

1      On the sensitivity of food webs to multiple  
2      disturbances

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## <sup>32</sup> Checklist

- <sup>33</sup>  Proposal letter Ecology Letters - Ideas and Perspectives
- <sup>34</sup>  Cover letter and novelty statement
- <sup>35</sup>  Conflict of interest statement
- <sup>36</sup>  Statement of authorship
- <sup>37</sup>  Data accessibility statement
- <sup>38</sup>  Reviewers
- <sup>39</sup>  Keywords
- <sup>40</sup>  Abstract
- <sup>41</sup>  Introduction
- <sup>42</sup>  Of food webs and multiple disturbances (concept)
- <sup>43</sup>  Simulations
- <sup>44</sup>  Sensitivity
- <sup>45</sup>  Amplification
- <sup>46</sup>  Food web sensitivity & amplification
- <sup>47</sup>  Conclusions
- <sup>48</sup>  Acknowledgements
- <sup>49</sup>  References
- <sup>50</sup>  Figure 1 - Concept
- <sup>51</sup>  Figure 2 - Sensitivity
- <sup>52</sup>  Figure 3 - Amplification
- <sup>53</sup>  Figure 4 - Food web scores table
- <sup>54</sup>  Figure 5 - Topological ~ Realised scores
- <sup>55</sup>  Figure 6 - Scores ~ Trophic level & degree
- <sup>56</sup>  Table S1 - Systems of equations
- <sup>57</sup>  Article formatting

58 **Plan**

59 • **Abstract**

60 • **Introduction**

- 61 – Global changes and disturbances propagation through food webs  
62 – Uncertainty associated with multiple disturbances  
63 – Limits of *in situ* and experimental approaches to study multiple disturbances  
64 – Limited insights from null model testing  
65 – Shift towards ecological modelling to better understand mechanisms  
66 – Insights on the effects of disturbances on ecological communities from theoretical  
67 ecology  
68 – Theoretical focus on single disturbances, coexistence and extinctions

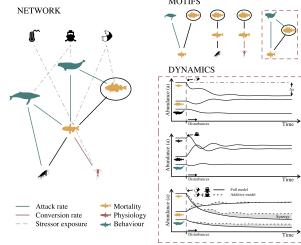
69 • **Objectives**

- 70 – Investigate the role of species and their interactions in mediating the effects of  
71 multiple disturbances on food webs.  
72 – Questions of particular significance to management:  
73     1) should interactions be considered in impact assessments?  
74     2) can the effects of stressors be evaluated separately or should they be consid-  
75         ered in combination?  
76     3) which species are most sensitive to disturbances based on their trophic posi-  
77         tion?

78 • **Of food webs and multiple disturbances**

- 79 – [1] Food web dynamics  
80 – [2] Indirect effects  
81 – [3] Environmental pressures  
82 – [4] Effects of disturbances on food webs  
83     \* What we know: robustness to extinctions, importance of indirect effects  
84 – [5] Pathways of effects  
85 – [6] Non-additive effects  
86 – [7] Topology (trophic position and interaction types)  
87 – [8] Motifs  
88     \* to understand how topology influences sensitivity to and amplification of  
89         disturbances  
90 – [9] Archetypes  
91 – [10] Subweb dynamics/insights (Holt 1997; Stouffer 2007)  
92 – [11] Definitions - pathway, trophic (position), biotic (species)  
93     \* Weak entry points  
94     \* Sinks

- 95                    \* Buffers (cite Montoya et al. 2009)  
 96                    \* Multipliers

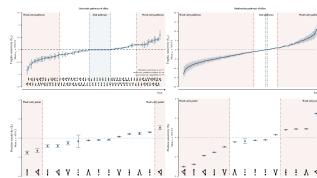


97                  • Simulating multiple disturbances on food webs

- 98                  – Method for simulations:  
 99                  \* Exhaustive investigation of how topology affects species abundance at  
 100                 \* equilibrium to univariate and multivariate pathways of effects

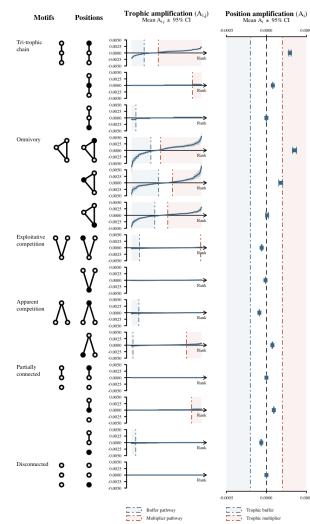
101                 • Topology and sensitivity

- 102                  – Method: Comparison between initial and disturbed abundance: trophic sensitiv-  
 103                 ity  
 104                  – Amplitude of effects is highly variable, and much higher for multivariate pathways  
 105                 of effects  
 106                  – Importance of considering species interactions  
 107                  \* Univariate pathways of effects simulations clearly show that interactions in-  
 108                 fluence the amplitude of the effects of disturbances  
 109                  \* Complex interactions = greater variability  
 110                  \* Control motifs (disconnected & )  
 111                  – Species position and interaction type leads to varying sensitivity  
 112                  \* Interactions generally amplify effects on species  
 113                  \* Control motifs largely unaffected  
 114                  \* Complex interactions more sensitive (i.e. tri-trophic food chain and omnivory)  
 115                  \* Competitive interactions (Competitive and apparent competition) less sensi-  
 116                 tive  
 117                  \* Basal resources and top predators generally more sensitive



118                 • Topology and amplification

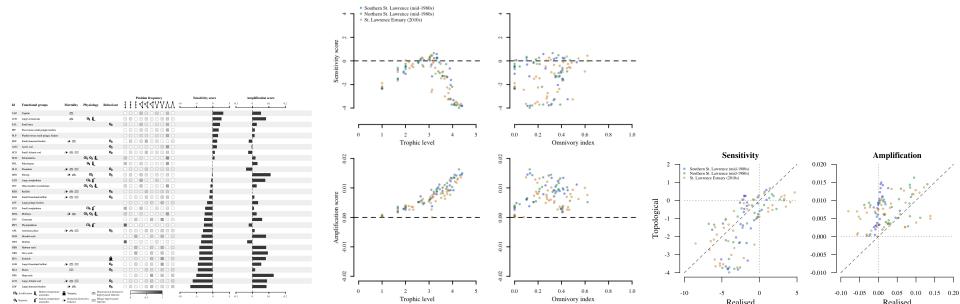
- 119 – Method: Comparison between full models considering all pathways of effects si-  
 120 multaneously and additive models considering the sum of the effects of univariate  
 121 pathways of effect to identify antagonistic, additive and synergistic pathways of  
 122 effect: trophic amplification  
 123 – Frequency and variability of non-additive effects more important for omnivory  
 124 and tri-trophic chain.  
 125 – Predator release for resources or meso-predators (positive effects)  
 126 – Limited non-additive effects for control motifs  
 127 – Competition: antagonism  
 128 – Complex interactions: more non-additive effects, dominated by synergistic effects  
 129 for consumers



### 130 • Complex food webs

- 131 – Method: Topological and realised sensitivity and amplification scores; expert  
 132 opinion on effects of drivers on mortality, physiology and behaviour.  
 133 – Empirical food web: Northern Gulf of St. Lawrence, prior to the groundfish stock  
 134 collapse in the 1990s  
 135 – Topological vs realised scores
  - 136     \* Interpret biplots
  - 137 – Trophic level
    - 138     \* Realised sensitivity non-linear with trophic level. Lower and higher trophic  
 139 levels have low sensitivity scores, while intermediate trophic levels have null  
 140 or positive sensitivity scores
    - 141     \* Realised Aaplification looks like a sinusoid, with antagonism at low trophic  
 142 levels which increases to synergism towards intermediate trophic levels. It  
 143 then drops to antagonisms again at intermediate trophic levels and then in-  
 144 creases again towards synergisms for higher trophic levels.
  - 145 – Food web:

- 146                    \* Few biotic sinks, more negative weak entry points  
 147                    \* Very few biotic buffers, many biotic multipliers  
 148                    \* A species does not have to be impacted directly to have large trophic sensitiv-  
 149                    ity and amplification scores (*e.g.* seals and seabirds), and direct disturbances  
 150                    do not necessarily result in sensitivity or amplification.  
 151                    \* Groundfish collapse: decrease in groundfish species and increase in inverte-  
 152                    brates, crustaceans and shrimp (economical shift ensued with fisheries now  
 153                    focused on those species)  
 154                        · Groundfish species are negative weak entry points and biotic multipliers  
 155                        · Large crustaceans positive weak entry point and biotic multiplier  
 156                        · Shrimp biotic sink  
 157                        · Check up on capelin populations post stock collapse



158                    • Conclusions

- 159                    – Complex interactions = more sensitive and non-additive effects  
 160                    – Meso-predator in complex interactions or resources in apparent competition =  
 161                    predator release  
 162                    – Competitive interactions = less sensitive and more antagonism  
 163                    – Mecanistic understanding  
 164                    – Probabilities  
 165                    – Management

