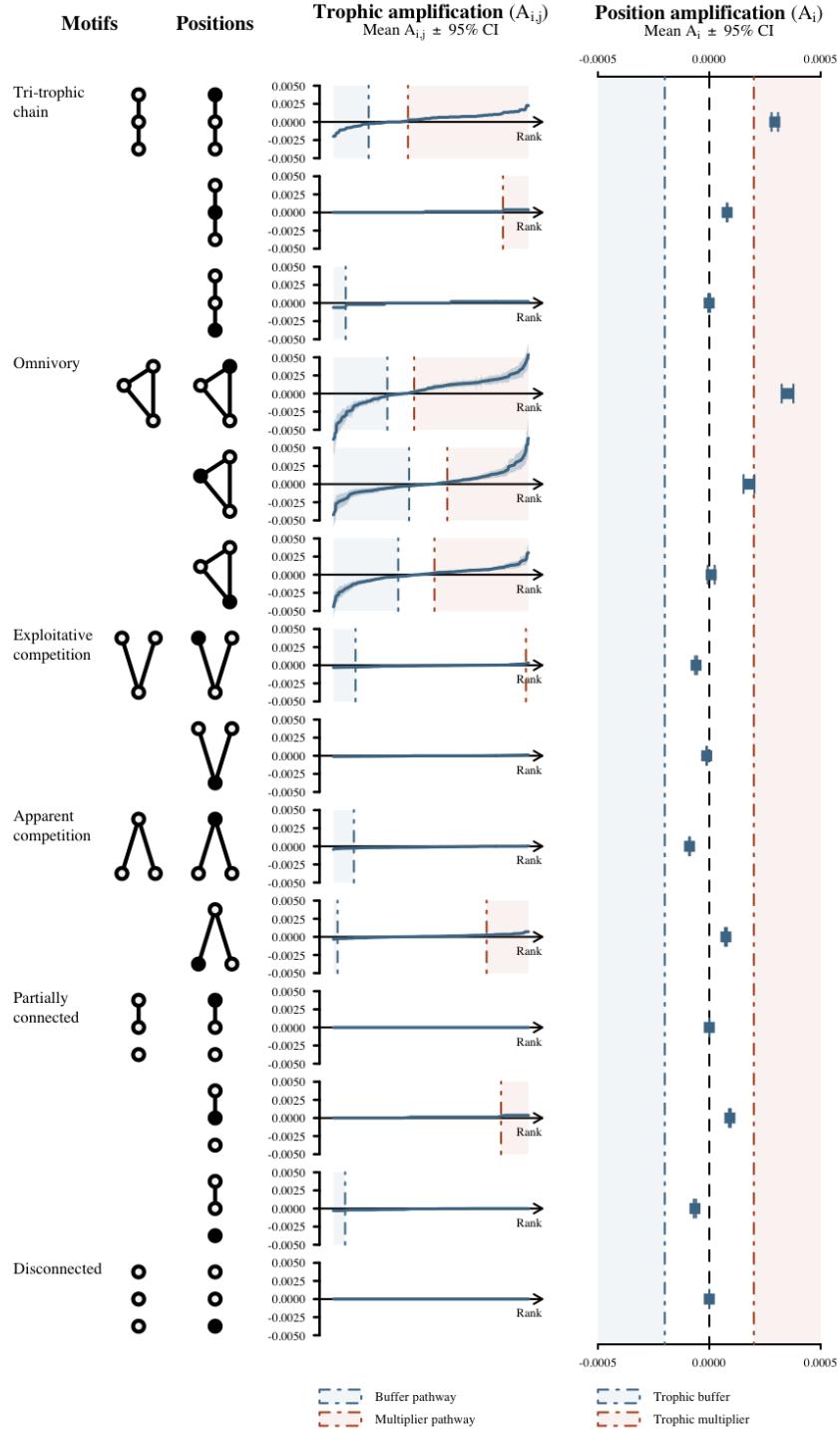


Figure 6: Ranking of all multivariate pathways of effect as a function of trophic and position amplification, for each motif position. Pathways and motif positions identified as biotic buffers (*i.e.* affected synergistically by disturbances) and biotic buffers (*i.e.* affected antagonistically by disturbances) are identified by the red and blue regions, respectively.

