

On the sensitivity of food webs to multiple disturbances

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

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

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

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

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

Correspondence:

David Beauchesne

david.beauchesne@uqar.ca

1 To do:

- ☒ Check and adjust for unique pathways of effect (exploitative and apparent competition).
 - They are all unique when you consider the position of the species, except for the disconnected motif.
- ☐ Think on the best way to establish position profile. At the moment what is used is the mean of individual pathways of effect per position, and I feel we could do better.
- ☐ Integrate (Hodgson et al., 2019) in the introduction
- ☐ 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. -> This will be discussed in this paper, and developed in the subsequent spatial paper
- ☐ Figure out methodology to evaluate species profile through two indices: sensitivity score and amplification score. These could be used to adjust Halpern's equation later on.
- ☐ Sensitivity and amplification scores for pathways of effect and motif positions, between [-1 1]
- ☐ Should the delta abundances (%) be divided by the delta parameter (%)?
- ☐ Should the median be used instead of the mean?
- ☐ Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frolicher, T.L., Lam, V.W.Y., Palomares, M.L.D., Watson, R., and Pauly, D. 2013. Shrinking of fishes exacerbates impacts of global ocean changes on marine ecosystems. Nature Climate Change 3: 254-258.
- ☐ Should the sensitivity score be divided by the number of unitary pathways disturbed?
- ☐ Uniformiser les indices dans les équations de l'article
- ☐ Modify the score for species using realised pathways of effects. I thought that this was done, but since we are not using probabilities, I'm not sure what I should be doing anymore with this. Ideally I would still use a probability and have a general function, but we might still want to keep this for the 4th chapter of the thesis.
- ☐ Verify all codes so that the proper equations are used
- ☐ Update thresholds used

2 Abstract

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

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

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

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

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

3 Introduction

3.1 Context

- **Global changes, multiple stressors and food webs**

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

- **Uncertainty associated with multiple stressors**

- Largest uncertainty in predicting environmental effects is the potential for complex driver interactions (Côté et al., 2016; Darling and Côté, 2008).
- Stressors can combine non-additively and result in effects that are greater (*i.e.* synergistic) or lower (*i.e.* antagonistic) than the sum of individual effects (Côté et al., 2016; Crain et al., 2008; Darling and Côté, 2008)
- Net effects of multiple stressors can be additive (*i.e.* joint effect equal to the sum of individual effects), synergistic (joint effect superior to the sum of individual effects), antagonistic (joint effect inferior to the sum of individual effects) or dominant (joint effect equal to an individual effect) (e.g. Crain et al., 2008; Côté et al., 2016; Darling and Côté, 2008).
- This is of particular significance for management, because we have mostly been operating under the assumption that stressors are mostly additive and thus can be managed independently.
- Maybe cite (Hodgson et al., 2019) (cite it for certain in the article).
- most research on driver effects in marine environments remains overwhelmingly focused on single driver assessments (O’Brien et al., 2019).

- **Limits of *in situ* and experimental approaches to study multiple disturbances**

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

- **Limited insights from null model testing**

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

- **Shift towards ecological modelling to better understand mechanisms**

- (De Laender, 2018; Schäfer and Piggott, 2018; Thompson et al., 2018a)

- **Some insights on the effects of disturbances on ecological communities from theoretical ecology**
 - Importance of interactions and web complexity
 - Indirect effects [Wootton (1993); Yodzis (2000); Wootton (2002); Montoya et al. (2009); ogorman2009]; see intro séminaire 1
 - Different types of interactions will lead to different overall effects (???).
 - * Different sensitivity for species involved in different types of interactions (segway to motifs)
 - How direct and indirect effects combine to affect food web sensitivity to disturbances
- **Theoretical has thus far mostly been concerned mostly with single disturbances and resistance of communities to extinctions**
 - Little insights into how different pathways of effect influences food webs, let alone pathways of multiple effects.
 - Little on the role of species and their interactions in propagating or buffering against disturbances

3.2 Objectives

1. Objective
2. Pathways of effect
3. Archetypes
4. Motifs
5. Terminology

- **State the objective**

- Here, we investigate the role of species in mediating the effects of multiple disturbances on food webs. We also seek to answer questions of particular significance for management: 1) should species interactions be considered in impact assessments, and 2) should the effects of stressors be evaluated separately or in combination?
- OR
- Here, we focus on evaluating the structural role of species and their trophic interactions in mediating food web sensitivity to multiple stressors. We also seek to answer questions of particular significance for management:
 - 1) should species interactions be considered in impact assessments, and
 - 2) should the effects of stressors be evaluated separately or in combination?

- **How we do this**

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

135 • **Transition to motifs**

136 – ...?

137 • **Motif description and use**

- 138 – A food web can be decomposed into a set of smaller n -species subgraphs called
139 motifs (Milo et al., 2004; Stouffer et al., 2007). For example, there are 13 distinct
140 3-species motifs composed of 30 unique positions (Stouffer et al., 2007, 2012).
141 Motifs are the backbone of food webs and their study has unearthed valuable
142 insights on community dynamics such as [...].
- 143 – Their type and frequency has been linked to food web stability and persistence
144 (???)
- 145 – Like many disturbance studies in theoretical ecology, however, these have focused
146 less on the dynamics of population abundances and more on the resistance of food
147 webs to extinctions.
- 148 – Motifs have been used to investigate the persistence of food web to species extinc-
149 tions (Stouffer and Bascompte, 2010) and the benefit associated to each species
150 in food web persistence (Stouffer et al., 2012).
- 151 – *The ecological role of a species in a network is a direct rest if its interactions with*
152 *other species (Luczkovich 2003; Olesen 2007; Allesina 2009) (in Stouffer 2012)*
- 153 – *The number and types of motifs that make up a food web are known to directly*
154 *affect the web's stability and persistence (Neutel 2002; Kondoh 2008; Allesina*
155 *2008; García-Domingo 2008; Stouffer 2010; in Stouffer 2012)*

156 • **Our focus**

- 157 – Here we focus on the most abundant types of interactions: omnivory, tri-trophic
158 food chain, exploitative competition and apparent competition (Camacho et al.,
159 2007; Stouffer and Bascompte, 2010)
- 160 – Two additional motifs, *i.e.* partially connected and disconnected were also consid-
161 ered in order to evaluate whether interactions in food webs are truly more likely
162 to be characterized by non-linear effects.
- 163 – To study the effects of multiple stressors in a trophic context, we rather focus on
164 the resulting disturbances following different pathways of effect rather than on
165 the disturbances themselves. This means that we will not investigate the effects
166 of multiple stressors applied to a single species in the food web. This precludes us
167 from investigating the sensitivity of species to each individual stressor. Rather,
168 we investigate the effects of disturbances to multiple species simultaneously. But
169 see Thompson et al. (2018b) and Thompson et al. (2018a) for a description of
170 a modelling approaching incorporating multiple sources of stress in a food web
171 model.
- 172 – We are interested in pathways that affect the trophic dynamic of food webs, *i.e.*
173 those that target population growth (*i.e.* birth and death rates) and the rates at
174 which species interact (*i.e.* attack and conversion rates).