166 **To do:**

- 167     Proposal for Ecology Letters Ideas and Perspectives  
168     Check and adjust for unique pathways of effect (exploitative and apparent competition).  
169        – They are all unique when you consider the position of the species, except for the disconnected motif.
- 170     Think on the best way to establish position profile. At the moment what is used is  
171        the mean of individual pathways of effect per position, and I feel we could do better.  
172        ***Perhaps with maximal positional scores.***  
173     Integrate (Hodgson *et al.* 2019) in the introduction  
174     Figure out how to evaluate species motifs position as a probability rather than a frequency. This could make use of empirical diet % available in Ecopath models. ->  
175        This will be discussed in this paper, and developed in the subsequent spatial paper  
176     Figure out methodology to evaluate species profile through two indices: sensitivity score  
177        and amplification score. These could be used to adjust Halpern's equation later on.  
178     Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frolicher, T.L., Lam, V.W.Y., Palomares,  
179        M.L.D., Watson, R., and Pauly, D. 2013. Shrinking of fishes exacerbates  
180        impacts of global ocean changes on marine ecosystems. Nature Climate Change 3:  
181        254-258.  
182     Uniformiser les indices dans les équations de l'article  
183     Modify the score for species using realised pathways of effects. I thought that this was  
184        done, but since we are not using probabilities, I'm not sure what I should be doing  
185        anymore with this. Ideally I would still use a probability and have a general function,  
186        but we might still want to keep this for the 4th chapter of the thesis. -> in 4th chapter.  
187     Verify all codes so that the proper equations are used  
188     Update thresholds used  
189     Give proper credit to icons and images used  
190     Sensitivity and amplification ~ in- and out-degree  
191     Figure ex. biotic multiplier ~ position  
192     Evaluate realised score potential (maximum) for each position. Not all pathways could  
193        be realised simultaneously, since when a multivariate pathway of effect exists, all of  
194        its constituent pathways cannot exist anymore. We could therefore come up with a  
195        maximal sensitivity and amplification score. We could then check the maximal possible  
196        score for a species and see whether we are close to it or not. Since there can only be a  
197        single realised pathway between 3 species, the maximum score would be the pathway  
198        of effect with the highest sensitivity and the one with the higher amplification score.  
199     Check whether the unsensitivity of resources in competitive exploitation is due to the  
200        competitive parameters added to the models to get to equilibrium  
201     If indirect effects are as important as direct effects, then it means that to better understand  
202        the impacts of disturbances, it may be as important to look at species beyond  
203        our focal species of interest.  
204     ***Have to look into the importance of direct vs indirect effects***

208 **Proposal letter**

<sup>209</sup> **Cover letter and novelty statement**

<sup>210</sup> **Letter**

<sup>211</sup> **Documents joined**

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- <sup>214</sup>     • Reviewer 1
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- <sup>218</sup>     • In-conflict individual and reason

<sup>219</sup> **Conflict of interest statement**

<sup>220</sup> The authors declare that the submitted work was carried out in the absence of any personal,  
<sup>221</sup> professional or financial relationships that could potentially be construed as a conflict of  
<sup>222</sup> interest.

## 223 1 Abstract

224 Global changes are resulting in increasingly intricate environmental stress exposure regimes.  
225 These can in turn induce complex and unpredictable environmental effects permeating entire  
226 ecological communities by way of species interactions.

227 The role of species and their interactions in mediating the effects of multiple disturbances  
228 on food webs is however still understudied. Experimental and *in situ* approaches provide  
229 limited insight, while theoretical approaches have yet to fully tackle the issue.

230 Using Lotka-Volterra equilibria models of the 4 most common 3-species motifs in empirical  
231 food webs, we show that trophic position and interaction type influence the sensitivity to  
232 and the amplification of the effects of multiple disturbances.

233 We then show that how species are embedded in complex food webs and the types of dis-  
234 turbances they are exposed to dictates their sensitivity to multiple sources of stress.

235 Our results illustrate the importance of explicitly considering species interactions to properly  
236 capture the effects of multiple stressors and safeguard ecological communities against global  
237 changes.

238 Global changes are creating intricate stress exposure regimes that induce unpredictable en-  
239 vironmental effects permeating entire ecological communities by way of species interactions.  
240 The role of species and their interactions in mediating the effects of multiple disturbances on  
241 food webs remains understudied. Experimental and *in situ* approaches provide contextual  
242 insights, while theory has yet to fully tackle the issue. Using Lotka-Volterra models, we  
243 show that topology (i.e. trophic position and interaction type) influences the sensitivity to  
244 and the amplification of the effects of multiple disturbances. We show that species position  
245 in complex food webs and the types and combinations of disturbances they are exposed to  
246 dictates their sensitivity to multiple sources of stress. Our results illustrate the importance  
247 of considering species interactions and non-additive effects to capture the effects of multiple  
248 disturbances and safeguard ecological communities against global changes.

249 Contribution: we define multiple types of ecological outcomes from different pathways of  
250 effects, i.e. weak entry points, biotic sinks, biotic buffers and biotic amplifiers.

251 Surprises: non-additive effects Interactions: affects the amplitude of the predicted effects of  
252 disturbances Explain why 2 disturbances make the situation more complex when considering  
253 interactions

254 **2 Introduction**

255 • **Global changes, multiple stressors and food webs**

- 256 – Global changes are resulting in increasingly intricate environmental stress expo-  
257 sure regimes (Halpern *et al.* 2015; Côté *et al.* 2016; Bowler *et al.* 2019). These can  
258 in turn induce complex and unpredictable environmental effects that propagate  
259 through entire ecological communities by way of species interactions (Bascompte  
260 2009; Montoya *et al.* 2009).

261 • **Uncertainty associated with mutliple stressors**

- 262 – Largest uncertainty in predicting environmental effects is the potential for com-  
263 plex driver interactions (Darling & Côté 2008; Côté *et al.* 2016).  
264 – Stressors can combine non-additively and result in effects that are greater (*i.e.*  
265 synergistic) or lower (*i.e.* antagonistic) than the sum of individual effects (Crain  
266 *et al.* 2008; Darling & Côté 2008; Côté *et al.* 2016)  
267 – Net effects of multiple stressors can be additive (*i.e.* joint effect equal to the sum  
268 of individual effects), synergistic (joint effect superior to the sum of individual  
269 effects), antagonistic (joint effect inferior to the sum of individual effects) or dom-  
270 inant (joint effect equal to an individual effect) (e.g. Crain *et al.* 2008; Darling &  
271 Côté 2008; Côté *et al.* 2016).  
272 – This is of particular significance for management, because we have mostly been  
273 operating under the assumption that stressors are mostly additive and thus can  
274 be managed independently.  
275 – Maybe cite (Hodgson *et al.* 2019) (cite it for certain in the article).  
276 – most research on driver effects in marine environments remains overwhelmingly  
277 focused on single driver assessments (O'Brien *et al.* 2019).

278 • **Limits of *in situ* and experimental approaches to study multiple distur-  
279 bances**

- 280 – The number of stressors and of their potential interactions limits the insights we  
281 can glean into the effects of multiple disturbances *in situ* and in experimental  
282 settings such as mesocosm (Côté *et al.* 2016).  
283 – In food webs, this is compounded by the myriad of possible interactions  
284 – between species

285 • **Limited insights from null model testing**

- 286 – The knowledge we do have has mostly been gleaned from null model testing  
287 providing little insights into ecological mecanisms underlying non-additive stressor  
288 effects (De Laender 2018).

289 • **Shift towards ecological modelling to better understand mecanisms**

- 290 – (De Laender 2018; Schäfer & Piggott 2018; Thompson *et al.* 2018a)

291 • **Some insights on the effects of disturbances on ecological communities from  
292 theoretical ecology**

- 293     – Importance of interactions and web complexity  
 294     – Indirect effects [Wootton (1993); Yodzis (2000); Wootton (2002); Montoya *et al.*  
 295       (2009); ogorman2009]; see intro séminaire 1  
 296     – Different types of interactions will lead to different overall effects (???).  
 297       \* Different sensitivity for species involved in different types of interactions (seg-  
 298       way to motifs)  
 299     – How direct and indirect effects combine to affect food web sensitivity to distur-  
 300       bances
- 301     • **Theoretical has thus far mostly been concerned mostly with single distur-  
302       bances and resistance of communities to extinctions**
    - 303       – Little insights into how different pathways of effect influences food webs, let alone  
 304       pathways of multiple effects.
    - 305       – Little on the role of species and their interactions in propagating or buffering  
 306       against disturbances
  - 307     • **State the objective**
    - 308       – Here, we investigate the role of species in mediating the effects of multiple dis-  
 309       turbances on food webs. In doing so, we seek to answer questions of particular  
 310       significance to management: 1) should species interactions be considered in im-  
 311       pact assessments, 2) should the effects of stressors be evaluated separately or in  
 312       combination, and 3) which species are most sensitive to disturbances?

### 313     3 Of food webs and multiple disturbances

- 314     • Species are linked  
 315     • Disturbing one means that you will likely disturb another one  
 316     • The position and types of interactions a species is involved in will affect its sensitivity  
 317       to multiple disturbances  
 318     • In real systems, food webs are threatened by many environmental pressures that can  
 319       penetrate them in many different ways.