412 4.2 Species vulnerability

413 Based on their trophic position, the most vulnerable species in the Northern St. Lawrence
414 are large predators that are never or rarely resources themselves such large demersal fish
415 (*i.e.* demersals, atlantic cod and greenland halibut; Figure 7). These species largely appear
416 to be both weak entry points and biotic amplifiers (Figure 7). Resources are generally less
417 sensitive, depending on their position in food webs. Large crustaceans, for example, are
418 positive weak entry points and biotic amplifiers, which is likely due to their position as both
419 predator and resource in the food web (*e.g.* resource in apparent competition; Figure 7).
420 Other species like redfish and shrimp are in motif positions leading both to positive (*e.g.*
421 meso-predator in omnivory interaction) and negative (*e.g.* resources in omnivory interations)
422 effects in motif-scale simulations (Figure 7). This likely leads to counteracting effects that
423 dampen their overall sensitivity to disturbances. Species sensitivity and amplification scores
424 do not co-vary. In fact, few species are biotic buffers, with most acting as biotic amplifiers to
425 some degree (Figure 7).

426 Species targeted by multiple drivers are not necessarily the most vulnerable based on their
427 trophic position. For example, even though the mortality, physiology and behaviour of shrimp
428 were expected to be impacted by drivers, it is nonetheless insensitive based on its trophic
429 position (Figure 7). In contrast, species impacted by few drivers like cetaceans, or no drivers
430 at all like harbour seals, may nonetheless be highly vulnerable due to their trophic position
431 (Figure 7).

432 Focusing on cod, shrimp and large crustaceans, 3 species with contrasting vulnerabilities in
433 the St. Lawrence, we see that different driver combinations and food web topologies lead to
434 differet species vulnerability (Figure 8). Combinations of drivers may increase or dampen
435 over effects on species sensitivity. For instance, fisheries and climate combine to increase and
436 decrease sensitivity of cod and shrimp, respectively (Figure 8). Driver combinations may also
437 lead to effect amplification even though a driver group has no effect. The combined effect

⁴³⁸ of fisheries and climate drivers on shrimp leads to drastically increased amplification scores
⁴³⁹ even if fisheries in isolation does not lead to non-additive effects (Figure 8).

⁴⁴⁰ Food web topology also impacts a species vulnerability. Based on topology, cod seem more
⁴⁴¹ vulnerable in the Northern Gulf of St. Lawrence than in the Estuary and Southern Gulf
⁴⁴² (Figure 8). Shrimp and crustaceans, meanwhile, are more sensitive in the Estuary, although
⁴⁴³ amplification is more important in the Gulf (Figure 8). Contrasts between food webs may
⁴⁴⁴ even lead to flipped species vulnerabilities. Large crustaceans seem to be negative entry points
⁴⁴⁵ and biotic buffers in the Estuary, yet they positive weak entry points and biotic amplifiers in
⁴⁴⁶ the Gulf (Figure 8).