175 • **Pathways of effect**

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

• Terminology for types of pathways and position profile

- Species can occupy different roles in these pathways of multiple effects. Investigating 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 multiple disturbances.
- We define 4 key roles in species propagating or buffering against multiple disturbances:

Role	Description	Mathematically	Example
Weak entry point	Species directly or indirectly more affected than expected	Synergistic effect on focal species	S_i in $\Delta i D_{i,j} \gg \Delta i D_i + \Delta i D_j$
Biotic multiplier	Species propagating disturbances	Peripheral species involved in synergistic effect	S_j in $\Delta i D_{i,j} \gg \Delta i D_i + \Delta i D_j$
Biotic sink	Species directly or indirectly affected less than expected	Antagonistic effect on focal species	S_i in $\Delta i D_{i,j} \ll \Delta i D_i + \Delta i D_j$
Biotic buffer	Species blocking the propagation of disturbances	Peripheral species involved in antagonistic effect	S_j in $\Delta i D_{i,j} \ll \Delta i D_i + \Delta i D_j$
Biotic dominant	Species whose individual effect dictates the response of other species	Focal or peripheral species driving dominance effect	S_j in $\Delta i D_{i,j} = \Delta i D_j$

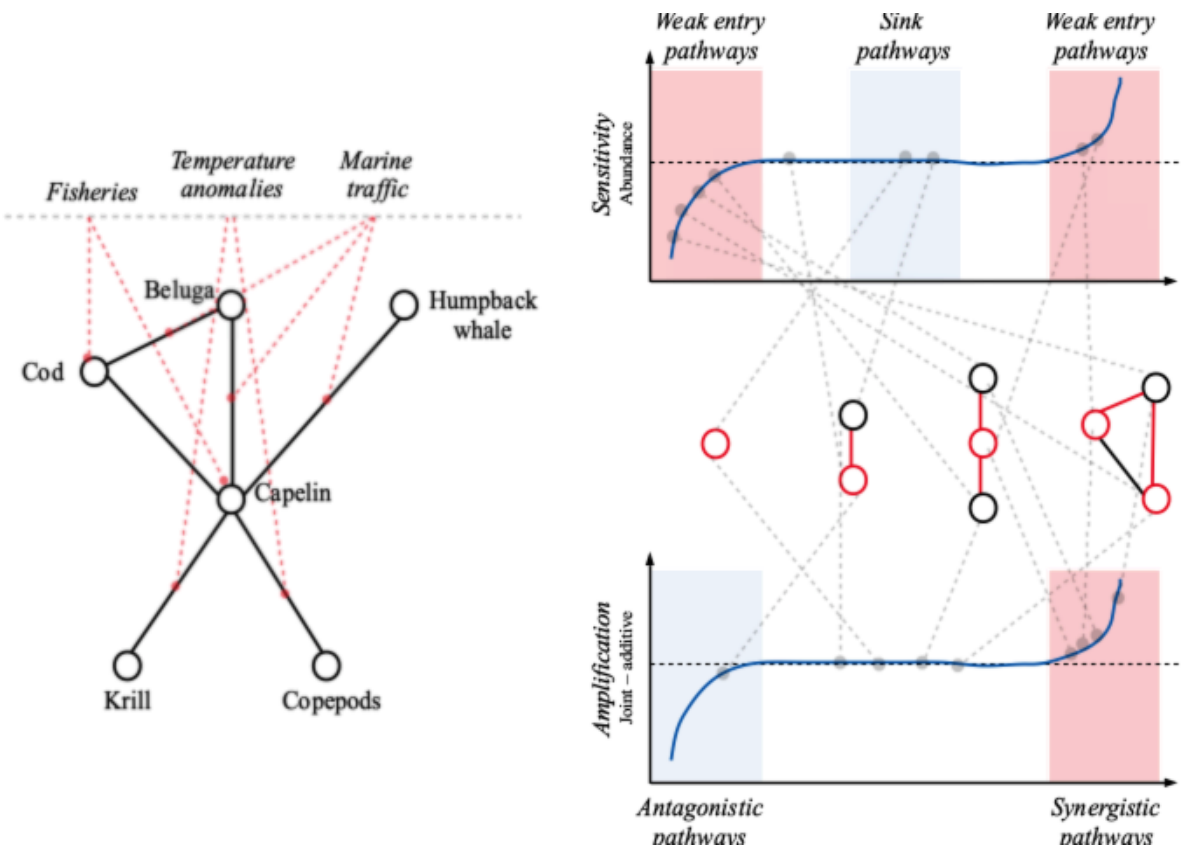


Figure 1: Conceptualize the effects of multiple disturbances on food webs

4 Methodology

4.1 Models

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

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

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

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

4.2 Disturbances

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

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

4.3 Trophic sensitivity

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

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

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

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

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

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

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

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

4.4 Trophic amplification

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

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

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

where K_j is a multivariate pathway of effect j and k_j are unitary pathways of effect composition j . The amplification score evaluates the deviance of a multivariate pathway of effect and the sum of the univariate effects composing the pathway of effect, *i.e.* the additive

model. Thus, a value of 0 identifies a null of additive effect, a value below 0 identifies an antagonistic effect, and a value over 0 identifies synergistic effects.

We define *antagonistic pathways* and *synergistic pathways* as those pathways whose effect on the abundance of a motif position is significantly different than the additive model, while *additive pathways* are those pathways whose effect is not significantly different than the additive model (1).

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

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

We define *biotic buffers* and *biotic multipliers* as positions whose amplification score is significantly different than 0, while *biotic invariants* are positions whose amplification score is not significantly different than 0 (1).

