

¹ On the vulnerability of food webs to multiple
² stressors

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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 (Boonstra *et al.* 2015; Halpern *et al.* 2019). Pressures may
98 be driven by natural or human-induced biophysical processes such as ocean acidification and
99 warming, or directly from anthropogenic activities such as fisheries. These drivers can be
100 defined as any externality that affects environmental processes and disturbs natural systems.
101 Individually, drivers have been found to impact all levels of biological organization and cause
102 dramatic changes to whole ecosystems. Ocean acidification can reduce coral and mollusk
103 calcification, metabolic, growth and mortality rates, and has been linked to altered carbon
104 fluxes in ecological networks (Fabry *et al.* 2008; Kroeker *et al.* 2013; Bove *et al.* 2019).
105 Fisheries have caused the collapse of commercial species, decreased the mean trophic level
106 in coastal and oceanic environments by targetting large predators and impaired a variety of
107 essential ecosystem services (Pauly *et al.* 1998; Myers & Worm 2003; Worm *et al.* 2006).
108 Rarely do drivers occur individually, and the list of potentially interacting drivers affecting an
109 ecosystem at any given point in time or space can be extensive (Halpern *et al.* 2019). Global
110 changes and local human activities thus result in increasingly intricate environmental stress
111 exposure regimes, compounding the pathways of effects through which natural systems can be
112 impacted (Halpern *et al.* 2019). For example, coral reefs contend with a suite of pressures
113 including fishing, warming temperatures, ocean acidification and water quality that may
114 impact species in contrasting ways (McClanahan *et al.* 2014; Harborne *et al.* 2017). Drivers
115 can then combine to induce complex and sometimes unpredictable effects (Côté *et al.* 2016).
116 Dramatic examples include up to 100-fold increases of the sensitivity of certain organisms
117 to toxicants (*e.g.* pesticides) when exposed to other environmental stressors (*e.g.* parasites;
118 Liess *et al.* 2016) and the reversal of the positive effects of acidification on primary producer
119 biomass by warmer waters in boreal lakes (Christensen *et al.* 2006).
120 The potential for complex interactions between drivers remains the largest uncertainty when

¹²¹ studying or predicting environmental impacts (Darling & Côté 2008; Côté *et al.* 2016).
¹²² Interactive drivers effects have thus been extensively investigated to uncover instances of
¹²³ non-additive effects, *i.e.* when the effect of multiple interacting drivers is greater (synergism)
¹²⁴ or lower (antagonism) than the sum of their individual parts. These studies have found non-
¹²⁵ additive effects of multiple drivers to be the norm rather than the exception across ecosystems
¹²⁶ globally (*e.g.* Darling & Côté 2008; Crain *et al.* 2008; Piggott *et al.* 2015; Jackson *et al.*
¹²⁷ 2016).

¹²⁸ Species sensitivity to environmental pressures can be highly variable, which further com-
¹²⁹ pounds the complexity of mutliple drivers studies. For example, hypoxia decreases overall
¹³⁰ habitat quality but has species-dependent effects, ranging from well-adapted (*e.g.* north-
¹³¹ ern shrimp *Pandalus borealis* and Greenland halibut *Reinhardtius hippoglossoides*; Pillet *et*
¹³² *al.* 2016) to avoidance behaviour (*e.g.* Atlantic cod *Gadus morhua*; Chabot & Claireaux
¹³³ 2008), and mortality (*e.g.* sessile benthic invertebrates; Eby *et al.* 2005; Belley *et al.*
¹³⁴ 2010). Moreovers, species are also embedded in a complex web of interactions that provides
¹³⁵ indirect pathways of effects through which pressures may permeate entire ecological com-
¹³⁶ munities (Wootton 2002; Bascompte 2009; Montoya *et al.* 2009; O’Gorman & Emmerson
¹³⁷ 2009; O’Gorman *et al.* 2012). Indirect effects, *i.e.* when two or more direct effects are
¹³⁸ linked by a single species involved in both effects, may be as important of, and propagate
¹³⁹ faster than, direct effects (Wootton 1993, 2002; Menge 1995; Yodzis 2000). Empirical ex-
¹⁴⁰ amples of trophic cascades are abundant throughout all types of ecosystems globally (Estes
¹⁴¹ *et al.* 2011). In multi-species systems, where both direct and indirect effects are operating
¹⁴² simultaneously, it is expected that the effects of environmental pressures will be amplified
¹⁴³ or dampened through biotic interactions (Ives 1995; Wootton 2002; Thompson *et al.* 2018).
¹⁴⁴ Community dynamics and how species are embedded in complex networks is therefore likely
¹⁴⁵ to affect their sensitivity to environmental pressures.

¹⁴⁶ Confronted with the challenge of managing and preserving complex systems, there is an
¹⁴⁷ urgent need for the development of theoretical frameworks that properly consider the com-

plexities of multiple drivers and ecological networks in ways that are informative to management. From a practical standpoint, single-driver and single-species assessments remain overwhelmingly applied (O'Brien *et al.* 2019), while most multiple drivers studies have typically focused on habitats (*e.g.* Ban *et al.* 2010; Halpern *et al.* 2019). This conveniently circumscribes assessments to a set of tractable units, but it also ignores systems complexity and aggregates biological processes operating at lower levels organization (Halpern & Fujita 2013; Giakoumi *et al.* 2015). Studies have also relied on the use of null models that provide little insights into the mechanisms underlying ecological responses to the effects of multiple drivers (Griffen *et al.* 2016; Jackson *et al.* 2016; De Laender 2018; Schäfer & Piggott 2018). Theoretically, species interactions have long been identified as key components to the sensitivity of whole networks to disturbances (*e.g.* Ives 1995; Wootton 2002; O'Gorman & Emmerson 2009; O'Gorman *et al.* 2012), but the effects of multiple disturbances on networks have yet to be formally explored.

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

3 Of food web and multiple disturbances

3.1 Conceptualizing disturbances

Drivers can disturb the dynamics of ecological communities by disrupting a variety of biological processes (Figure 1A) such as behaviour (*e.g.* Chabot & Claireaux 2008; Hale *et*

¹⁷² *al.* 2017), reproduction [*e.g.* ref], physiology (*e.g.* Dupont-Prinet *et al.* 2013), mortality
¹⁷³ (*e.g.* Belley *et al.* 2010), and species interactions (*e.g.* Wootton 2002; Guiden *et al.* 2019).

¹⁷⁴ Multiple processes may be affected by a single driver, while multiple drivers may target a
¹⁷⁵ single process. For instance, fishing could affect the behaviour and the mortality of cod,
¹⁷⁶ while ocean warming and ocean acidification may affect physiological processes of benthic
¹⁷⁷ invertebrates such as calcification rates. The potential number of univariate and multivari-
¹⁷⁸ ate pathways of effects through which community dynamics may be affected is extensive and
¹⁷⁹ increases exponentially with the number of species and the number on links in a network.

¹⁸⁰ A thorough understanding of the impacts of disturbance regimes and community dynamics
¹⁸¹ would be necessary to fully capture the effects of multiple drivers, but the complexity of
¹⁸² empirical food webs in itself is prohibitive to investigations of community dynamics. Studying
¹⁸³ smaller subgraphs - community motifs or modules - has thus emerged as an alternative to
¹⁸⁴ gather insights into the dynamics and stability of complex ecological communities (Holt
¹⁸⁵ 1997; Holt & Hochberg 2001). Motifs are collections of n -species that, when put together,
¹⁸⁶ construct whole food webs (Milo *et al.* 2002; Stouffer *et al.* 2007). They form the backbone
¹⁸⁷ of food webs and provide a mesoscale characterization of community structure (Bascompte
¹⁸⁸ & Melián 2005; Stouffer *et al.* 2007). A species can be described as a function of all n -species
¹⁸⁹ motifs it is involved in in an empirical food web (Figure 1B; Stouffer *et al.* 2012).