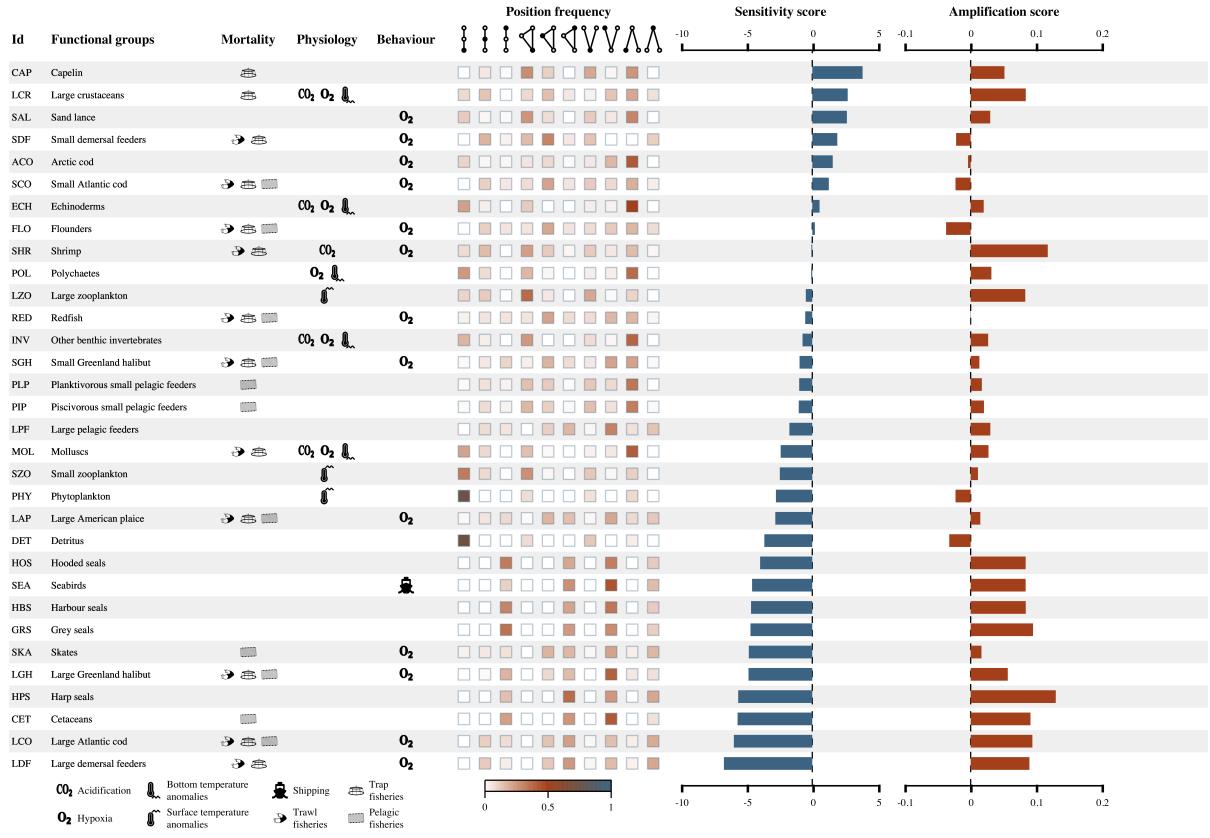


Figure 7: Change in species and functional groups sensitivity and amplification scores as a function of realized pathways of effects for an empirical food web of the Northern Gulf of St. Lawrence in the mid-1980s [?]. The left-hand side of the table presents the species and functional groups, the drivers 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.