320     The role of species and their interactions in food web sensitivity to multiple Disturbances  
 321     “The prevailing notion is that the ecological role of a species in a network is a direct result  
 322     of its interactions with other species” - Stouffer “Unclear how to extrapolate the structural  
 323     role of species to its dynamic relevance to complex food webs” - Stouffer

324 **3.1 Other thoughts, clean up**

325 • **How we do this**

- 326 – To do so, we focus on how trophic position and interaction types affect species  
327 sensitivity to disturbances and the likelihood of species acting as buffer against  
328 or amplifiers of the effects of multiple disturbances.

329 • **Transition to motifs**

- 330 – ...?

331 • **Motif description and use**

- 332 – A food web can be decomposed into a set of smaller  $n$ -species subgraphs called  
333 motifs (Milo *et al.* 2004; Stouffer *et al.* 2007). For example, there are 13 distinct  
334 3-species motifs composed of 30 unique positions (Stouffer *et al.* 2007, 2012).  
335 Motifs are the backbone of food webs and their study has unearthed valuable  
336 insights on community dynamics such as [...].
- 337 – Their type and frequency has been linked to food web stability and persistence  
338 (???)
- 339 – Like many disturbance studies in theoretical ecology, however, these have focused  
340 less on the dynamics of population abundances and more on the resistance of food  
341 webs to extinctions.
- 342 – Motifs have been used to investigate the persistence of food web to species ex-  
343 tinctions (Stouffer & Bascompte 2010) and the benefit associated to each species  
344 in food web persistence (Stouffer *et al.* 2012).
- 345 – *The ecological role of a species in a network is a direct rest if its interactions with*  
346 *other species (Luczkovich 2003; Olesen 2007; Allesina 2009) (in Stouffer 2012)*
- 347 – *The number and types of motifs that make up a food web are known to directly*  
348 *affect the web's stability and persistence (Neutel 2002; Kondoh 2008; Allesina*  
349 *2008; García-Domingo 2008; Stouffer 2010; in Stouffer 2012)*

350 • **Our focus**

- 351 – Here we focus on the most abundant types of interactions: omnivory, tri-trophic  
352 food chain, exploitative competition and apparent competition (Camacho *et al.*  
353 2007; Stouffer & Bascompte 2010)
- 354 – Two additional motifs, *i.e.* partially connected and disconnected were also consid-  
355 ered in order to evaluate whether interactions in food webs are truly more likely  
356 to be characterized by non-linear effects.
- 357 – To study the effects of multiple stressors in a trophic context, we rather focus on  
358 the resulting disturbances following different pathways of effect rather than on  
359 the disturbances themselves. This means that we will not investigate the effects  
360 of multiple stressors applied to a single species in the food web. This precludes us  
361 from investigating the sensitivity of species to each individual stressor. Rather,  
362 we investigate the effects of disturbances to multiple species simultaneously. But  
363 see Thompson *et al.* (2018b) and Thompson *et al.* (2018a) for a description of

364 a modelling approach incorporating multiple sources of stress in a food web  
365 model.

- 366 – We are interested in pathways that affect the trophic dynamic of food webs, *i.e.*  
367 those that target population growth (*i.e.* birth and death rates) and the rates at  
368 which species interact (*i.e.* attack and conversion rates).

369 • **Pathways of effect**

- 370 – Studying the effects of multiple disturbances means that we will be focusing on  
371 disturbances affecting multiple species, referred to as pathways of multiple effects  
372 ( $D_{i,j}$ ,  $D_{i,k}$ ,  $D_{j,k}$ , and  $D_{i,j,k}$ ).  
373 – In a food web context, we will define linear and non-linear effect as a function of  
374 whether these pathways of multiple effects result in additive ( $D_{i,j} = D_i + D_j$ ),  
375 synergistic ( $D_{i,j} >> D_i + D_j$ ), antagonistic ( $D_{i,j} << D_i + D_j$ ) or dominant  
376 ( $D_{i,j} = D_i \vee D_j$ ) effects.

377 • **Terminology for types of pathways and position profile**

- 378 – Species can occupy different roles in these pathways of multiple effects. Investigating  
379 species profile (e.g.\* Stouffer *et al.* 2012) could thus inform us on the role played by individual species in buffering against or amplifying the effects of  
380 multiple disturbances.  
381 – We define 4 key roles in species propagating or buffering against multiple disturbances:  
382  
383

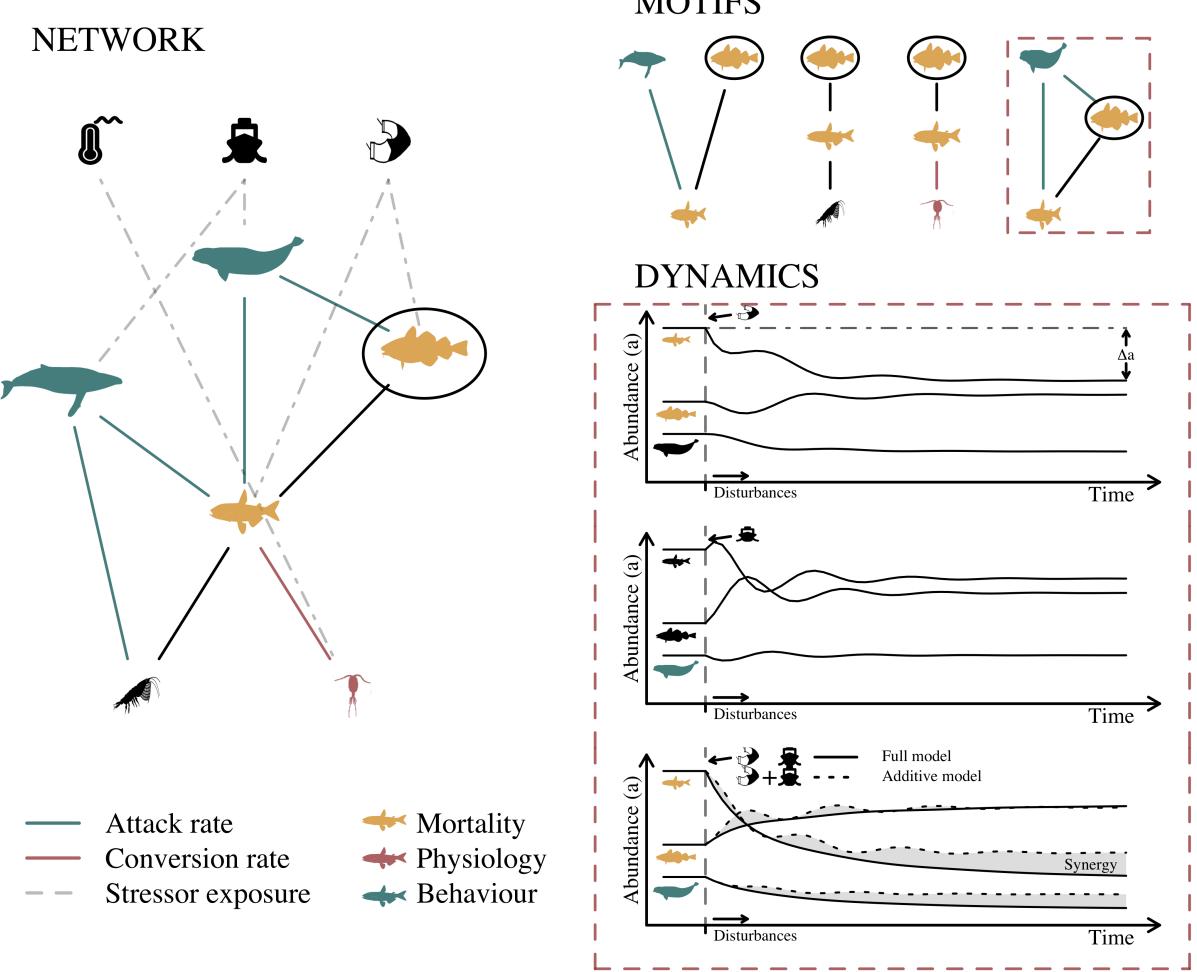


Figure 2: Conceptualize the effects of multiple disturbances on food webs

384 **4 Sumulating disturbances on food webs**

385 **4.1 Models**

386 The dynamics of the four most abundant 3-species motifs (*i.e.* tri-trophic food chain, om-  
387 nivory, exploitative and apparent competition) in empirical food webs (Stouffer & Bascompte  
388 2010) were modeled using Lotka-Volterra equation systems (Table S1). Two additional motifs  
389 were included to serve as controls to test the importance of considering species interactions  
390 when evaluating environmental effects, *i.e.* a partially connected motifs with a disconnected  
391 species and a predator-prey interaction, and a fully disconnected motif with three indepen-  
392 dent species.

393 Resources were modeled using logistic growth equations of the form  $\frac{dX_i}{dt} = X_i(r_i - \alpha_{ii}X_i -$   
394  $\sum \alpha_{ij}X_j)$ , where  $X$  are species,  $i$  is the resource,  $j$  are the consumers,  $r_i$  is the intrinsic  
395 resource growth rate,  $\alpha_{ii}$  is the density-dependent effect of the resource on itself and  $\alpha_{ij}$  is  
396 the rate at which consumer  $j$  affects resource  $i$ , *i.e.* the attack rate.