¹⁹⁰ There are 13 distinct 3-species motifs composed of 30 unique positions (Milo *et al.* 2002;
¹⁹¹ Stouffer *et al.* 2007, 2012). Four 3-species motifs have received particular attention in
¹⁹² theoretical and empirical studies due to their roles [ref] and prevalence (Camacho *et al.* 2007;
¹⁹³ Stouffer & Bascompte 2010) in food webs: tri-trophic food chain, omnivory or intraguild
¹⁹⁴ predation, exploitative competition and apparent competition.

¹⁹⁵ Motif dynamics has been studied extensively to uncover how structural properties of food
¹⁹⁶ webs can benefit community persistence and stability (Allesina & Pascual 2008; Kondoh
¹⁹⁷ 2008; Stouffer & Bascompte 2010, 2011; Monteiro & Faria 2016) and to assess the structural

198 roles of species within food webs (Stouffer *et al.* 2012; Cirtwill & Stouffer 2015). These
199 provide meaningful insights for conservation efforts. For example, results from Stouffer *et*
200 *al.* (2012) suggest that certain species may benefit whole community persistence based on
201 their trophic position, and that the diversity of trophic roles found in empirical food webs
202 does not correlate to species richness. This means that strictly using species richness as
203 a conservation measure may ignore the benefits to community persistence provided by the
204 trophic roles of individual species. Using trophic roles as targets may thus be valuable for
205 community conservation (Stouffer *et al.* 2012).

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

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

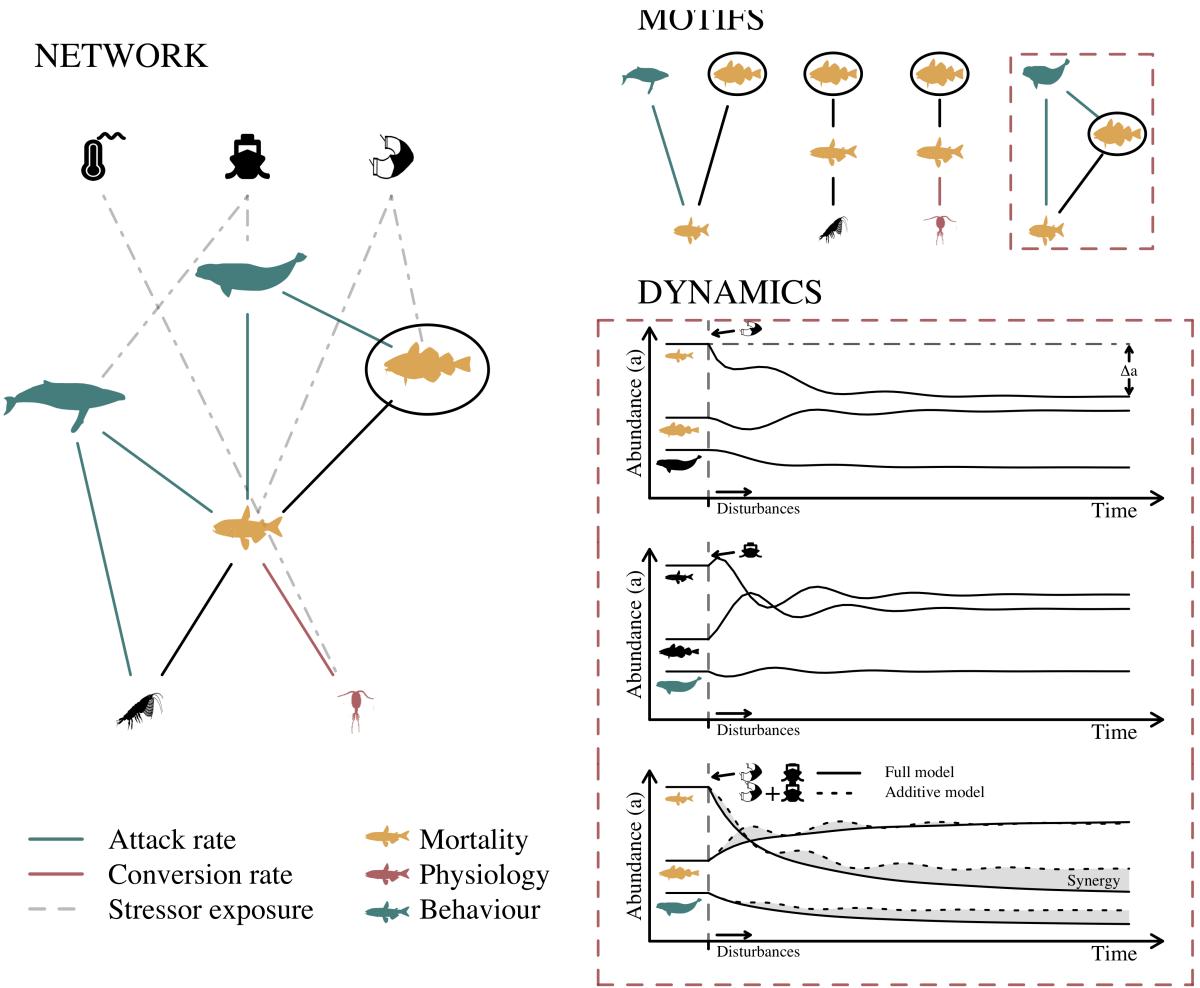


Figure 1: Conceptualization of the effects of multiple sources of environmental stress on the dynamics of a theoretical food web. A) Drivers such as sea surface temperature, marine traffic and fisheries penetrate food webs through various pathways of effects by disturbing ecological processes governing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

219 **3.2 Sumulating disturbances**

220 **3.2.1 Models formulation**

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

227 Resources were modeled using logistic growth equations of the form

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

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

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

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

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

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

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

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

240 **3.2.2 Models parameterization**

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

252 **3.2.3 Disturbances**

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

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

265 3.3 Motifs vulnerability

266 3.3.1 Trophic sensitivity

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

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

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

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

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

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

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

279 3.3.2 Trophic amplification

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

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

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

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

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

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

293 **3.4 Species vulnerability**

294 **3.4.1 Scores**

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

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

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

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

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

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

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

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

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

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

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

317 **3.4.2 Empirical food webs**

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

330 \rightarrow

³³¹ **3.4.3 Drivers**

³³² Climate change related drivers (*i.e.* acidification, hypoxia, and bottom and surface temper-
³³³ ature anomalies) are prevalent in the St. Lawrence System, with the exception of hypoxia in
³³⁴ the Southern Gulf (???). Marine traffic is widespread, especially in the Northern Gulf and
³³⁵ the Estuary, which serve as the main seaway to inland North-America (???). Fisheries have
³³⁶ changed through time after the collapse of groundfish stocks in the early 1990s. Species af-
³³⁷ fected by fisheries were identified using the catch data provided in the description of the food
³³⁸ web models (???: ???; Morissette *et al.* 2003). Gearnype used was identified using landing
³³⁹ data from logbooks from the Department of Fisheries and Ocean's Canada [dfo2016b].

³⁴⁰ The impacts of specific drivers on species and functional groups was done following broad
³⁴¹ rules to simplify the number of assumptions required. Our approach does not seek to establish
³⁴² the vulnerability of a particular species to all types of drivers, but rather to make general
³⁴³ inference on species trophic vulnerability based of its trophic position and the supposed
³⁴⁴ effects of drivers on biological processes driving community dynamics. Detailed literature
³⁴⁵ search or expert knowledge could be used to get a better sense of the proximate effects of
³⁴⁶ drivers on species, but this is beyond the scope of our objective.