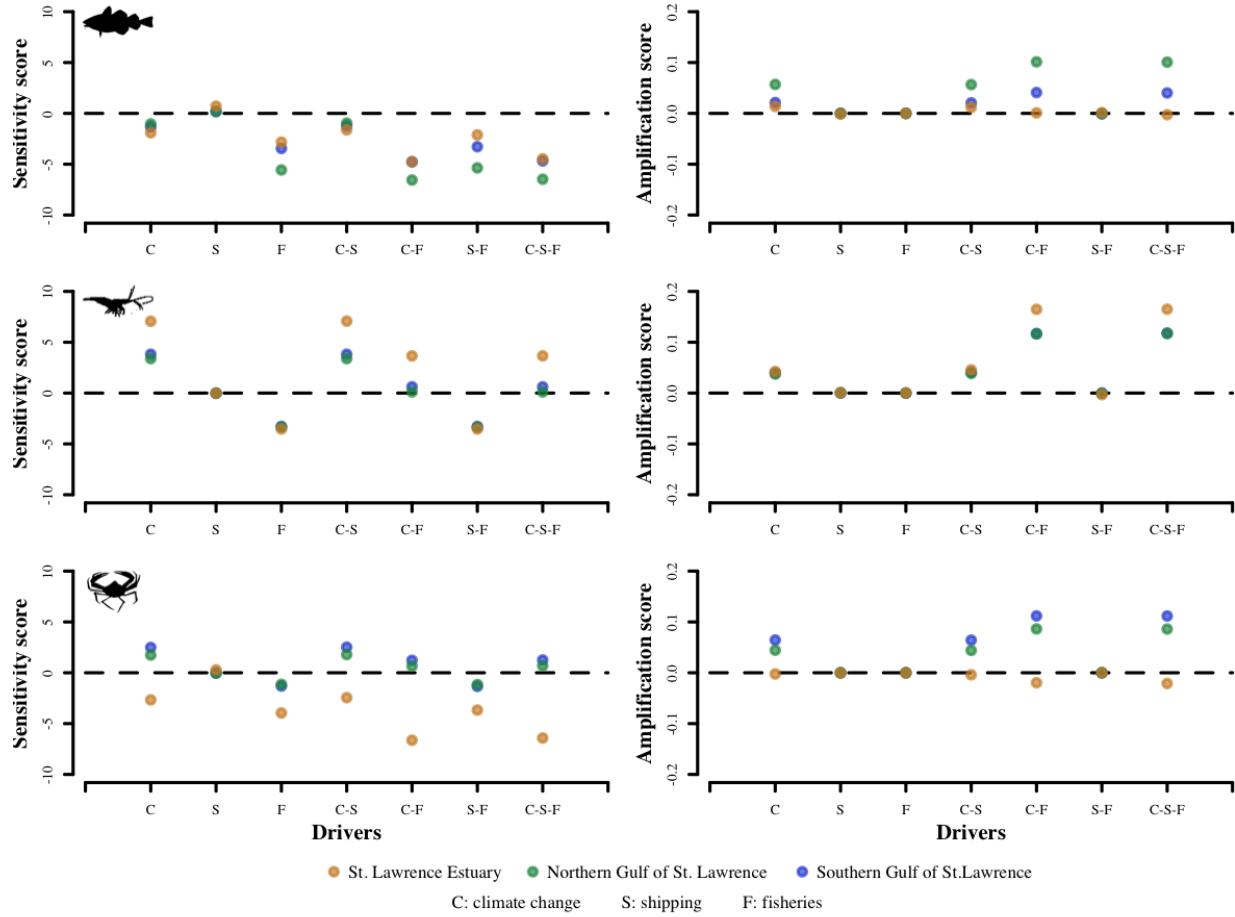


Figure 8: Realized sensitivity (S_m^*) and amplification (A_m^*) scores for Atlantic cod (*Gadus morhua*), shrimp (*Pandalus borealis*) and large crustaceans (*Crustacea*), 3 species or functional groups part of the food webs of the Southern and Northern Gulf of St. Lawrence in the mid-1980s [?] and the St. Lawrence Estuary [?]. Scores are presented when groups of drivers are considered individually and in combination.