397 Consumers were modeled using a Type I functional response of the form  $\frac{dX_j}{dt} = X_j(-m_j +$   
398  $\sum e_{ij}\alpha_{ij}X_i - \alpha_{jk}X_k)$ , where  $m$  is the mortality rate and  $e$  is the rate at which resource biomass  
399 is transformed into consumer biomass, *i.e.* the conversion rate, and is a scaling parameter  
400 of the attack rate which cannot exceed 1.

401 Models were solved at equilibrium to study the effects of disturbances on persistent motif dy-  
402 namics. As no equilibrium exists for the exploitative competition motif with Lotka-Volterra  
403 models of the selected forms, competitive parameters of the form  $\alpha_{jj}\alpha_{jk}X_jX_k - \alpha_{jj}X_j^2$  were  
404 included in the consumer models to constrain their growth.

405 **4.2 Disturbances**

406 For each motif, a 1% change in initial equilibria equations parameter values was applied  
407 to simulate negative disturbances through all possible unique pathways of univariate and  
408 multivariate effects. Parameters selected to simulate disturbances were those related to  
409 population growth ( $r$  and  $m$ ) and interaction rates ( $e$  and  $\alpha_{ij}$ ), as their effects on population  
410 dynamics can readily be attributed to environmental pressure effects. For example, cod  
411 mortality will increase through fishing activities, whale attack rates on krill will be altered  
412 by behavioural changes induced by marine traffic, and conversion rates of copepods by capelin  
413 will be reduced through physiological effects of temperature anomalies on copepods.

414 Initial parameter values for intrinsic growth ( $r$ ) and resource density-dependence ( $\alpha_{ii}$ ) were  
415 fixed to 1 and 0.001, respectively, to bound all resource solutions. Competitive parameters  
416 for the exploitative competition motif were also fixed at 0.001 since those parameters were  
417 not to be investigated in our analyses. Conversion rates ( $e$ ) were fixed to 0.5. Finally, a  
418 total of 100 sets of mortality ( $m$ ) and attack rates ( $\alpha_{ij}$ ) were evaluated using a simulated  
419 annealing algorithm optimizing for consumer abundance.

## 420 5 Trophic sensitivity

421 For each 13 unique motif positions considered and all unique pathways of effects, the variation  
422 in abundance between the 100 sets of initial conditions and disturbed conditions was used  
423 as a proxy of trophic sensitivity ( $s_{i,j}$ ) to disturbances:

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

424 where  $i$  is a motif position,  $j$  is a unique pathway of effect,  $a_i$  is the initial abundance at  
425 position  $i$ , and  $a_{i,j}$  is the abundance at position  $i$  after the simulation of the pathway of effect  
426  $j$ . Sensitivity scores are bounded negatively to -1, as abundances cannot fall below 0. The  
427 sensitivity score used for a single pathway of effect ( $S_{i,j}$ ) is the mean of the 100 simulation  
428 using all initial conditions:

$$S_{i,j} = \frac{1}{n} \sum_{l=1}^n s_{i,j}$$

429 We define *weak entry pathways* and *sink pathways* as those pathways whose effect on the  
430 abundance of a motif position exceeds 1% ( $S_{i,j} < -1\%$  or  $S_{i,j} > 1\%$ ) and is null (*i.e.*  
431  $S_{i,j} = 0$ ), respectively (2).

432 A score of position sensitivity ( $S_i$ ) was evaluated using the mean of the set of all possible  
433 pathways of effect ( $K^i$ ) for a give position  $i$ :

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

434 We define *weak entry points* and *biotic sinks* as positions whose sensitivity score is signifi-  
435 cantly different than 1% ( $S_i < -1\%$  or  $S_i > 1\%$ ) and is null ( $S_i = 0$ ), respectively.

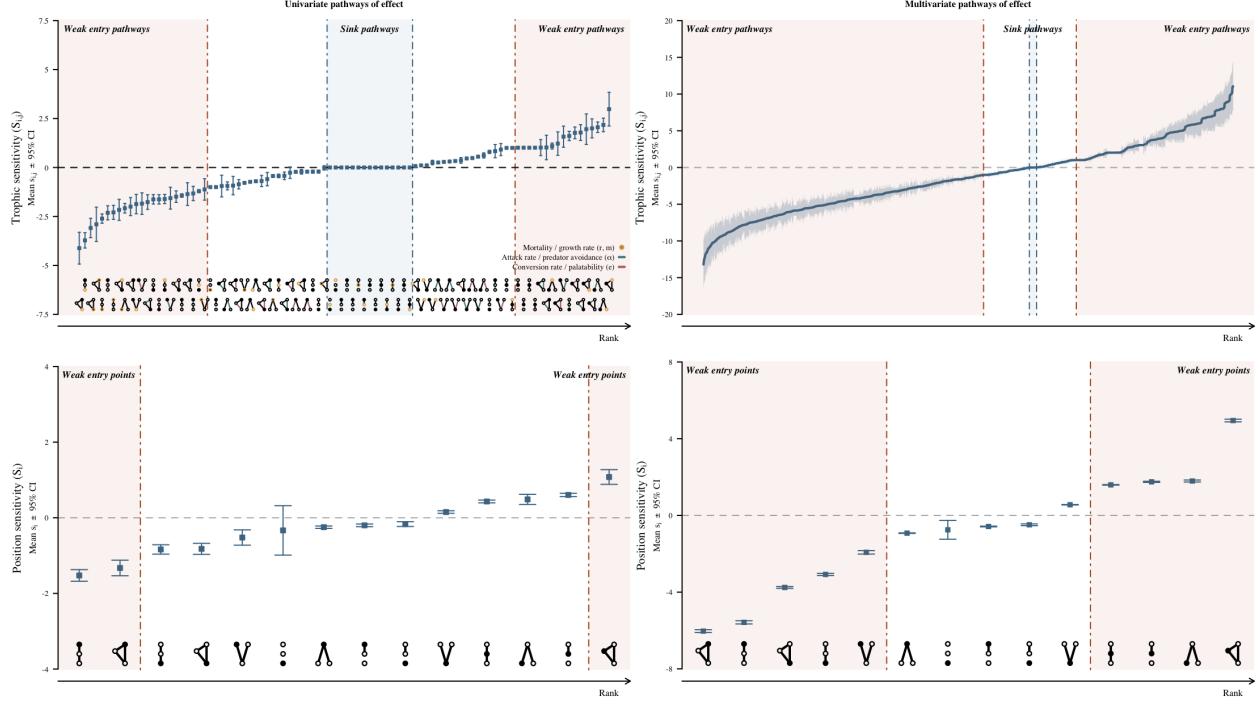


Figure 3: Disturbances. Line 1: Univariate disturbances; Line 2: Multivariate disturbances

## 436 6 Trophic amplification

437 To evaluate whether the effects of disturbances should be investigated in combination, a  
 438 score of trophic amplification was evaluated to

439 A score of trophic amplification ( $A_{i,j}$ ) was measured to evaluate the potential of pathways  
 440 of effects to result in non-additive effects:

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

441 where  $K_j$  is a multivariate pathway of effect  $j$  and  $k_j$  are unitary pathways of effect compo-  
 442 nition  $j$ . The amplification score evaluates the deviance of a multivariate pathway of effect  
 443 and the sum of the univariate effects composing the pathway of effect, *i.e.* the additive  
 444 model. Thus, a value of 0 identifies a null of additive effect, a value below 0 identifies an  
 445 antagonistic effect, and a value over 0 identifies synergistic effects.

446 We define *antagonistic pathways* and *synergistic pathways* as those pathways whose effect on  
 447 the abundance of a motif position is significantly different than the additive model, while  
 448 *additive pathways* are those pathways whose effect is not significantly different than the  
 449 additive model (2).

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

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

- 452 We define *biotic buffers* and *biotic multipliers* as positions whose amplification score is sig-  
453 nificantly different than 0, while *biotic invariants* are positions whose amplification score is  
454 not significantly different than 0 (2).