³⁴⁷ The first criteria used to evaluate the effect of drivers on species and functional groups was a
³⁴⁸ broad evaluation of direct exposure to individual drivers. Acidification, hypoxia and bottom
³⁴⁹ temperature anomalies are widespread in the deep habitats of the St. Lawrence, while surface
³⁵⁰ temperature anomalies and marine traffic are operating on the surface layer (???). As such,
³⁵¹ species of functional groups in deep or surface habitats were considered as exposed to deep
³⁵² or surface drivers, respectively. The effects of hypoxia and temperature anomalies was then
³⁵³ considered as impacting the physiology or behaviour of exposed species with low or high
³⁵⁴ mobility, respectively. Ocean acidification was assumed to affect the physiology of exposed
³⁵⁵ carbonate-secreting organisms (*e.g.* mollusks and crustaceans; Kroeker *et al.* 2013). Marine
³⁵⁶ traffic was considered as primarily impacting whale behaviour (???: ???). The impact

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

362 4 Results

363 4.1 Motifs vulnerability

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

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

375 Species position also greatly influences trophic sensitivity to and amplification of distur-
376 bances. In general, top predators are weak entry points for all interaction types (Figure 3).
377 In contrast, non-additive effects on top predators depends on interaction type. Pathways of
378 effect on top predators in omnivory and food chain interactions largely result in synergistic
379 or antagonistic effects, and predators are, on average, biotic amplifiers (Figure {position}).
380 Predators in competitive interactions, meanwhile, are less affected by non-additive effects

381 and are fringe biotic buffers (Figure {position}).

382 Resources are largely weak entry points for all motifs, yet the effect are typically negative
383 in food chain and omnivory interactions, and positive in competitive interactions (Figures
384 2, ref{position}). Altough resources are, on average, neither biotic buffers or amplifiers, the
385 effects of individual pathways of effects are mostly non-additive (Figure 2). The effects of
386 disturbances on other interactions are mostly additive. (Figure 2).

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

392 The nature of the pathways of effects also influences trophic sensitivity and amplification.
393 Unsurprisingly, multivariate pathways of effects are generally more impactful to species sen-
394 sitivity and hold a higher proportion of weak entry points than univariate pathways (Figure
395 2). Similarly, targeting multiple biological processes results in greater sensitivity and am-
396 plification (Figure 2). There are however a few generalities worth noting. Mortality and
397 growth rates are driving heightened trophic sensitivities, yet do not individually contribute
398 to non-additive effects (Figure ??). Instead, trophic amplification is largely driven by dis-
399 turbances on species species interactions (*i.e.* attack (α_{ij}) and conversion (e) rates; Figure
400 ??).

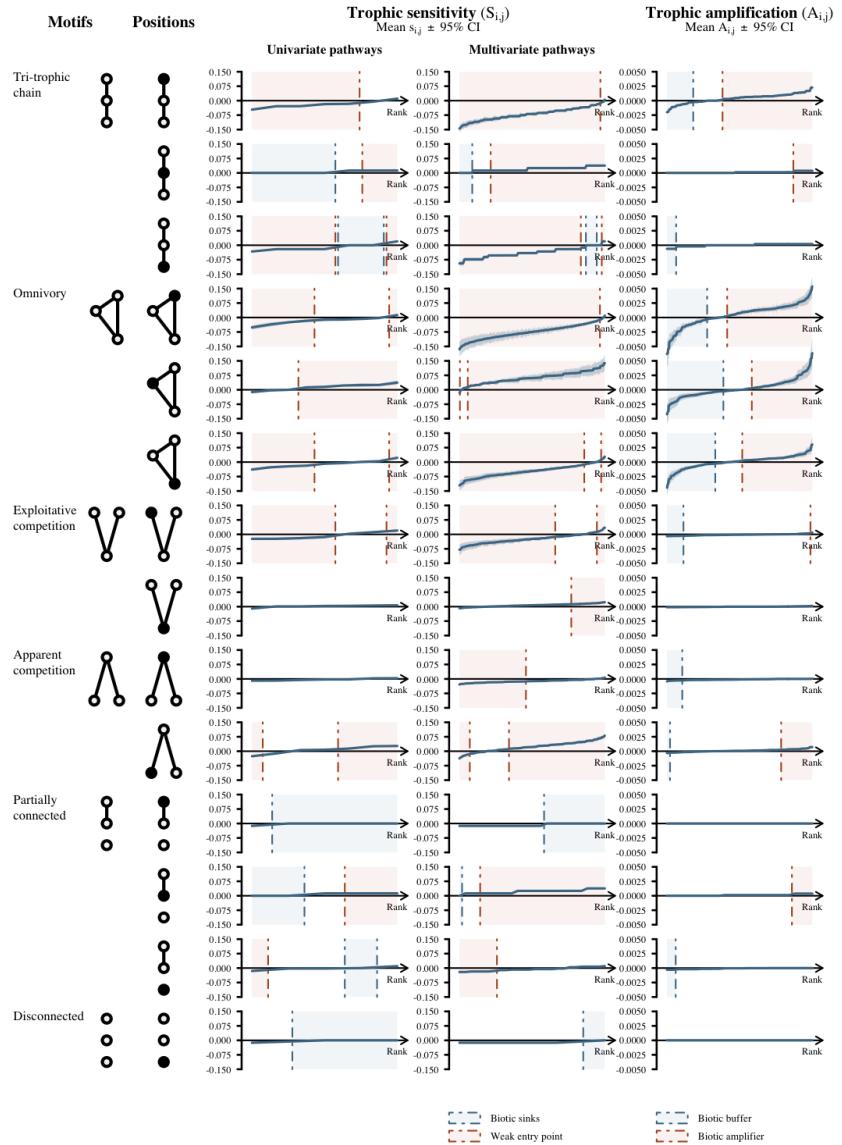


Figure 2: Ranking of all univariate and multivariate pathways of effect as a function of trophic (A,B) and position (C,D) sensitivity. Pathways and motif positions identified as weak entry points (*i.e.* highly sensitive to disturbances) and biotic sinks (*i.e.* insensitive to disturbances) are identified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