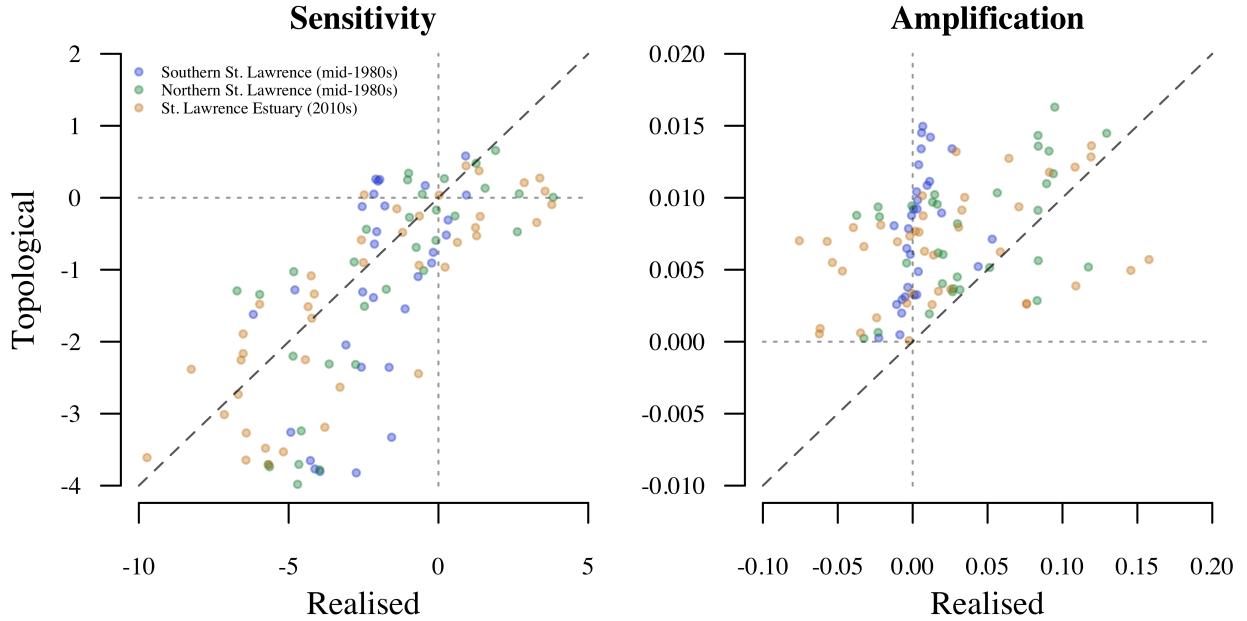


Figure 9: Biplot of the realized and topological species sensitivity (S_m^* , S_m) and amplification (A_m^* , A_m) scores in the food webs of the Southern and Northern Gulf of St. Lawrence in the mid-1980s [?] and the St. Lawrence Estuary [?].

447 5 What it all means

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

451 *Should species interactions be considered in impact assessments?*

452 We first find, as expected, that species interactions should be explicitly considered in impact
 453 assessments, as they greatly influence trophic vulnerability to the effects of disturbances.
 454 This supports longstanding evidence that interactions play a crucial role in spreading the
 455 effects of individual disturbances through food webs (e.g. Menge 1995; Wootton 1993, 2002;
 456 Yodzis 2000), and unsurprisingly extends this conclusion to multiple disturbances.

457 We further uncover the that type of interactions a species is involved in influences its
 458 vulnerability to disturbances. Omnivory and food chain in particular are highly responsive

⁴⁵⁹ to disturbances, while exploitative and apparent competition are less vulnerable. [...]

⁴⁶⁰ **Notes:**

- ⁴⁶¹ • Read up on individual modules and the work done by Stouffer
- ⁴⁶² • “Additionally, note that the exploitative competition module is unstable in isolation
- ⁴⁶³ due to competitive exclusion.” (In Stouffer2012, but I doubt I should cite him for this.
- ⁴⁶⁴ This is just a placeholder)

⁴⁶⁵ We also provide evidence that species interactions rather than population growth or mortality
⁴⁶⁶ are driving non-additive effects at the community scale. [...] This means that the effects of
⁴⁶⁷ drivers should not be studied outside of the context of species interactions when studying
⁴⁶⁸ population dynamics.

⁴⁶⁹ **Notes:**

- ⁴⁷⁰ • KEV: Importance of interaction paramters (McCann, from Kev, about reactivity(?) of
- ⁴⁷¹ interaction paramters in Lotka-Voltera models)

⁴⁷² ***Should the effects of stressors be evaluated separately or in combination?***

⁴⁷³ Secondly, we find that the effects of multiple disturbances should be considered in combination,
⁴⁷⁴ as non-additive effects often arise from disturbances to two or more biological processes.

⁴⁷⁵ **Notes:**

- ⁴⁷⁶ • Species in omnivory interactions and top predator in food chain are particularly
- ⁴⁷⁷ susceptible to non-additive effects, with most pathways resulting in either synergistic
- ⁴⁷⁸ or antagonistic effects.
- ⁴⁷⁹ • There is a lot of variability among individual pathways of effect, so that predicting
- ⁴⁸⁰ whether a species will be a biotic buffer or a biotic amplifier is particularly challenging.
- ⁴⁸¹ Indeed, differentiating between biotic buffers and amplifiers seems to require a thorough
- ⁴⁸² understanding of the pathways of effects at play, as there is so much variability.