4.5 Species sensitivity and amplification

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

$$S_m = \sum_i f_m i S_i$$

$$A_m = \sum_i f_m i A_i$$

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

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

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

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

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

4.6 Empirical food webs

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

281 5 Results

282 5.1 Disturbances

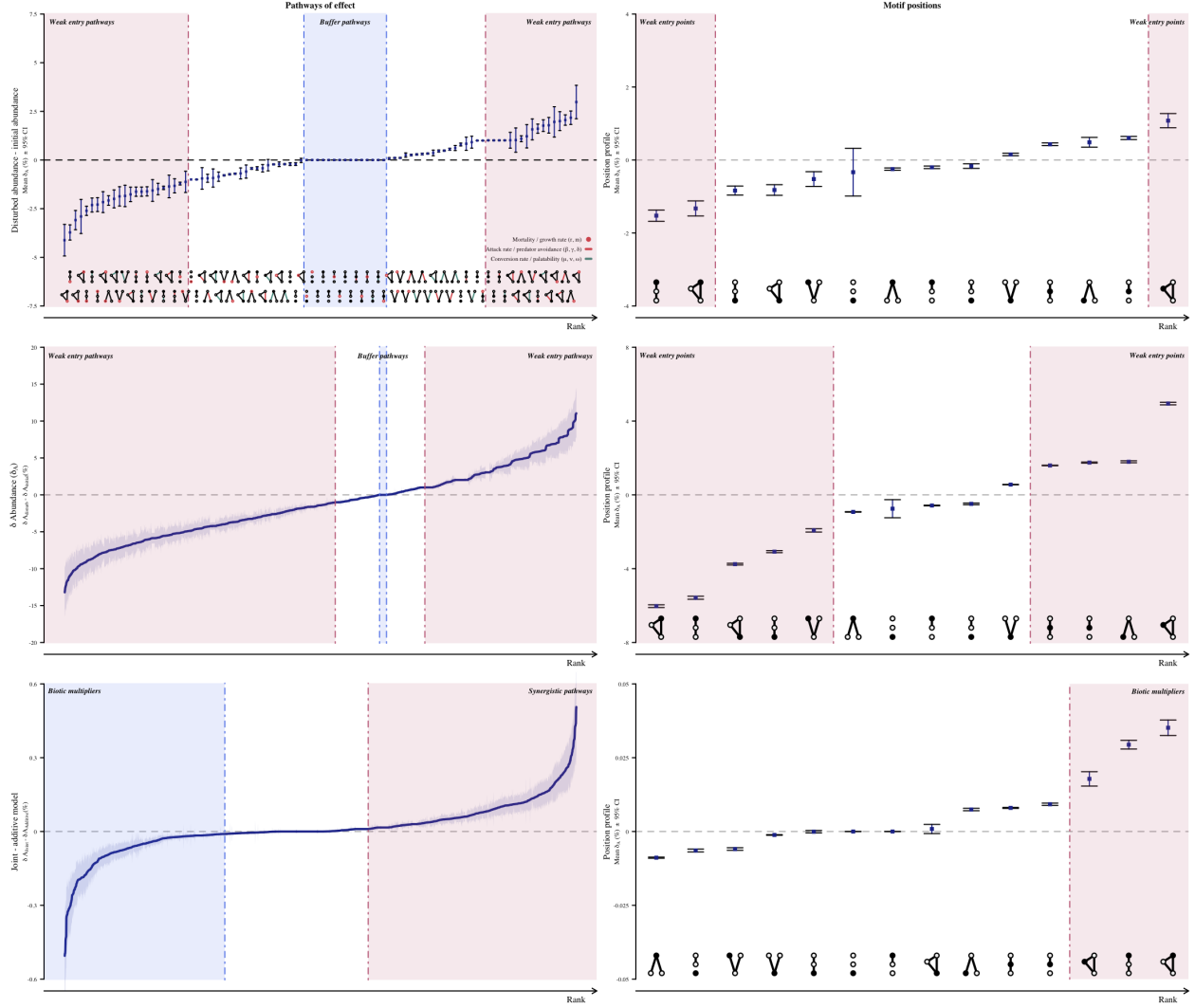


Figure 2: Disturbances. Line 1: Univariate disturbances; Line 2: Multivariate disturbances; Line 3: Joint - additive disturbances