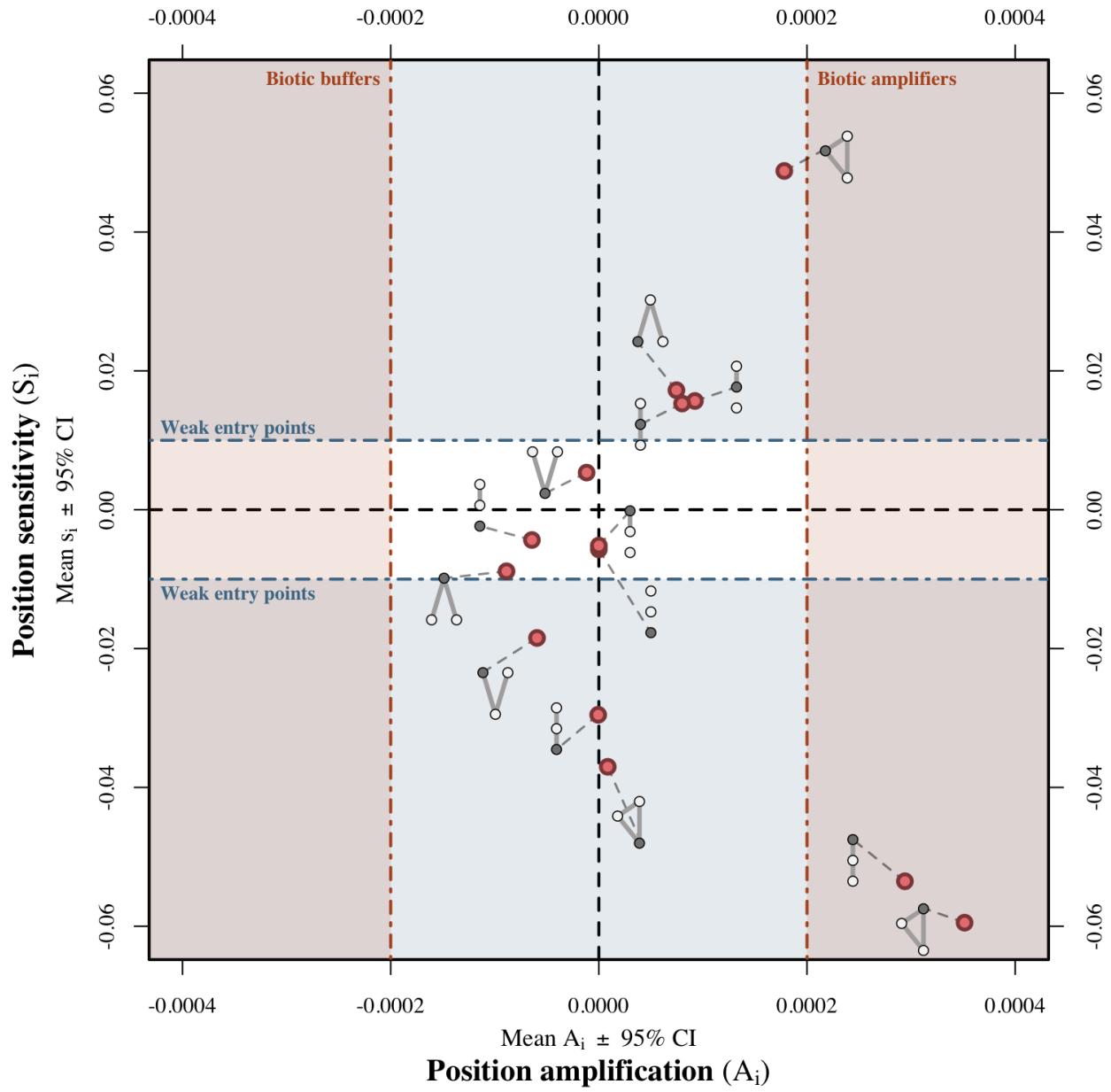


Figure 3: Ranking of all univariate and multivariate pathways of effect as a function of trophic (A,B) and position (C,D) sensitivity. Pathways and motif positions identified as weak entry points (*i.e.* highly sensitive to disturbances) and biotic sinks (*i.e.* insensitive to disturbances) are identified by the red and blue regions, respectively.

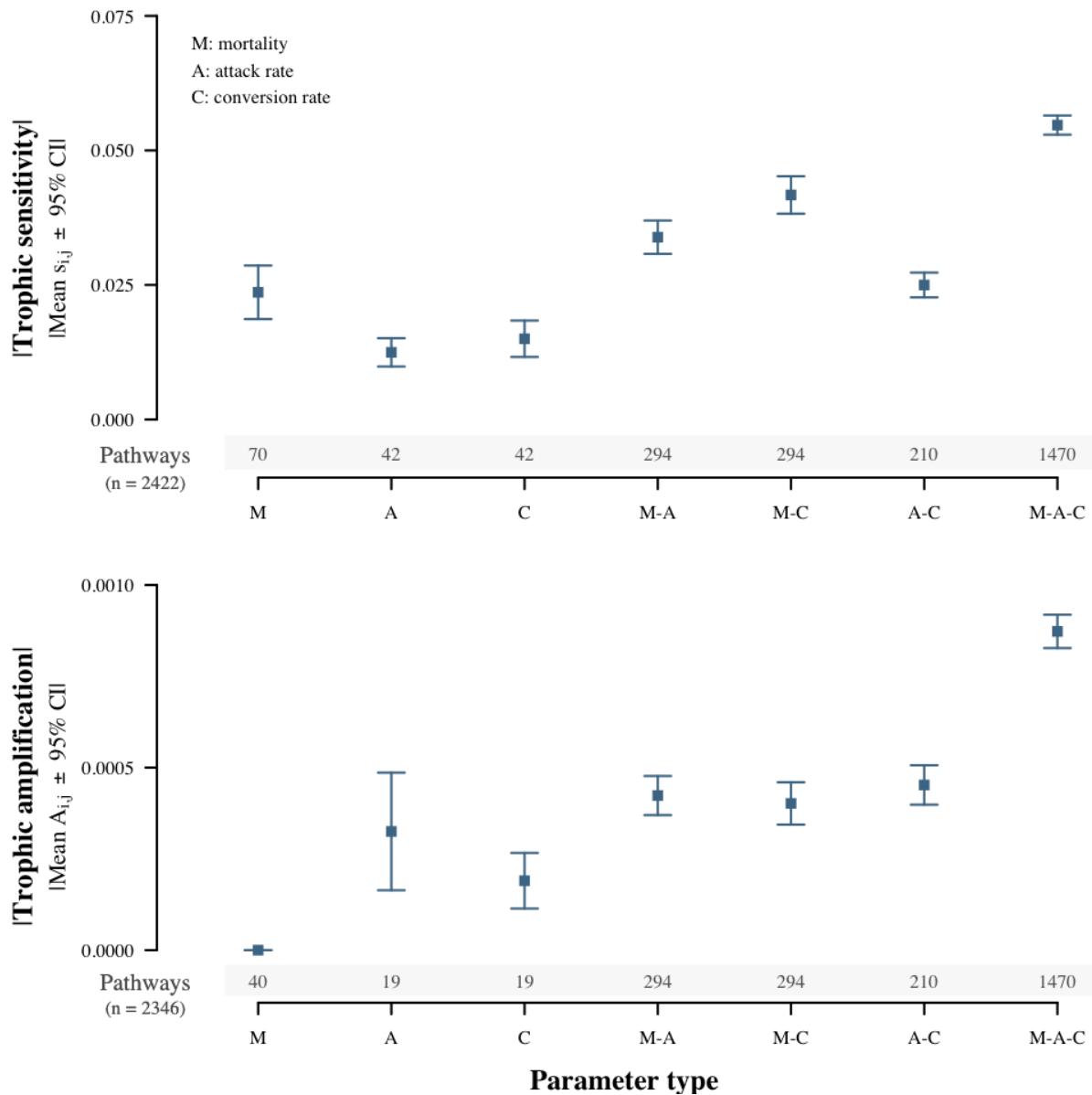


Figure 4: Absolute values of the mean trophic sensitivity (A) and amplification (B) as a function of disturbed parameter type and direct or indirect effects. All pathways of effect targeting a specific parameter type (*i.e.* mortality, attack and conversion rates) were grouped to evaluate their respective and combined effect on trophic sensitivity and amplification.