- 483 • Lot of variability in the nature of the non-additive effect, with no precise indication
484 of what drives a species to be a biotic buffer or a biotic amplifier, suggesting that
485 considering effects of pressures in combination is the only valid way to truly capture
486 the effects of multiple disturbances.

487 ***Which species are most vulnerable to disturbances based on their trophic posi-***
488 ***tion?***

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

492 At the motif scale, predators in food chain and omnivory interactions are the most vulnerable
493 by acting as both weak entry points and biotic amplifiers.

494 **Notes:** - Species themselves are more or less sensitivite, with predators in omnivory and
495 food chain both weak entry points and biotic amplifiers. - Trophic cascades, compensatory
496 effects - Estes *et al.* (2011); - Compensatory effect suppression Thompson *et al.* (2018) -
497 The fact that resources and predators are most affected, look at O'Gorman *et al.* (2012) -
498 Predators and resources

499 At the species scale:

500 **Notes:** - Groundfish stock collapse: a trophic hint? - Exploited species before the groundfish
501 stock collapse of the 1990s (\textit{e.g.} demersal feeders, Atlantic cod, Greenland halibut)
502 are all negative weak entry points and biotic amplifiers. - Exploited species after the collapse
503 are either positive weak entry points and biotic amplifiers (\textit{e.g.} large crustaceans) or
504 biotic sinks (\textit{e.g.} shrimp). - We find that heavily exploited species appear to be the
505 most vulnerable trophically, while fisheries transitioned to insensitive or beneficiary species
506 post-collapse. - Using the most common offshore environmental pressure in the St. Lawrence
507 System, food webs and simulations as heuristics, we find that [...] - Using the most common

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

512 6 The way forward

- 513 • Limits:
 - 514 – No interaction strength
 - 515 – No driver intensity
 - 516 – Simple model formulations
- 517 • In the absence of appropriate knowledge, it is reasonable to first explore the simplest
518 possibilities, which will provide novel hypotheses to test theoretically and empirically
519 in follow-up studies (Wootton 2002).
- 520 • Even if our simulations are simplifications of realworld system, they still provide
521 compelling evidence that reinforce the need to explicitly consider the complexity of
522 ecological systems.
- 523 • Name new hypotheses to test theoretically and empirically.
 - 524 – a) IDEAS?
 - 525 – b)
 - 526 – ...
- 527 • This framework is also so flexible that we could easily include other drivers typically
528 found in systems, such as pollution or seal hunting.
- 529 • Spatial and temporal vulnerability of species.

- 530 • Other models could be used to explicitly incorporate things like competition,
- 531 • Positive effects of drivers (*e.g.* nutrients on growth, at least initially)
- 532 • Management and conservation:
- 533 – Our results reinforce that holistic approaches are necessary to properly consider
- 534 the effects of environmental pressures on complex communities. Although this has
- 535 been hinted at, no other study [...]]
- 536 – Single species may be vulnerable (or not) in different contexts, so that the structure
- 537 of a network should be considered and conservation targets may change as the
- 538 vulnerability of species changes in time and space as a function of network structure
- 539 and driver combinations.

540 **7 Supplementary Material**

541 **7.1 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.