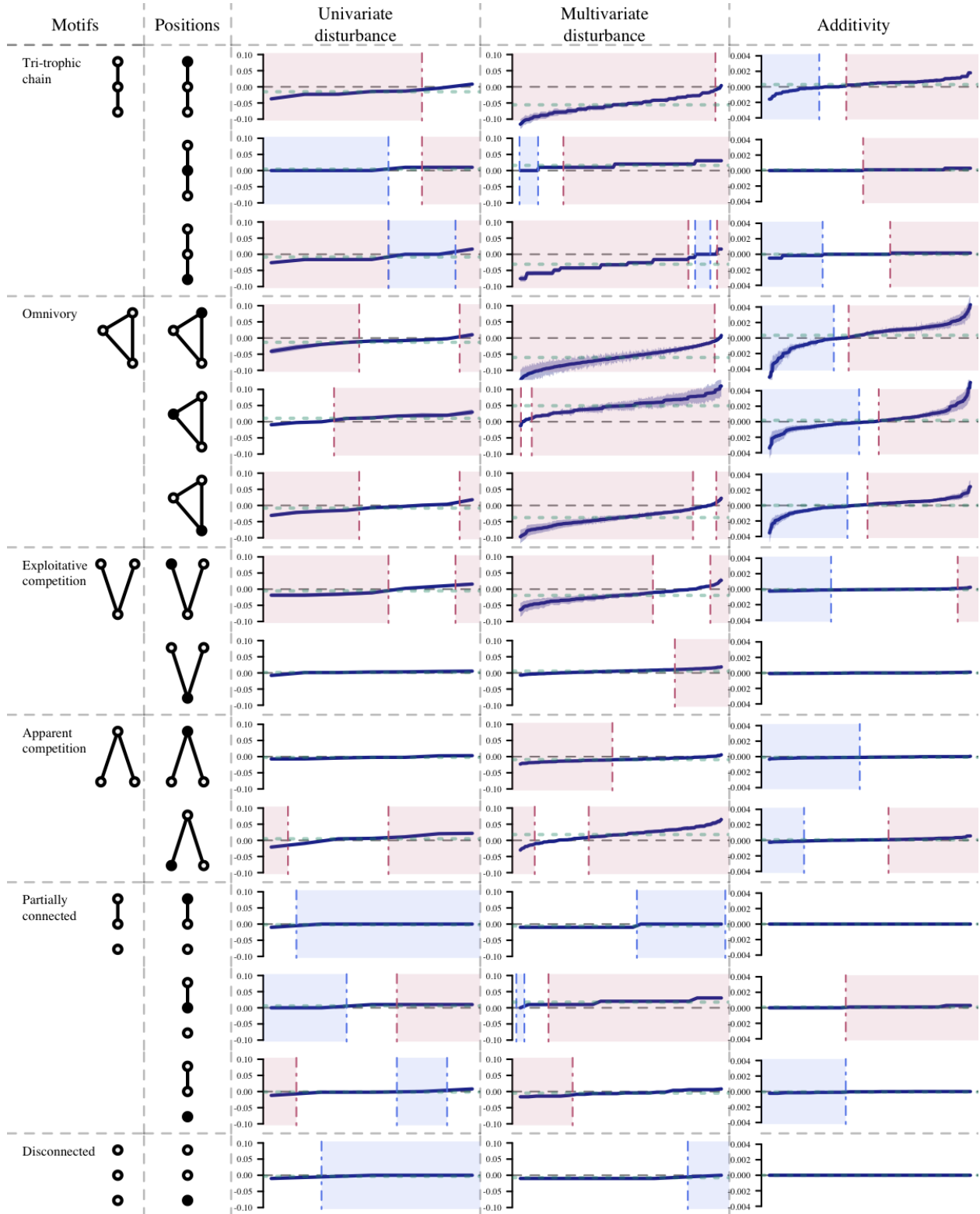


Figure 3: Morif positions and disturbances

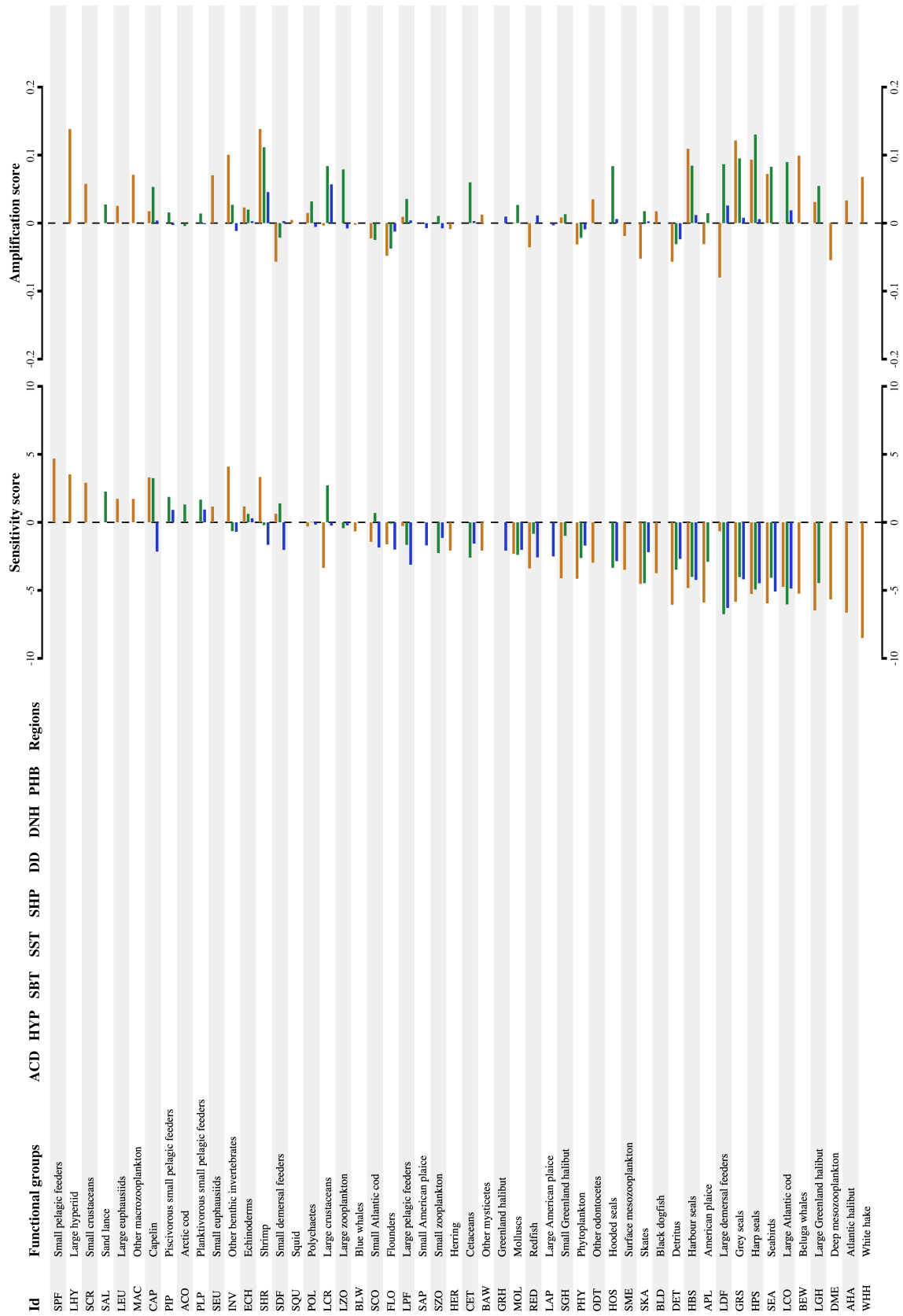


Figure 4: Species scores for the St. Lawrence

6 Supplementary Figures