401 ***Other figures:***

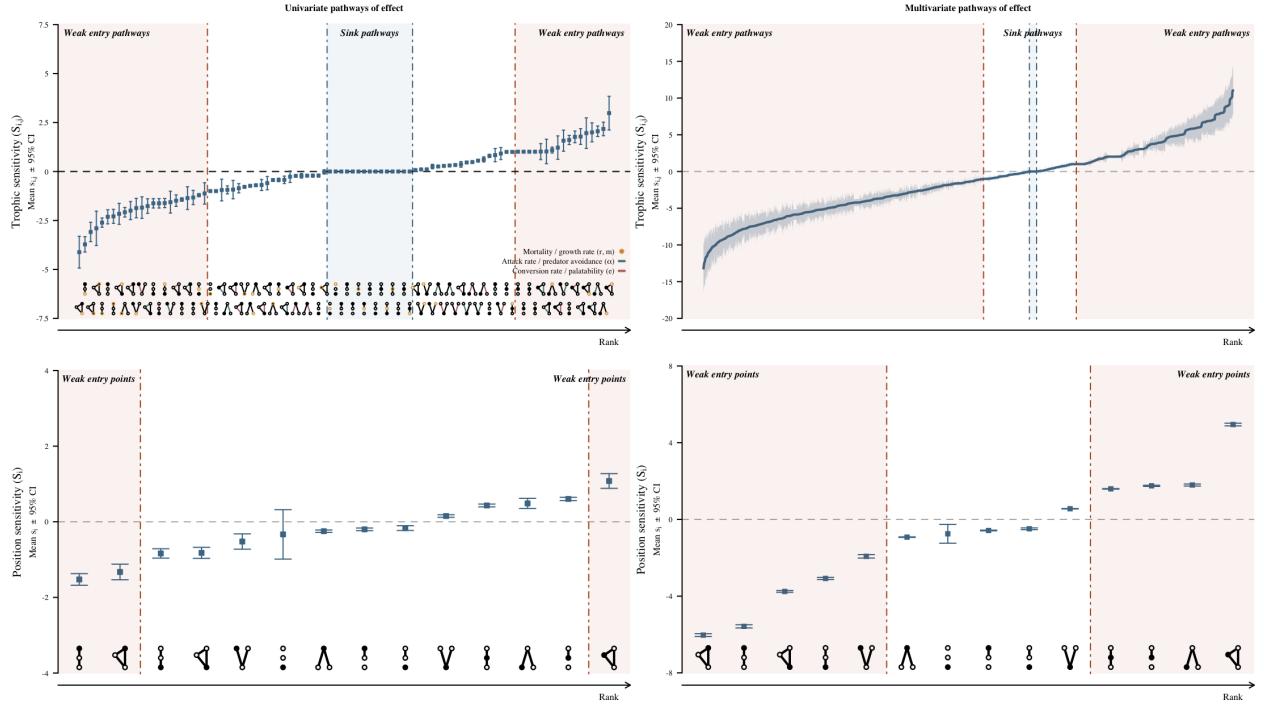


Figure 5: Ranking of all univariate and multivariate pathways of effect as a function of trophic (A,B) and position (C,D) sensitivity. Pathways and motif positions identified as weak entry points (*i.e.* highly sensitive to disturbances) and biotic sinks (*i.e.* insensitive to disturbances) are identified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

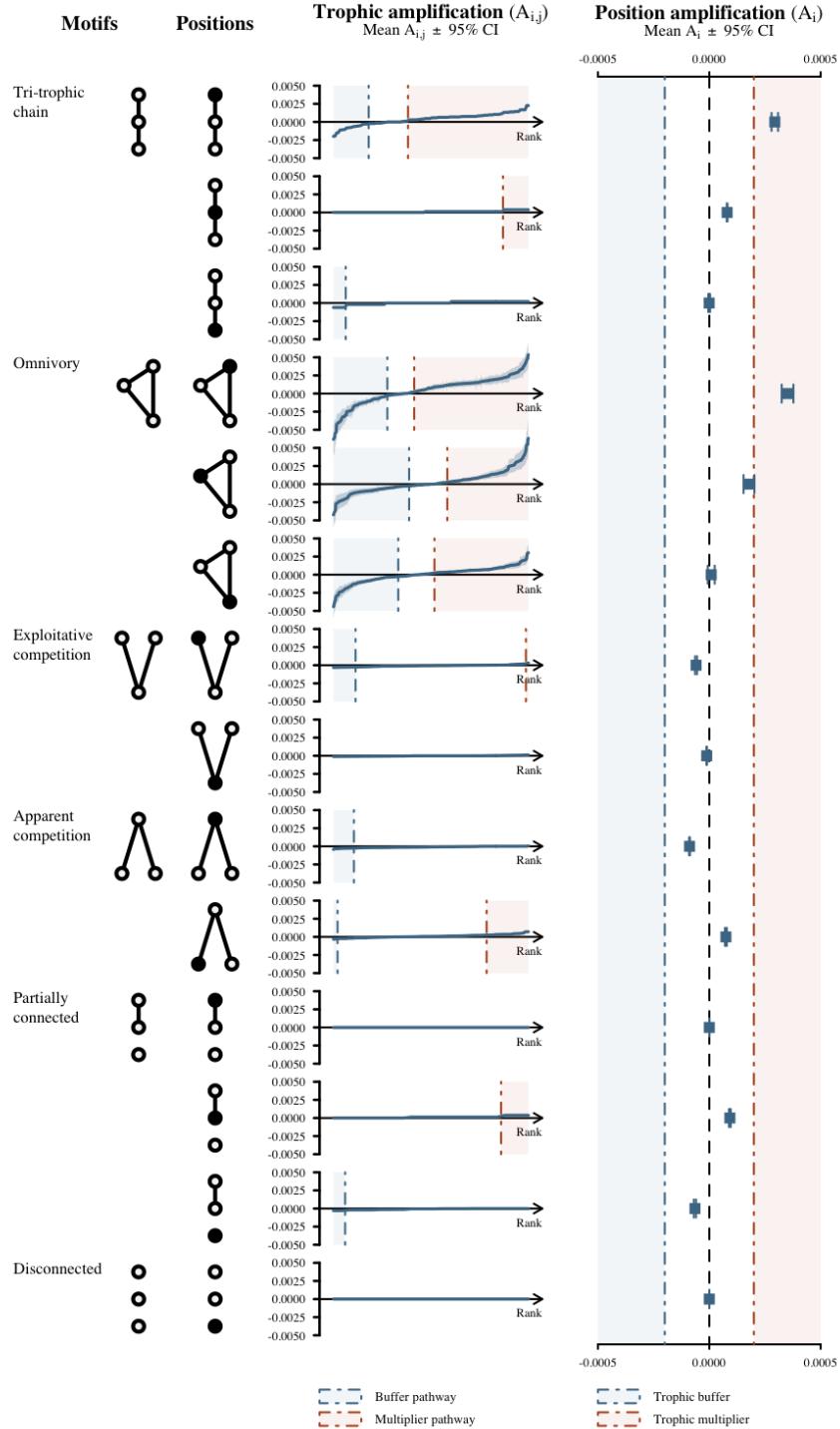


Figure 6: Ranking of all multivariate pathways of effect as a function of trophic and position amplification, for each motif position. Pathways and motif positions identified as biotic buffers (*i.e.* affected synergistically by disturbances) and biotic buffers (*i.e.* affected antagonistically by disturbances)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

402 **4.2 Network-scale vulnerability**

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

407 We find that sensitivity and amplification scores do not co-vary (Figure 7). We also find
408 that species targeted by multiple drivers are not necessarily the most vulnerable based on
409 their trophic position. For example, even though the mortality, physiology and behaviour
410 of shrimp were expected to be impacted by drivers, it is nonetheless insensitive based on
411 its trophic position (Figure 7). Similarly, species impacted by few drivers like sea birds, or
412 no drivers at all like seals, may nonetheless be highly vulnerable due to its trophic position
413 (Figure 7).

414 Large demersal predators, sea birds and seals are mostly weak entry points and biotic am-
415 plifiers (Figure 7). Prey species and large crustaceans appear to benefit from disturbances
416 and may act as positive weak entry points in the St. Lawrence (Figure 7). Invertebrates in
417 general and species like shrimp and redfish appear largely insensitive to disturbances (Figure
418 7).