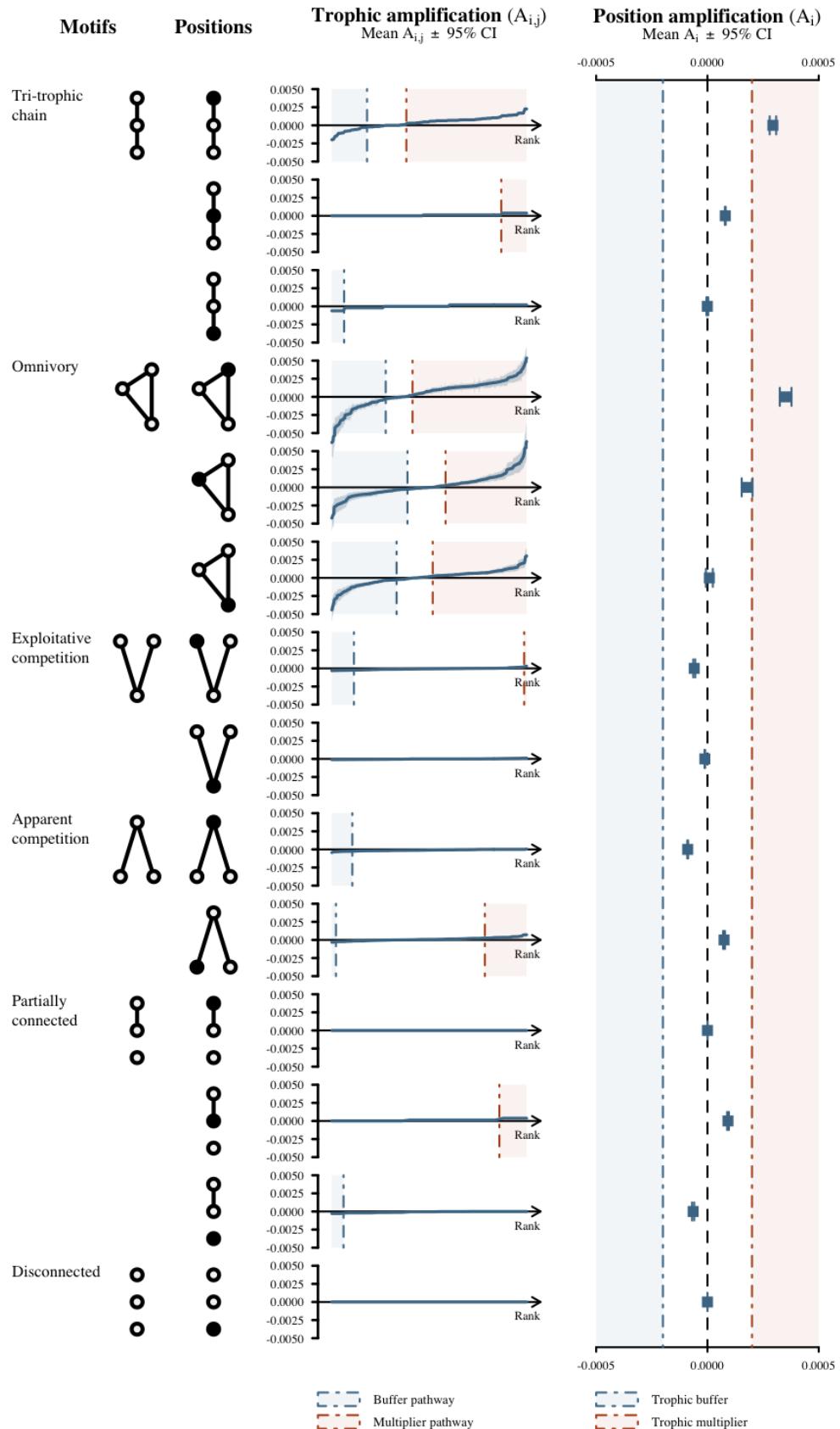


Figure 4: Motif positions and disturbances  
20

455 **7 Species role to food web sensitivity to multiple dis-**  
456 **turbances**

457 We define two sets of scores at the species level. The first requires no information on realised  
458 pathways of effect and provides a general evaluation of a species sensitivity and amplification  
459 potential based on the frequency of times it occupies a position in a food web:

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

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

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

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

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

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

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

467 **7.1 Empirical food webs**

468 We used empirical food web data from the Estuary and Gulf of St. Lawrence, in eastern  
469 Canada, to evaluate the sensitivity and amplification scores of its constituent species. The  
470 food webs come from different regions of the St. Lawrence and different time periods, and  
471 contain different yet overlapping functional groups. The Northern (???) and Southern (???)  
472 St. Lawrence food webs were for the mid-1980s, prior to the groundfish stock collapses of  
473 the early 1990s, and contain the same functional groups. The Estuary food web, mean-  
474 while, contains more functional groups and represents the beginning of the 2010s (???). See  
475 supplementary materials for a description of the food webs used for this analysis.