6.1 Simulation figures

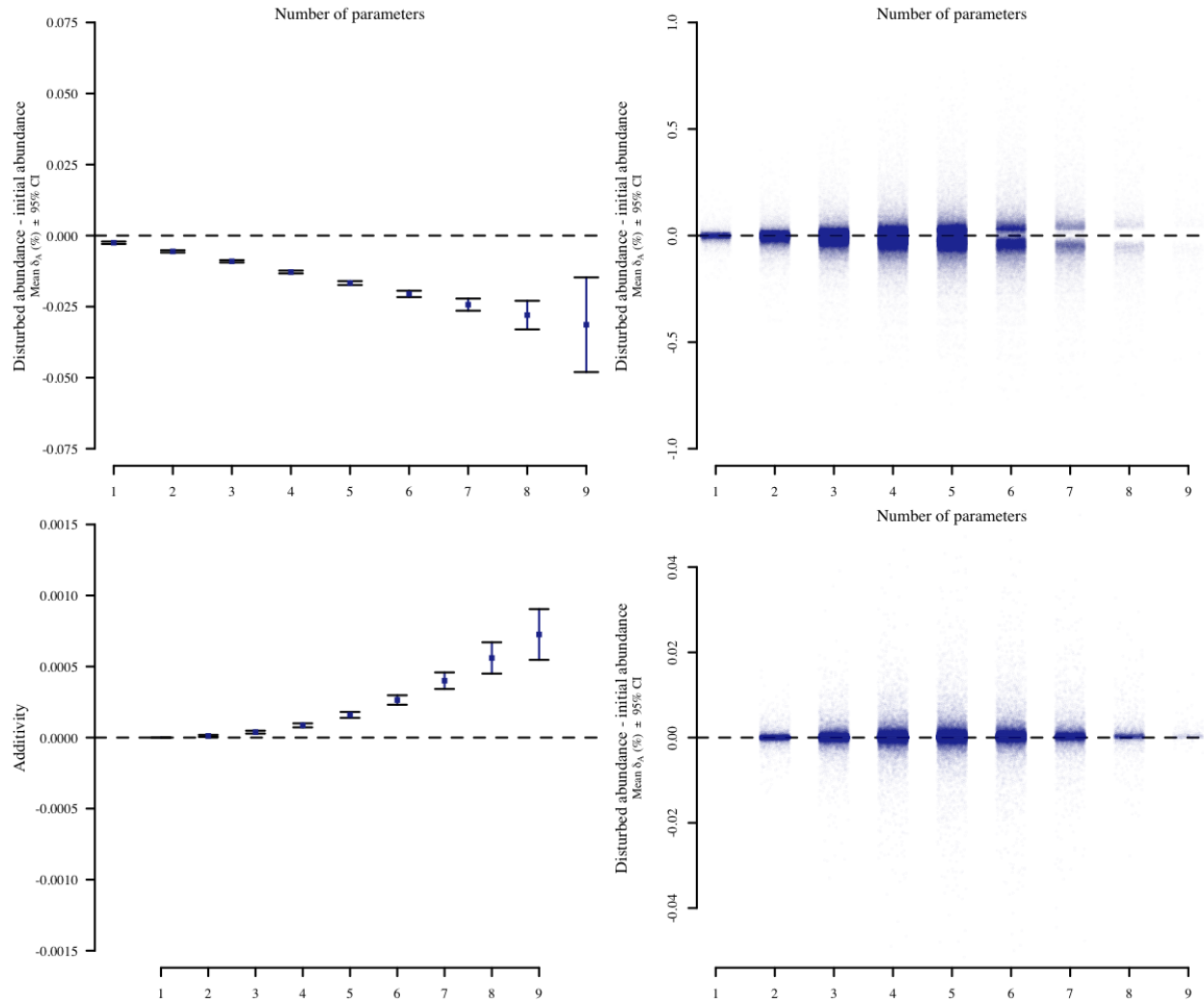


Figure 5: Mean delta abundance and difference between joint and additive models as a function of the number of parameters