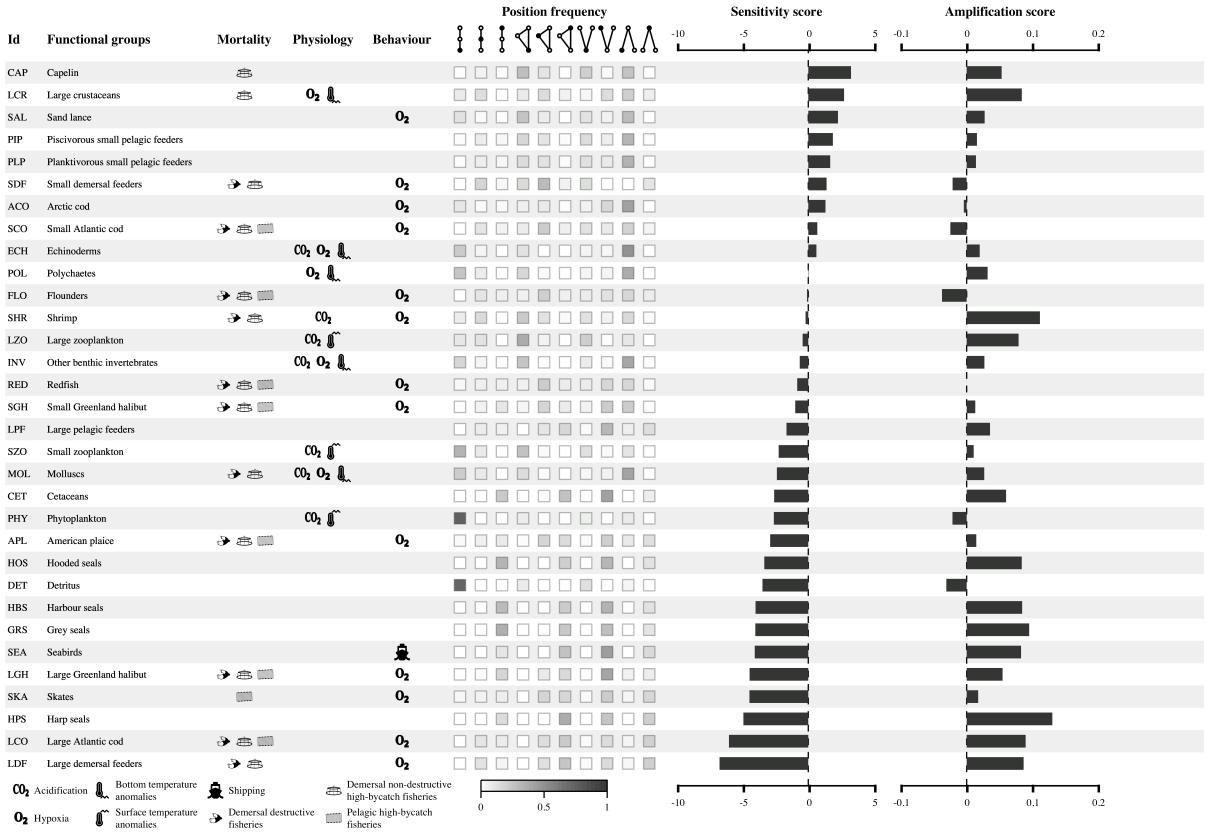


Figure 7: Change in species and functional groups sensitivity and amplification scores as a function of realised pathways of effects for an empirical food web of the Northern Gulf of St. Lawrence in the mid-1980s [?]. The left-hand side of the table presents the species and functional groups, the drivers supposed to be affecting population level mortality, physiology and behaviour, and the frequency at which they are found in each unique position of the food chain, omnivory, exploitative and apparent competition motifs. Important drivers in the Northern Gulf of St. Lawrence are fisheries (*i.e.* demersal destructive, demersal non-destructive high-bycatch and pelagic high-bycatch), climate change (*i.e.* ocean acidification, hypoxia and bottom and surface temperature anomalies), and shipping [?]. Species position and driver effects on biological processes were used to identify realised pathways of effects between all 3-species combinations in the food web. The right-hand side of the table presents the species sensitivity and amplification scores, which corresponds to the sum of the simulated effects of all realised pathways of effects for each species and functional group (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.

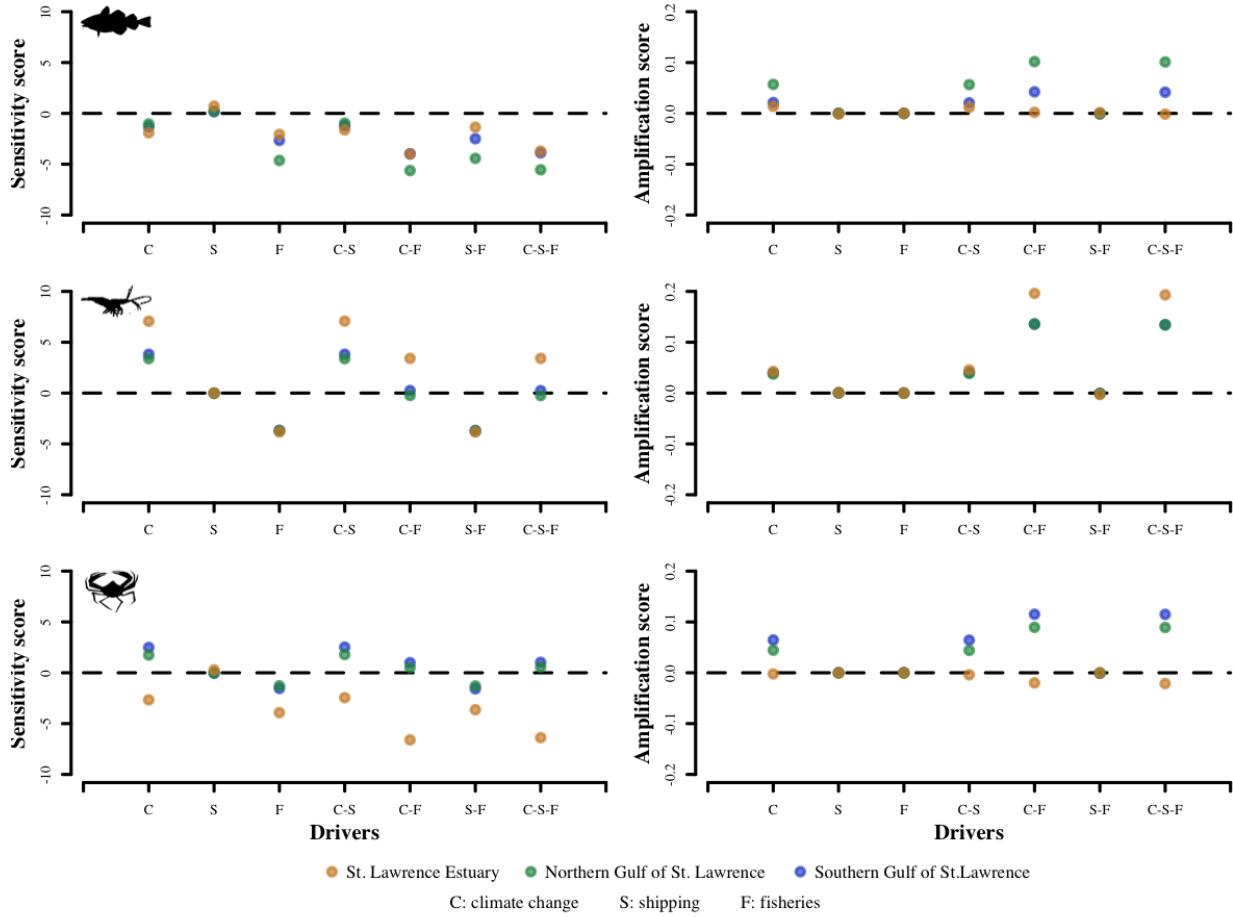


Figure 8: Species vulnerability in three different food webs.