542 7.2 Supplementary figures

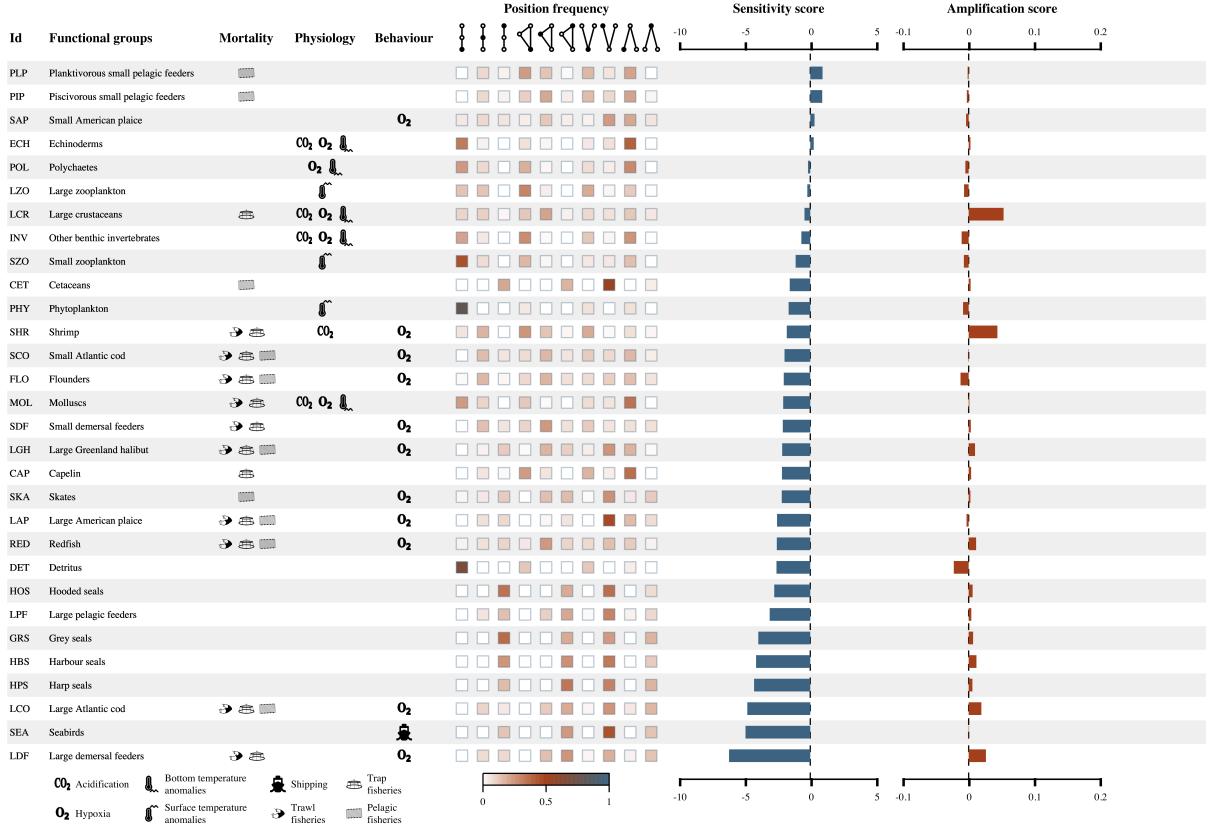


Figure 10: Change in species and functional groups sensitivity and amplification scores as a function of realized pathways of effects for an empirical food web of the Southern Gulf of St. Lawrence in the mid-1980s [?]. The left-hand side of the table presents the species and functional groups, the drivers 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.