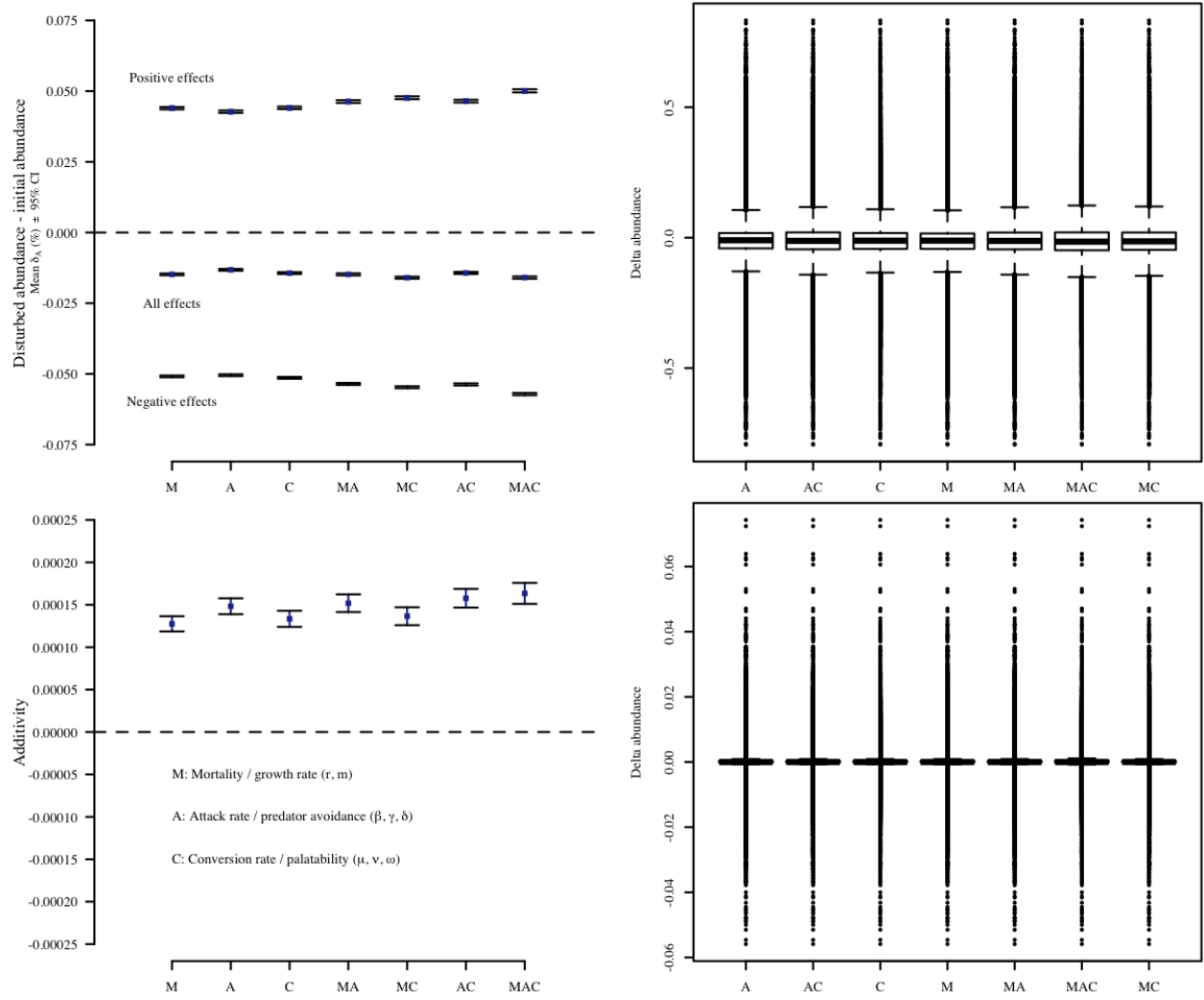


Figure 6: Mean delta abundance and difference between joint and additive models as a function of the types of parameters, i.e. growth/mortality rates, attack rates and conversion rates

6.2 Species position frequency

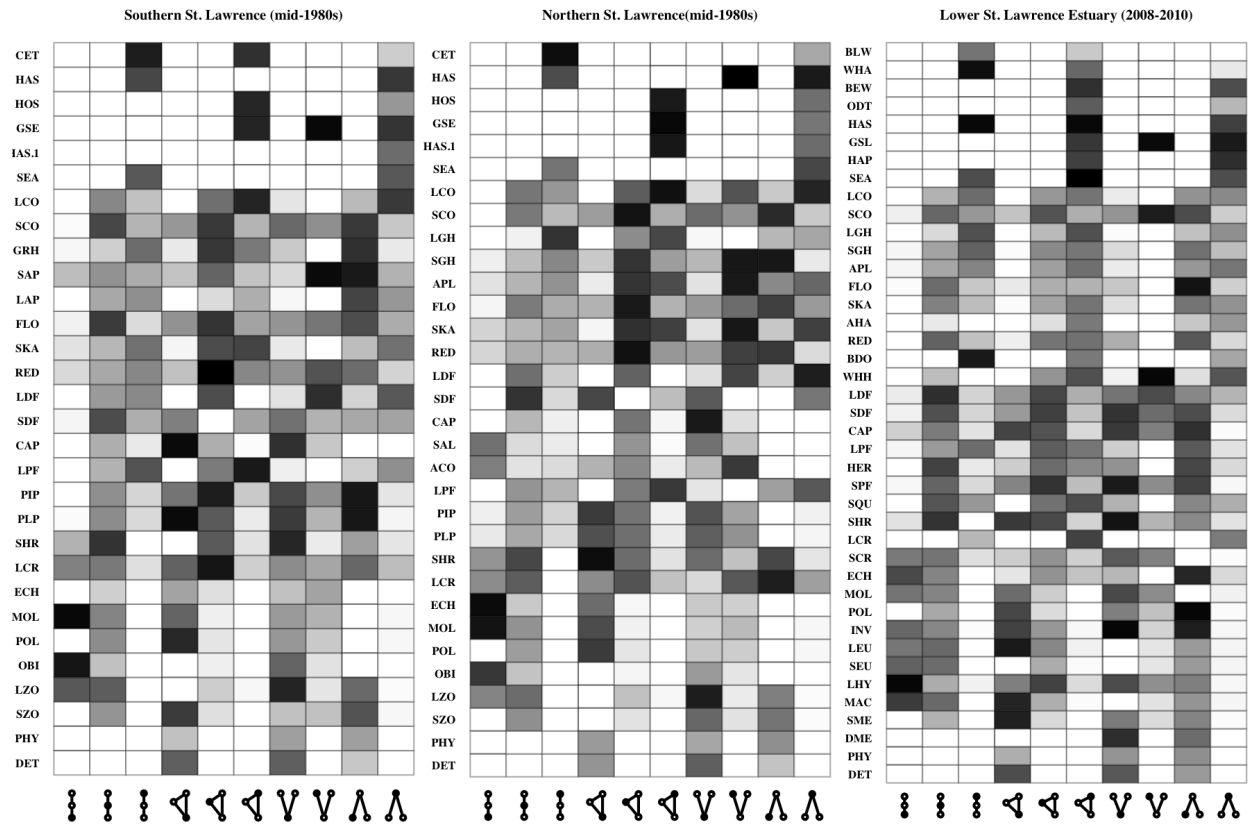


Figure 7: Frequency in which each species of three empirical food webs are found in each motif position.