419 5 What it all means

- 420 • Amplification increases with interaction complexity

421 ***First try: using introductory questions to structure discussion***

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

425 We first find, as expected, that species interactions should be explicitly considered in impact
 426 assessments, as they greatly influence trophic vulnerability to the effects of disturbances.

⁴²⁷ This supports longstanding evidence that interactions play a crucial role in spreading the
⁴²⁸ effects of individual disturbances through food webs (*e.g.*@menga1995; Wootton 1993, 2002;
⁴²⁹ Yodzis 2000), and unsurprisingly extends this conclusion to multiple disturbances.

⁴³⁰ We further uncover the that type of interactions a species is involved in influences its vul-
⁴³¹ nerability to disturbances.

⁴³² Omnivory and food chain in particular are responsive to disturbances, while exploitative and
⁴³³ apparent competition are less vulnerable. [...]

⁴³⁴ We provide evidence that indirect effects are at least as important as direct effects in driving
⁴³⁵ species vulnerability and that they are they seem to be the main source of non-additive
⁴³⁶ effects at the community scale. [...]. This means that when studying population dynamics,
⁴³⁷ the effects of multiple drivers cannot be studied outside of the context of species interactions.

⁴³⁸ Secondly, we find that the effects of multiple disturbances should be considered in combina-
⁴³⁹ tion, as non-additive effects often arise from disturbances to two or more biological processes.

⁴⁴⁰ Pathways of effect to omnivory and top predator in food chain interations

⁴⁴¹ Au final, ce que je veux dire c<et que les interactions d'omnivorie et le top prédateur de la
⁴⁴² chaîne tri-trophique en particulier sont caractérisés par des effects non-additifs. La majorité
⁴⁴³ des pathways

⁴⁴⁴ Ça va dépendre de chemins d'effects spécifiques, pas de généralité possible sur ces positions!

⁴⁴⁵ Additionally, there are no specific property of individual pathways of effect that conclusively
⁴⁴⁶ differentiate biotic buffers and amplifiers.

⁴⁴⁷ Pathways of effects

⁴⁴⁸ Omnivory interactions and the top predator in the food chain motif in particular are char-
⁴⁴⁹ acterized mostly

⁴⁵⁰ However, non-additive effects are however highly variable between interaction type and
⁴⁵¹ species position. In particular, pathways of effect on omnivory interacations largely lead

⁴⁵² to both biotic buffers and biotic amplifiers. Aditionnally, we

⁴⁵³ Predicting non-additive effects there seems pretty damn hard.

⁴⁵⁴ what differentiates biotic buffers and biotic amplifiers.

⁴⁵⁵ the types of pathways of effects that either

⁴⁵⁶ as to specific types of pathways of effects

⁴⁵⁷ accumulation of pathways of effects that lead to non-additive effects.

⁴⁵⁸ In general, omnivory and food chain interactions tend to

⁴⁵⁹ There is however a lot of variability

⁴⁶⁰ • Many non-additive effects arise from

⁴⁶¹ • Lot of variability in the nature of the non-additive effect, with no precise indication
⁴⁶² of what drives a species to be a biotic buffer or a biotic amplifier, suggesting that
⁴⁶³ considering effects of pressures in combination is the only valid way to truly capture
⁴⁶⁴ the effects of multiple disturbances.

⁴⁶⁵ • Multivariate pathways of effect result in heightened sensitivity (Figure 5B)

⁴⁶⁶ • Hypersensitivity when multiple pathways are targetted (jackson2016?) ## Good point
⁴⁶⁷ to use when I talk about sensitivity to multiple pathways of effect

⁴⁶⁸ • HARD TO PREDICT FOR OMNIVORY, LOTS OF VARIABILITY

⁴⁶⁹ • Non-additive effects

⁴⁷⁰ Lastly, we identify species that are particularly vulnerable to disturbances at the motif-
⁴⁷¹ scale, and use these generalities as heuristics to infer species trophic vulnerability in complex
⁴⁷² networks.

⁴⁷³ Finally, species themselves are more or less sensitivity, with predators in omnivory and food
⁴⁷⁴ chain both weak entry points and biotic amplifiers. - Trophic cascades, compensatory effects

⁴⁷⁵ - Estes *et al.* (2011); - Compensatory effect suppression Thompson *et al.* (2018) - The fact
⁴⁷⁶ that resources and predators are most affected, look at O'Gorman *et al.* (2012)

⁴⁷⁷ In particular, predators in food chain and omnivory interactions are both weak entry points
⁴⁷⁸ and biotic amplifiers.

⁴⁷⁹ Predators and resources

⁴⁸⁰ -Groundfish stock collapse: a trophic hint? - Exploited species before the groundfish stock
⁴⁸¹ collapse of the 1990s (\textit{e.g.} demersal feeders, Atlantic cod, Greenland halibut) are
⁴⁸² all negative weak entry points and biotic amplifiers. - Exploited species after the collapse
⁴⁸³ are either positive weak entry points and biotic amplifiers (\textit{e.g.} large crustaceans)
⁴⁸⁴ or biotic sinks (\textit{e.g.} shrimp). ->

⁴⁸⁵ We then use the simulated sensitivity and amplification scores as heuristics to infer trophic
⁴⁸⁶ vulnerability of species based on topology and realized pathways of effects in the food web
⁴⁸⁷ of the Northern Gulf of St. Lawrence, Canada, prior to a groundfish stock collapse in the
⁴⁸⁸ 1990s. We find that heavily exploited species appear to be the most vulnerable trophically,
⁴⁸⁹ while fisheries transitioned to insensitive or beneficiary species post-collapse.

⁴⁹⁰ 6 The way forward

- ⁴⁹¹ • Ignoring the importance of species interactions and pressure at bla bla
- ⁴⁹² • Provide novel hypothesis to test experimentally.
- ⁴⁹³ • Our results reinforce that holistic approaches are necessary to properly consider the
⁴⁹⁴ effects of environmental pressures on complex communities. Although this has been
⁴⁹⁵ hinted at, no other study [...]
- ⁴⁹⁶ • Management

497 **7 Supplementary Material**

498 **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 effect of multiple disturbances