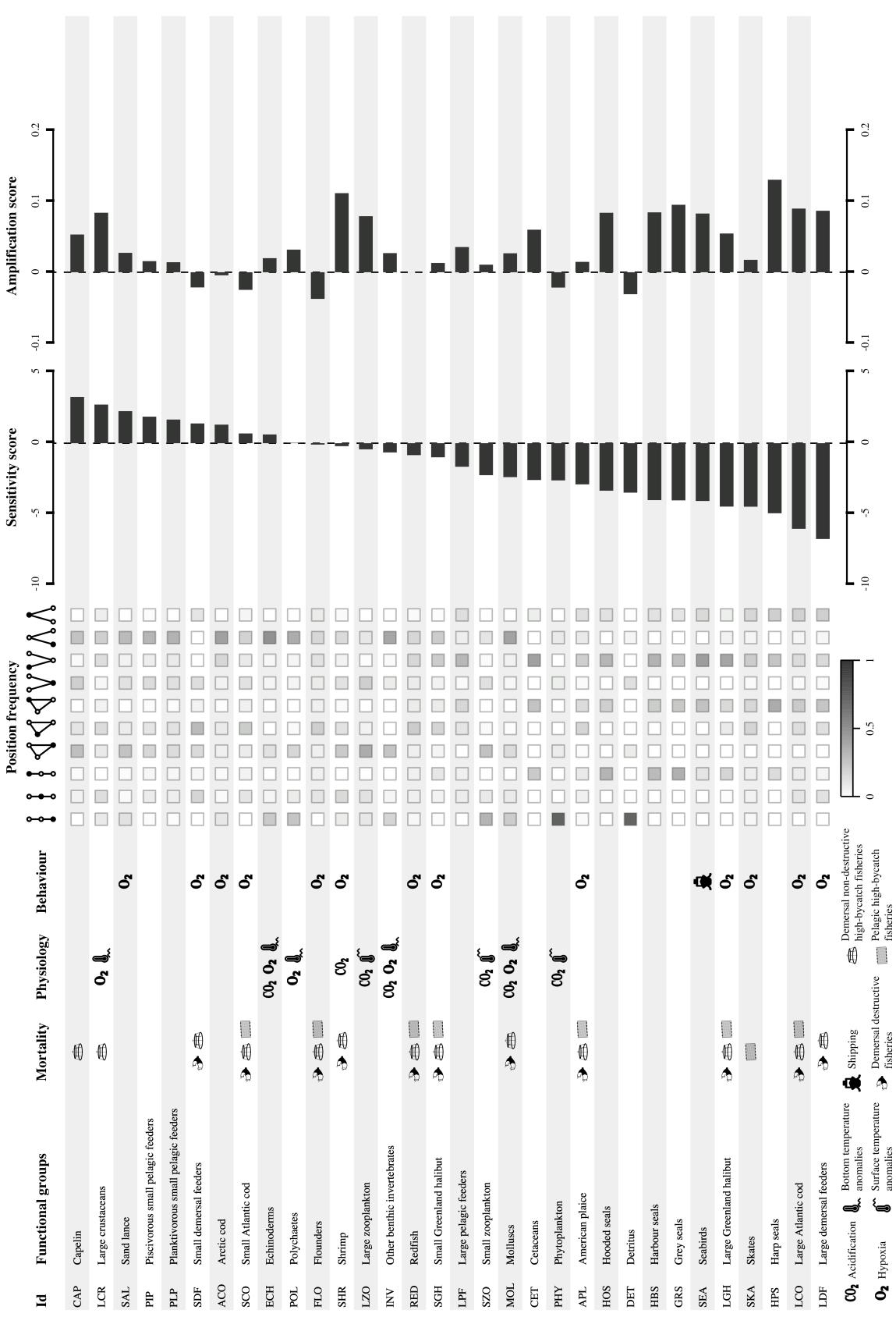


Figure 5: Species scores for the St. Lawrence

476 **8 Supplementary Figures**

477 **8.1 Simulation figures**

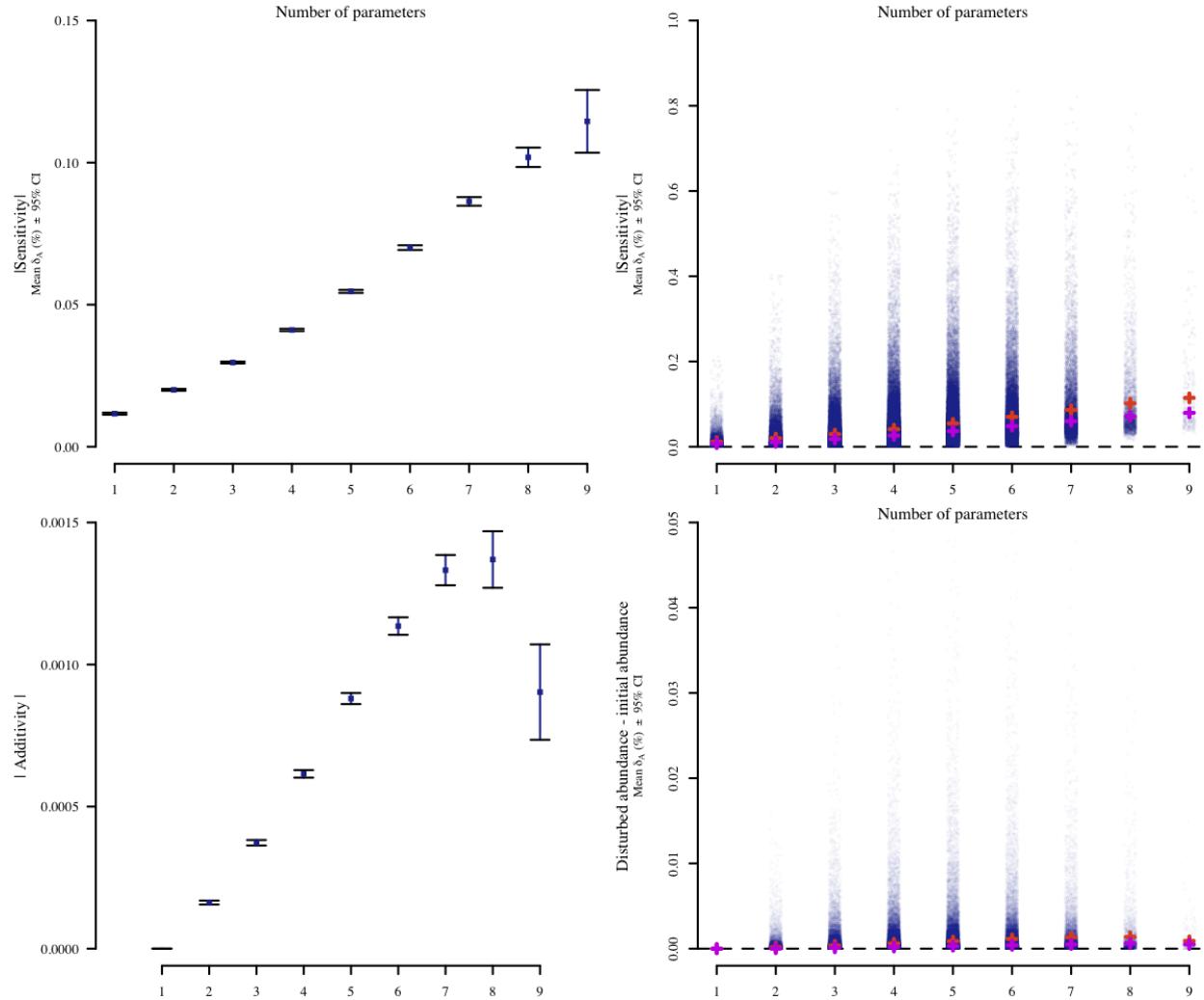


Figure 6: Mean delta abundance and difference between joint and additive models as a function of the number of parameters

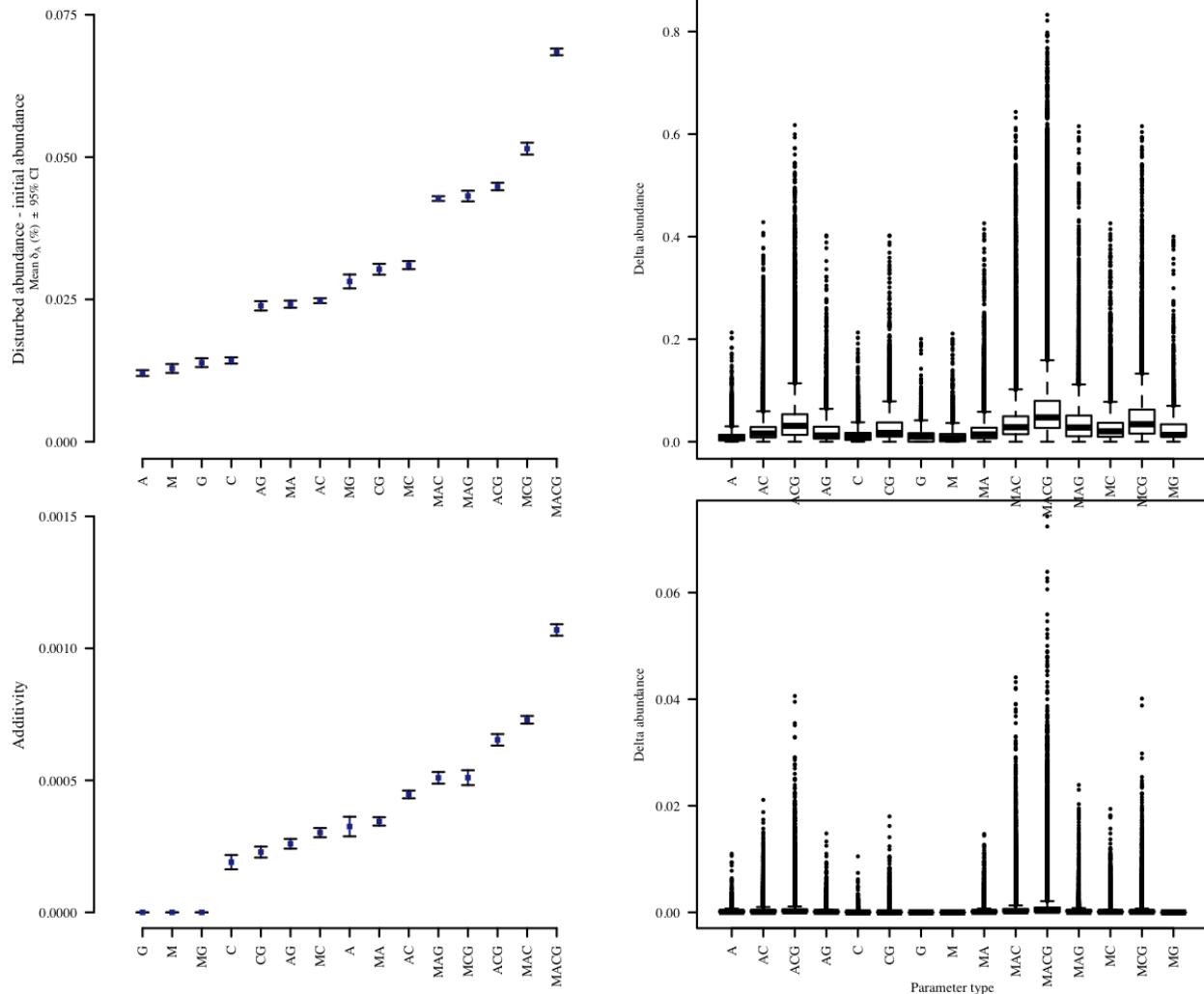


Figure 7: Mean delta abundance and difference between joint and additive models as a function of the types of parameters, i.e. growth/mortality rates, attack rates and conversion rates