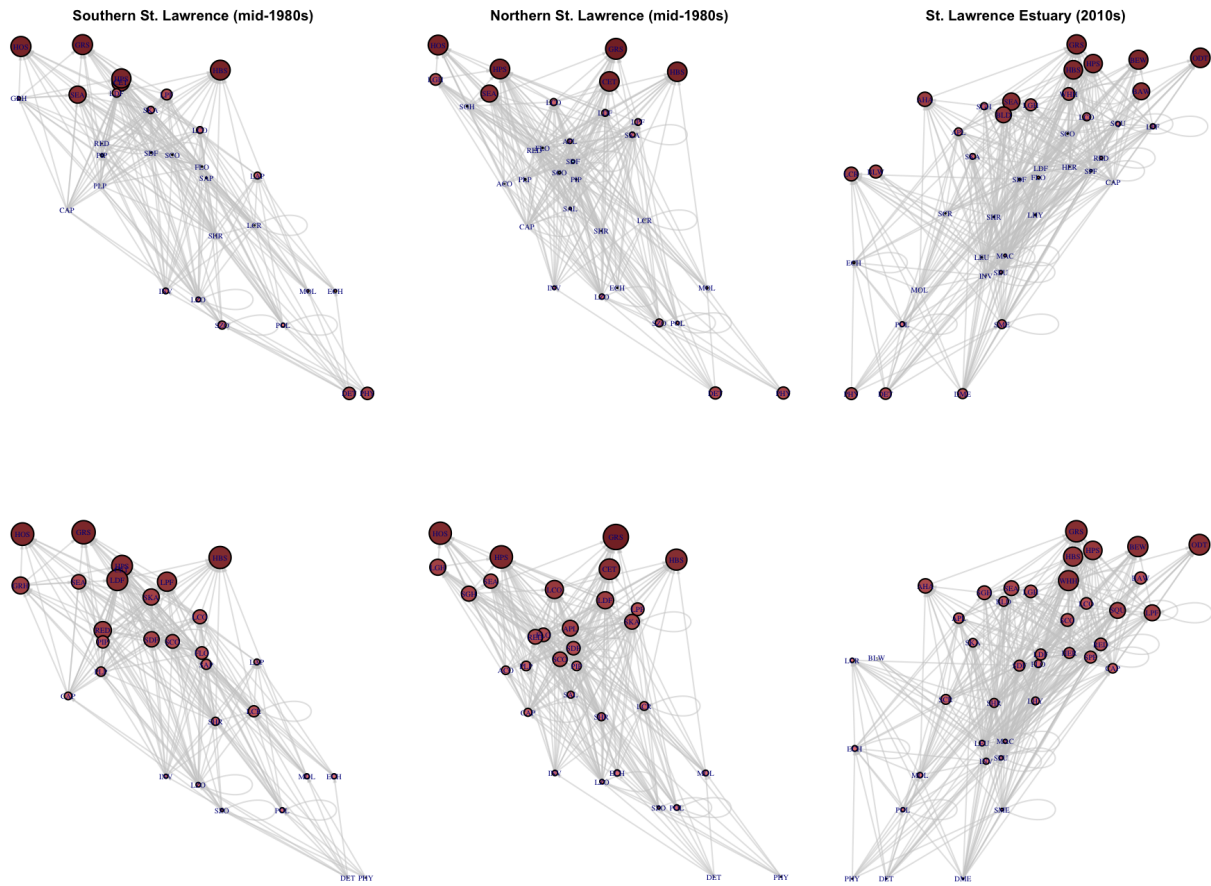


Figure 9: Sensitivity scores for species in the food webs of the southern St. Lawrence, northern St. Lawrence, and the estuary of St. Lawrence