499 7.2 Supplementary figures

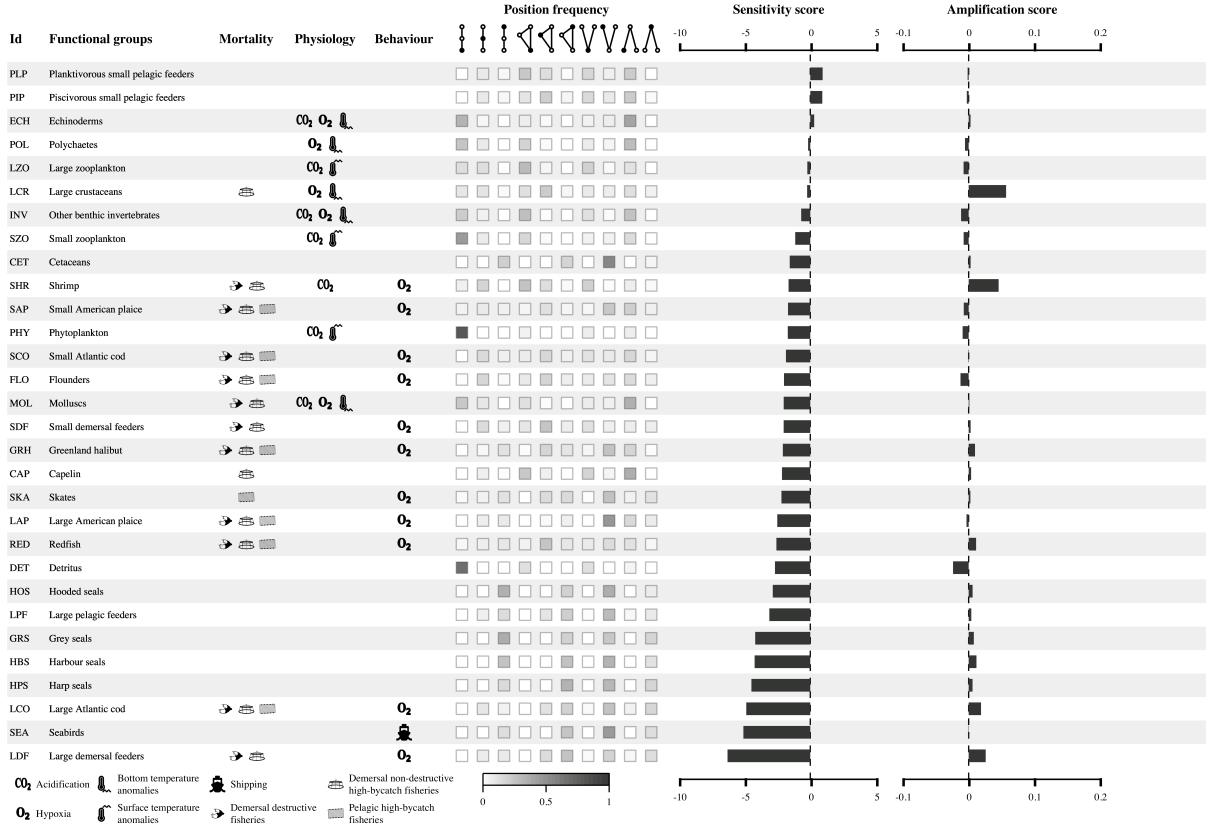
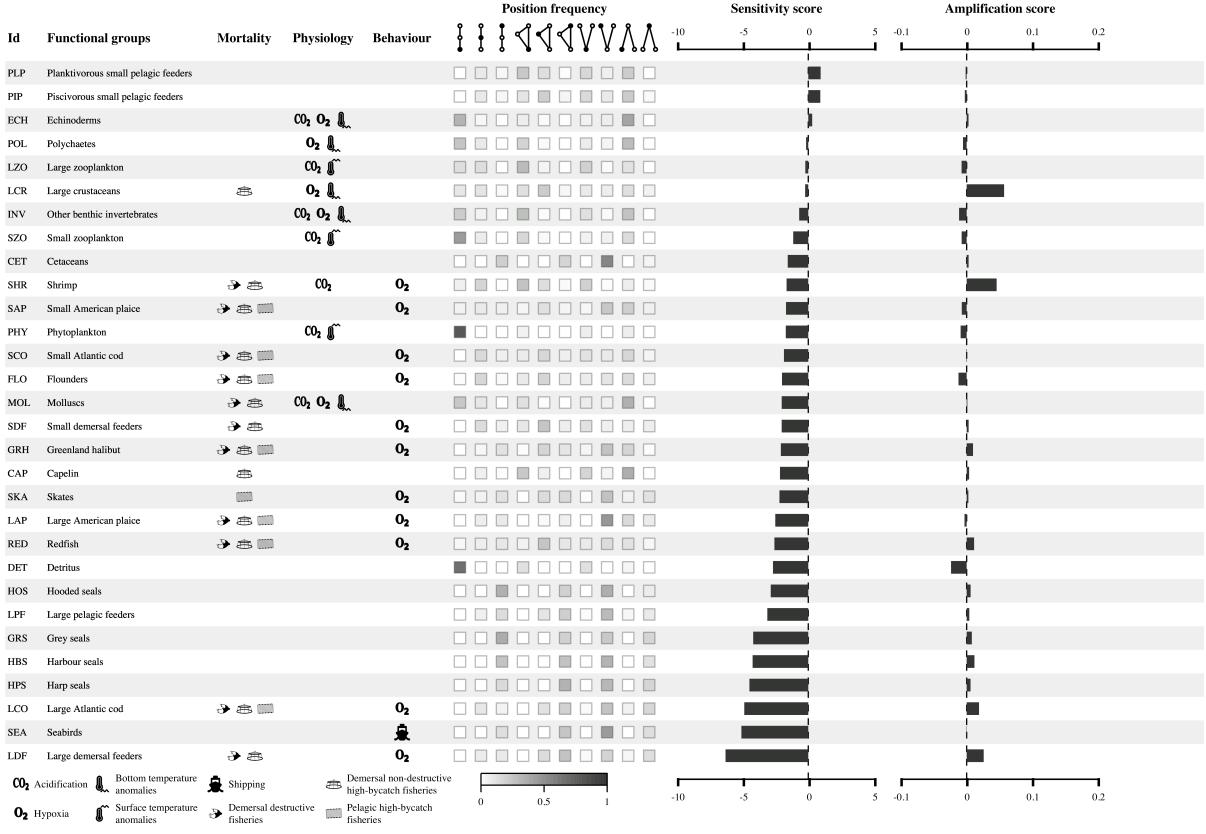


Figure 9: Change in species and functional groups sensitivity and amplification scores as a function of realised pathways of effects for an empirical food web of the Southern Gulf of St. Lawrence in the mid-1980s [?]. The left-hand side of the table presents the species and functional groups, the drivers 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 realised pathways of effects between all 3-species combinations in the food web. The right-hand side of the table presents the species sensitivity and amplification scores, which corresponds to the sum of the simulated effects of all realised pathways of effects for each species and functional group (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.



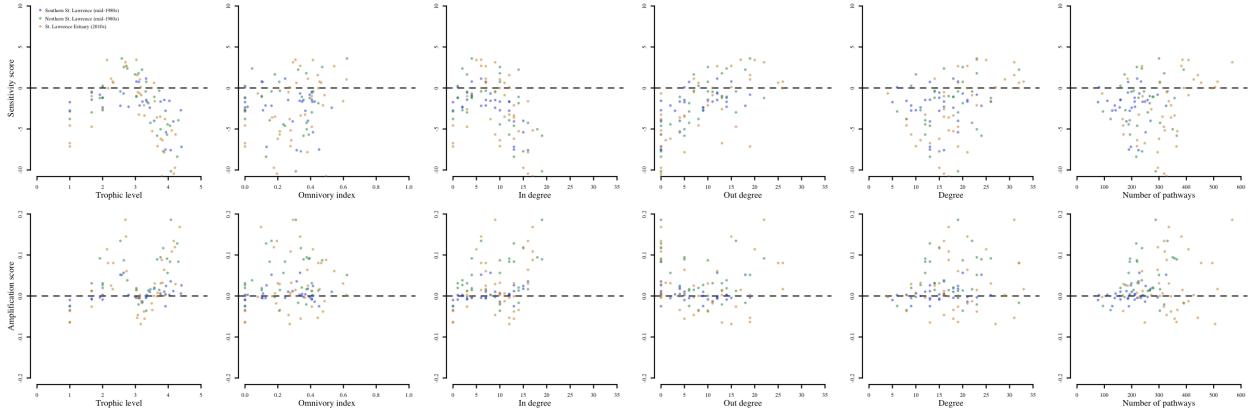


Figure 11: Sensitivity and amplification as a function of common network metrics.

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