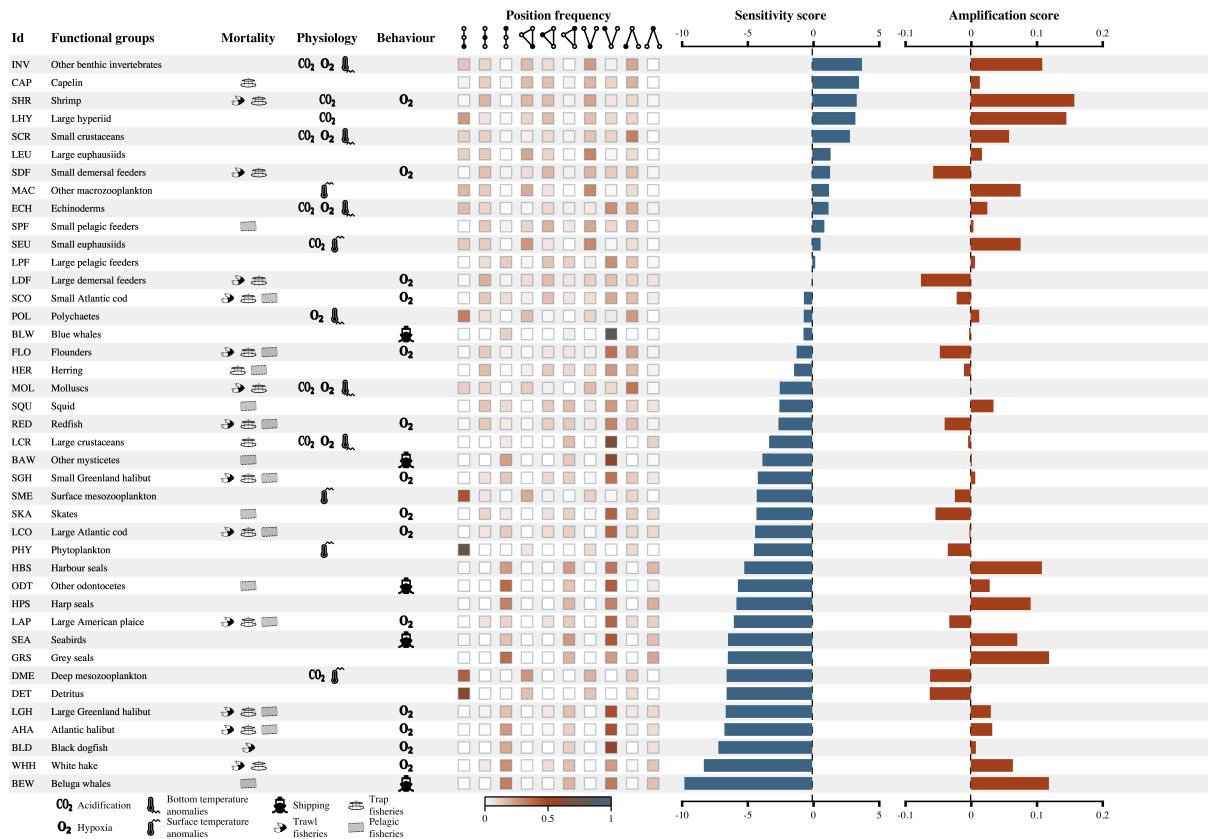


Figure 11: Change in species and functional groups sensitivity and amplification scores as a function of realized pathways of effects for an empirical food web of the St. Lawrence Estuary in the mid-1980s [?]. The left-hand side of the table presents the species and functional groups, the drivers supposed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

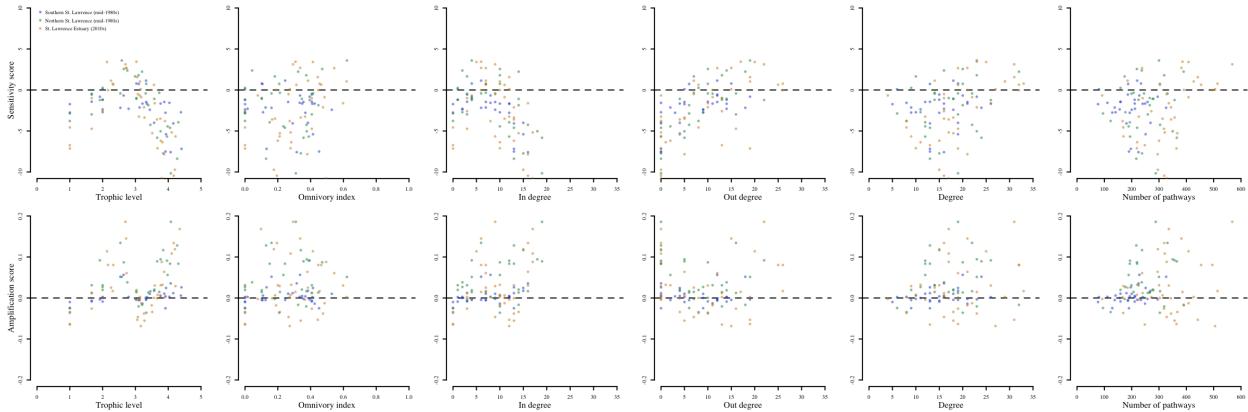


Figure 12: Species sensitivity and amplification scores as a function of network metrics: 1) trophic level, 2) omnivory index, 3) in-degree, 4) out-degree, 5) degree and 6) number of pathways of effect for the food webs of the Southern and Northern Gulf of St. Lawrence in the mid-1980s [?] and the St. Lawrence Estuary in the 2010s [?].

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