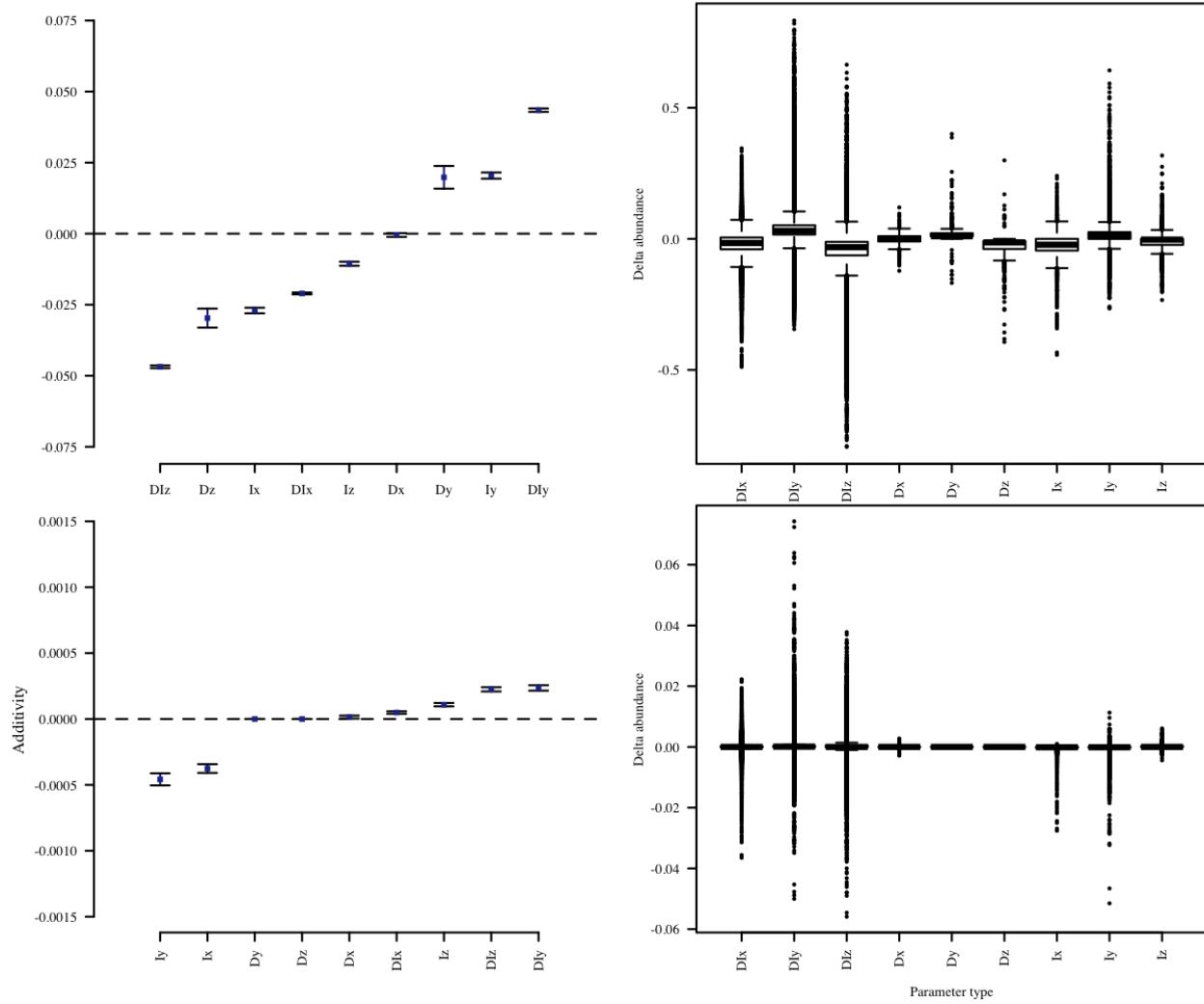


Figure 8: Direct vs indirect effects

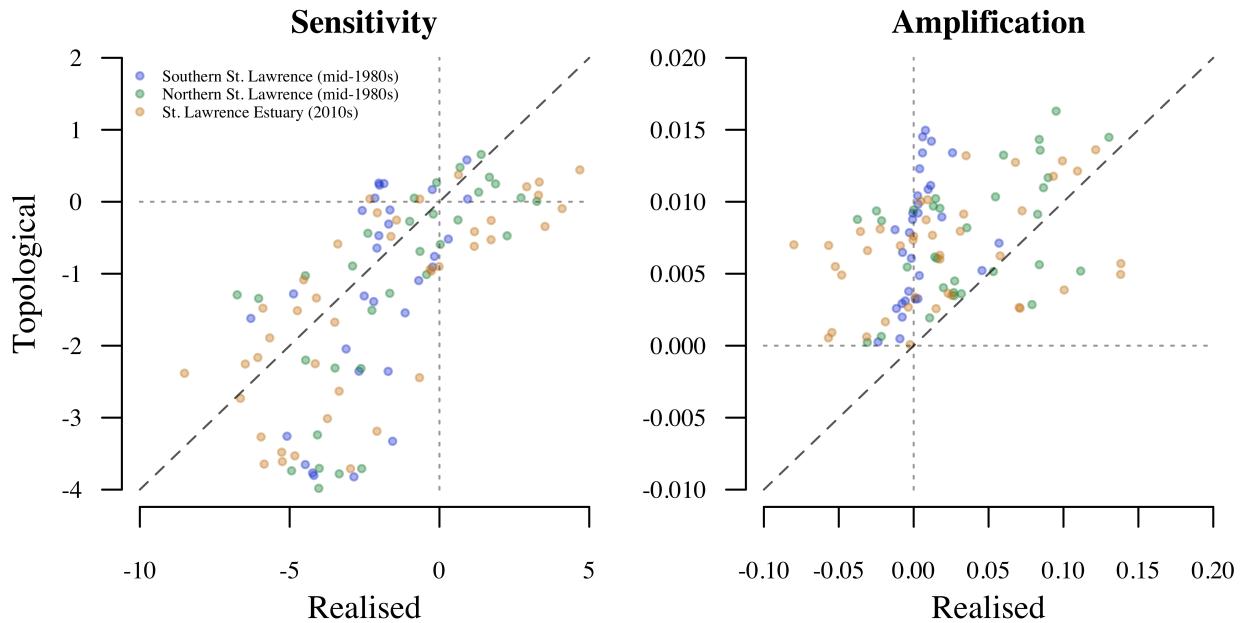


Figure 9: Realised vs topological scores

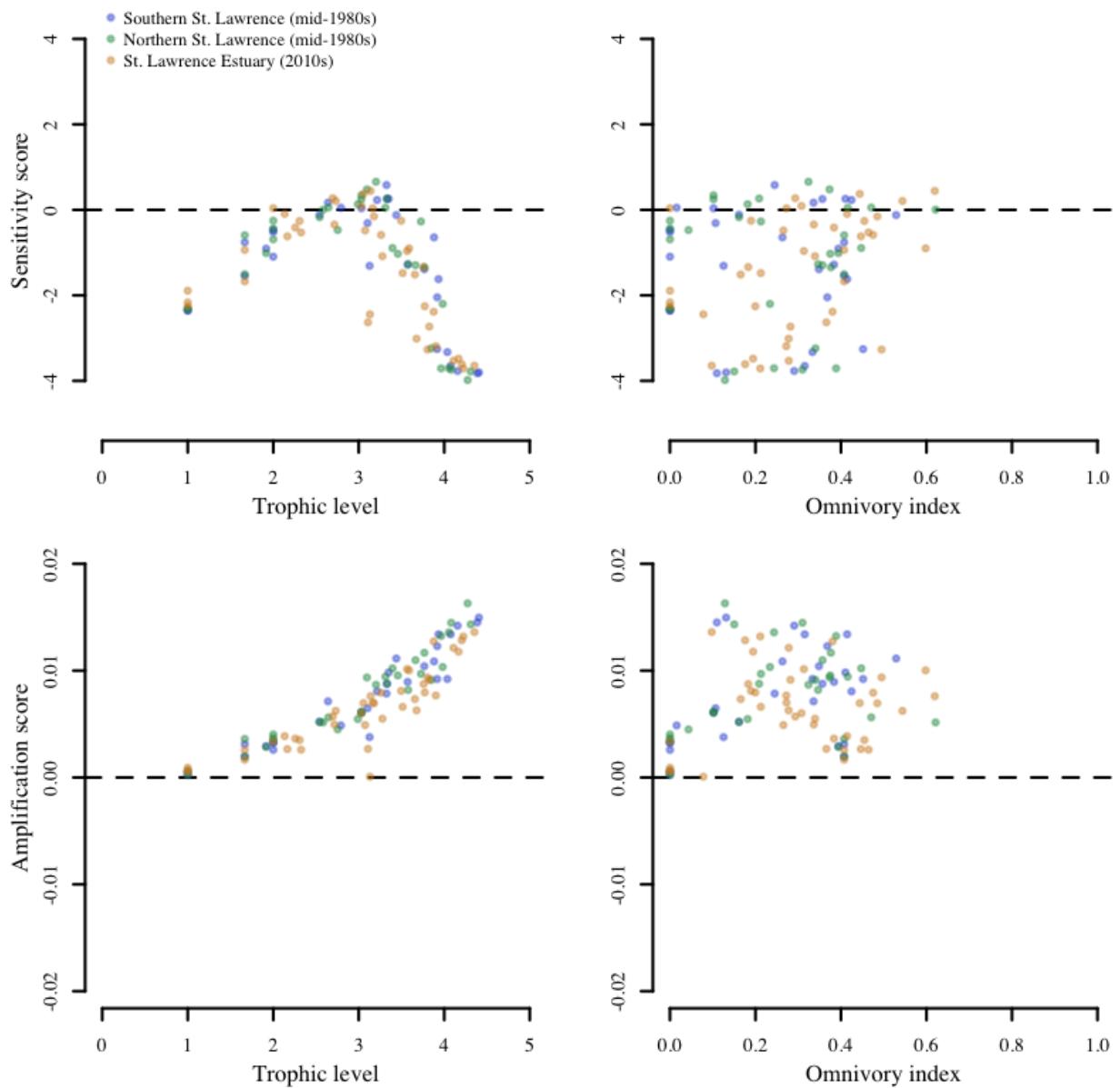


Figure 10: Sensitivity scores as a function of trophic level and omnivory index

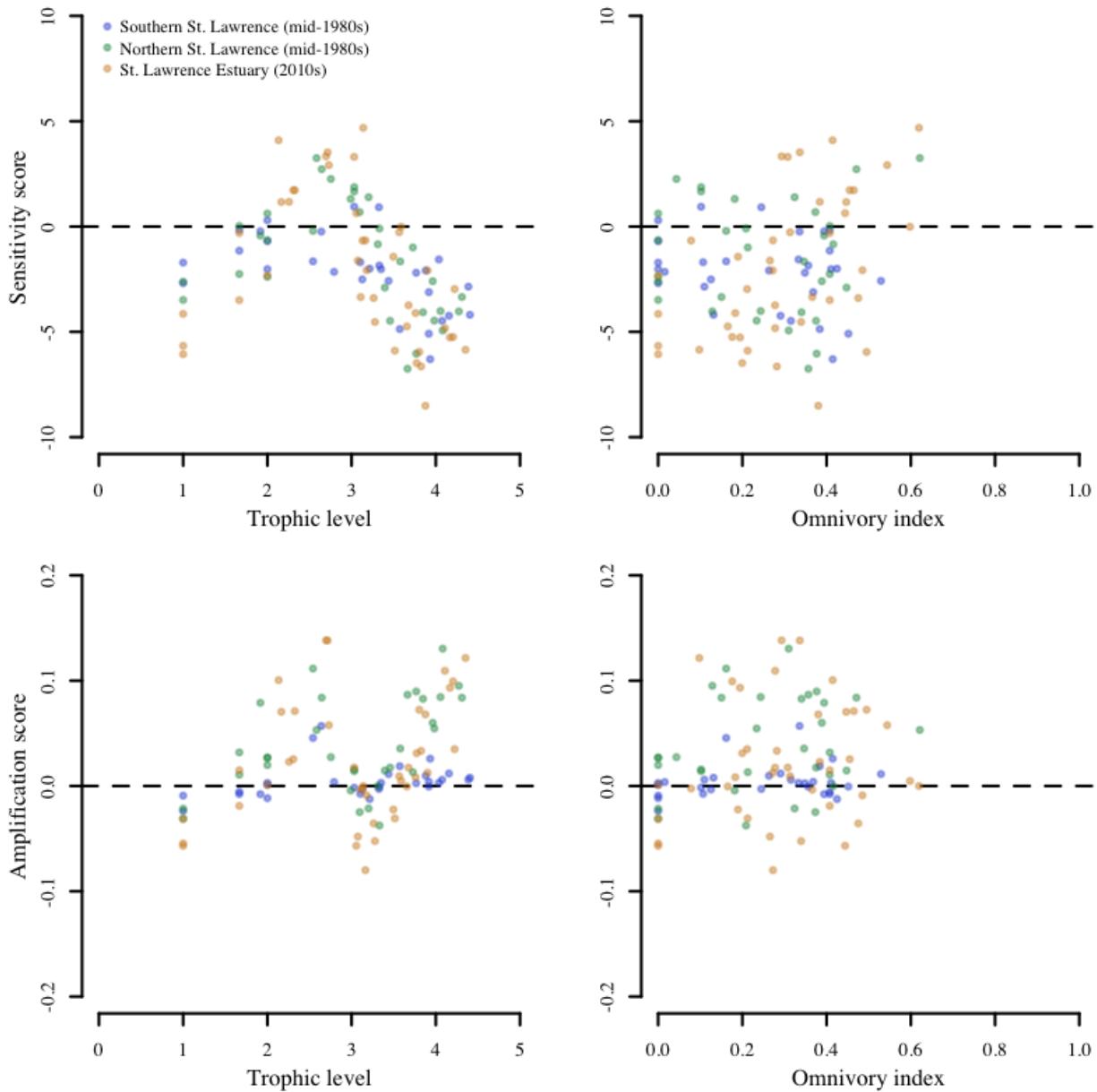


Figure 11: Impact scores as a function of trophic level and omnivory index

<sup>478</sup> **9 Supplementary Material**

<sup>479</sup> **9.1 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

480 **10 Next points**

- 481 • Non-linear effects in motifs  
482 • Species contribution to non-linear effects  
483 • Species profiles (frequency of times occupying roles that contribute to non-linear effects;  
484 see Stouffer *et al.* (2012))  
485 • Graphs to present these results  
486 • Methods

487 **11 Notes - to explore**

- 488 • With synergies, one should expect higher rates of community collapse, i.e. loss of  
489 species to extinction, because the effects increase more rapidly. Maybe look at Stouffer  
490 to better dissect their result on community persistence as a function of motifs. Perhaps  
491 they also explain which are the motif positions that tend to go extinct more rapidly?

492 **12 Interesting points**

- 493 • Effect limit (Schäfer & Piggott 2018): maximum effect size for a response (*e.g.* 100%  
494 mortality, zero growth or reproduction)

495 **13 Literature to cite - or at least look at!**

- 496 • Adams (2005)  
497 • Brown *et al.* (2013)  
498 • Brown *et al.* (2014)  
499 • Christensen *et al.* (2006)  
500 • Crain *et al.* (2008)  
501 • Darling *et al.* (2013)  
502 • Folt *et al.* (1999)  
503 • Galic *et al.* (2018) \*  
504 • Jackson *et al.* (2016)  
505 • Kath *et al.* (2018)  
506 • Lange *et al.* (2018)  
507 • Piggott *et al.* (2015)  
508 • Schäfer & Piggott (2018) \*  
509 • Segner *et al.* (2014)  
510 • Thompson *et al.* (2018a)  
511 • Thompson *et al.* (2018b)  
512 • Vinebrooke *et al.* (2004)

513 **14 References**

514 **15 Ecology Letters formatting and submission**

515 **15.1 Latex files**

516 **Instructions:** *Ecology Letters does not have a standard LaTex style file. Manuscripts sub-*  
517 *mitted using LaTeX should be accompanied by a PDF version of the paper. Upon final accep-*  
518 *tance for publication, authors will be requested to send their LaTeX source files accompanied*  
519 *by all figures in EPS or TIFF format and also any non-standard LaTeX style files used in*  
520 *the manuscript preparation.*

521 **15.2 Formatting**

- 522 • Numbered pages
- 523 • Text:
  - 524 – Double-spaced
  - 525 – No hyphenation
  - 526 – No automatic wordwrap
- 527 • Tables
  - 528 – As MS Excel or MS Word or equivalent
  - 529 – Cited consecutively in the text
  - 530 – Numbered with Arabic numerals
  - 531 – Grouped together at the end od the paper or in a separate file
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  - 533 – Clearly indicate units for each entries in the table
  - 534 – Footnotes to tables hsould be identified by the symbols \* † ‡ § ¶ (in that order)
  - 535 – and placed at the bottom of the table.
  - 536 – No vertical rules should be used
- 537 • Figures
  - 538 – Cited consecutively in the text
  - 539 – Numbered with Arabic numerals
  - 540 – Grouped together at the end od the paper or in a separate file
  - 541 – Titles and typed double-spaced on a separate sheet
  - 542 – Line and combination figures should preferably be submitted in vector graphics
  - 543 – format (e.g. either embedded as vector graphics in a Word document or saved
  - 544 – separately in PDF or eps format). If this is not possible, they should be saved
  - 545 – separately as pixel-based graphics at 600 dpi at the required print size, and they
  - 546 – should be saved in TIFF (not jpg) format or embedded as such in Word.

- 547 – Photographic figures should be saved at 300 dpi in TIFF format, or jpg format  
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553 must be large enough to allow for the necessary reduction. For full instructions on  
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555 and the electronic artwork guidelines.

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- 557 – Text boxes may be used for standalone definitions, equations, necessary explana-  
558 tions of concepts, a glossary (if needed only), and other items that disrupt the  
559 flow of the manuscript or where repeated reference to them is necessary. Text  
560 boxes can include equations and references (included in the main reference list),  
561 but not tables, figures or footnotes. Text boxes are limited to 750 words including  
562 a title. Items in text boxes that are not logically separate from the main text of  
563 the manuscript should be incorporated into the main text. A glossary should  
564 only be given if the language is complex enough that it may not be understood  
565 by the general readership of the journal or if requested by an editor for the jour-  
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568 manuscript and the text should begin with a short descriptive title, for instance  
569 “Box 1: Calculation of a trophic complexity index.”

570 • Scientific names

- 571 – The Latin names of each species should be given in full. Scientific names should  
572 be given priority in the text, with colloquial names in parentheses if desired.  
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574 unless these are very well known (e.g., *Homo sapiens*, *Drosophila melanogaster*,  
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576 identified, it must be cited. If fresh data are presented, the name of the taxonomist  
577 who identified the specimens should be given, as well as the name of the company  
578 or provider of the organisms (e.g., a culture collection or seed company) and/or the  
579 reference work used to make the identification. Lodgement of voucher specimens  
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581 and should be stated in the manuscript.

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599 nical Comments)
- 600 • the number of words in the abstract, the number of words in the main text (excluding  
601 abstract, acknowledgements, references, table and figure legends), and the number of  
602 words in each text box
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606 e-mail address) of the person to whom correspondence should be sent
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608 and will be printed at the end of the manuscript. This statement should be appropriate  
609 to the study described in the manuscript and should clarify who designed the study,  
610 who performed the research, who provided new methods or materials, and who wrote  
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616 be accepted, the data supporting the results will be archived in an appropriate public  
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618 the article.

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621 and Perspectives and Reviews and Syntheses.

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- 623 • (a)Introduction. The introduction should summarize briefly the background and aims,  
624 and end with a very brief statement of what has been achieved by the work.

- (b) Material and methods. This section should contain sufficient detail so that all procedures can be repeated (in conjunction with cited references). A checklist is provided so that authors can check that their methods report details which our editors regard as essential (please refer to the Checklist). Where specific equipment and materials are named, the manufacturer's name, city and country should be given (generally in parentheses after first mention).
- (c) Results. The Results section should present the experiments that support the conclusions to be drawn later in the Discussion. The Results section should conform to a high standard of rigour. Extended lines of inference, arguments or speculations should not be placed in the Results.
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- (e) Acknowledgements. Acknowledgements should be brief and concise.
- (f) References. See below for detailed information to in-text citations and Reference list.

#### 15.2.4 In-text citations

- Chronological order
- Fully, except if > 2 authors

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- 663 • “In press”: only permissible for papers that have been accepted for publication (documentary evidence of acceptance must be provided). Example: Vázquez, D.P. & Simberloff, D.  
664 (2003). Changes in interaction biodiversity induced by an introduced ungulate. *Ecol. Lett.*,  
665 in press (accepted). • “Personal communication”: Citation must be accompanied by the  
666 names of all persons concerned. Any person cited as the source of a ‘personal communication’  
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671 and remain usable in future decades. *Ecology Letters* requires, as a condition for  
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681 should be included in each Supporting Information file. It is published as supplied by the  
682 author, and a proof is not made available prior to publication; for these reasons, authors  
683 should provide any Supporting Information in the desired final format. - Include sensitivity  
684 and amplification score data?

685 Adams, S.M. (2005). Assessing cause and effect of multiple stressors on marine systems.  
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