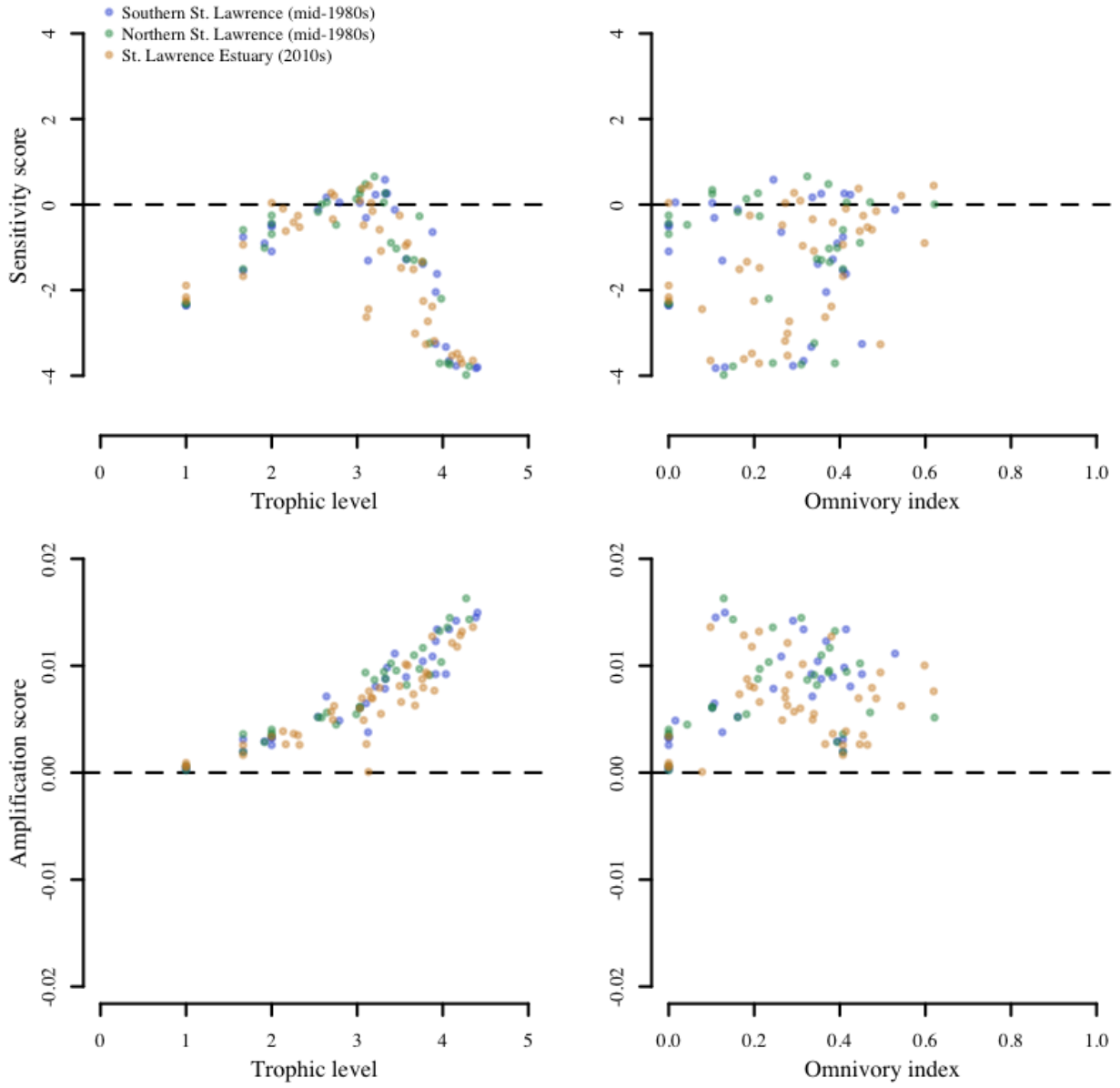


Figure 10: Sensitivity scores as a function of trophic level and omnivory index

6.4 Realised food web sensitivity and amplification scores

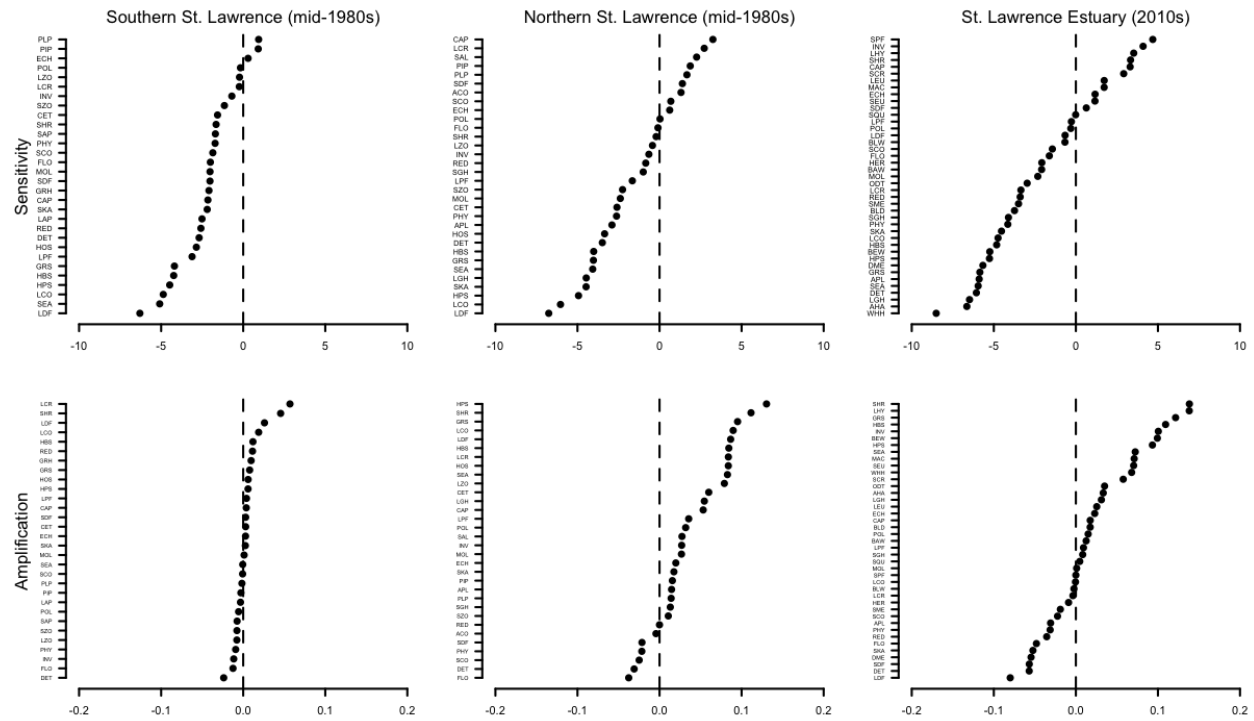


Figure 11: Impact scores for species in the food webs of the southern St. Lawrence, northern St. Lawrence, and the estuary of St. Lawrence

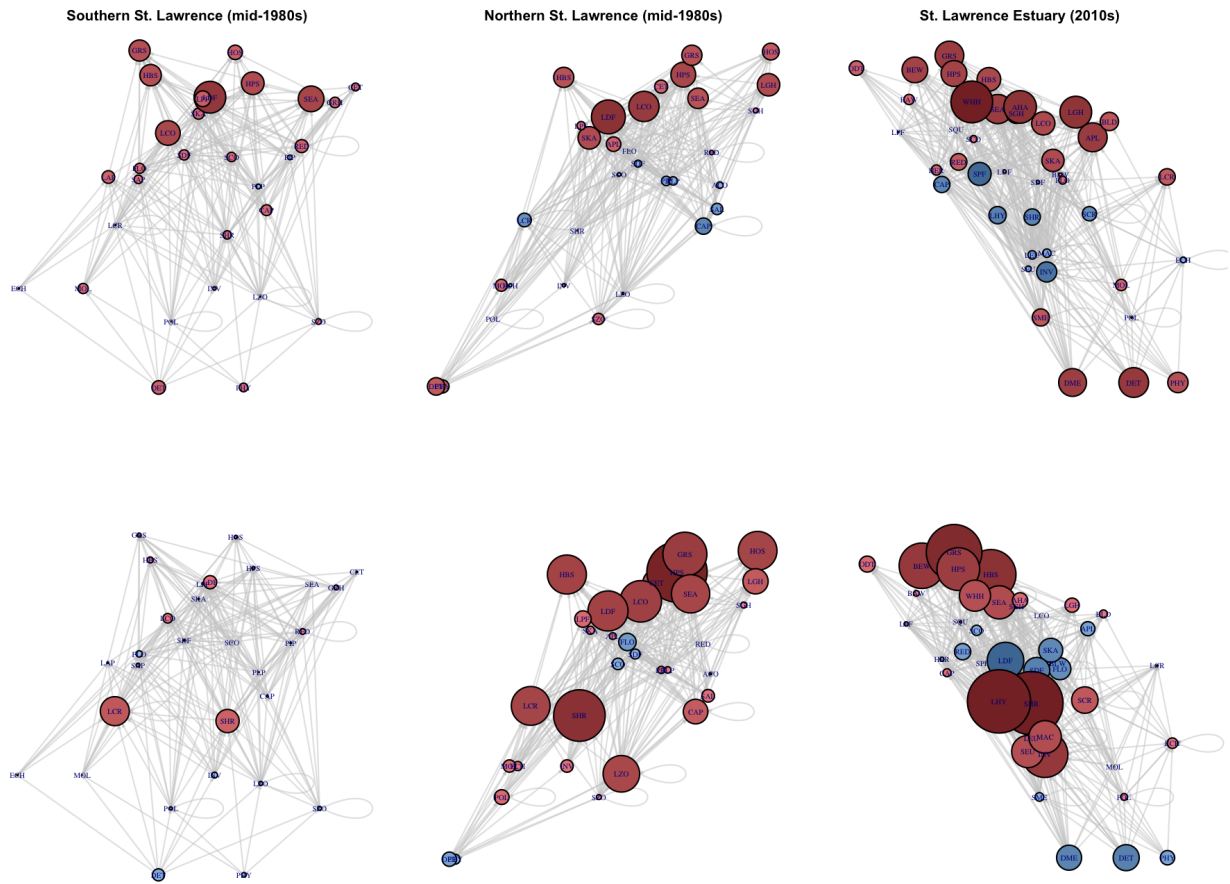


Figure 12: Sensitivity scores for species in the food webs of the southern St. Lawrence, northern St. Lawrence, and the estuary of St. Lawrence

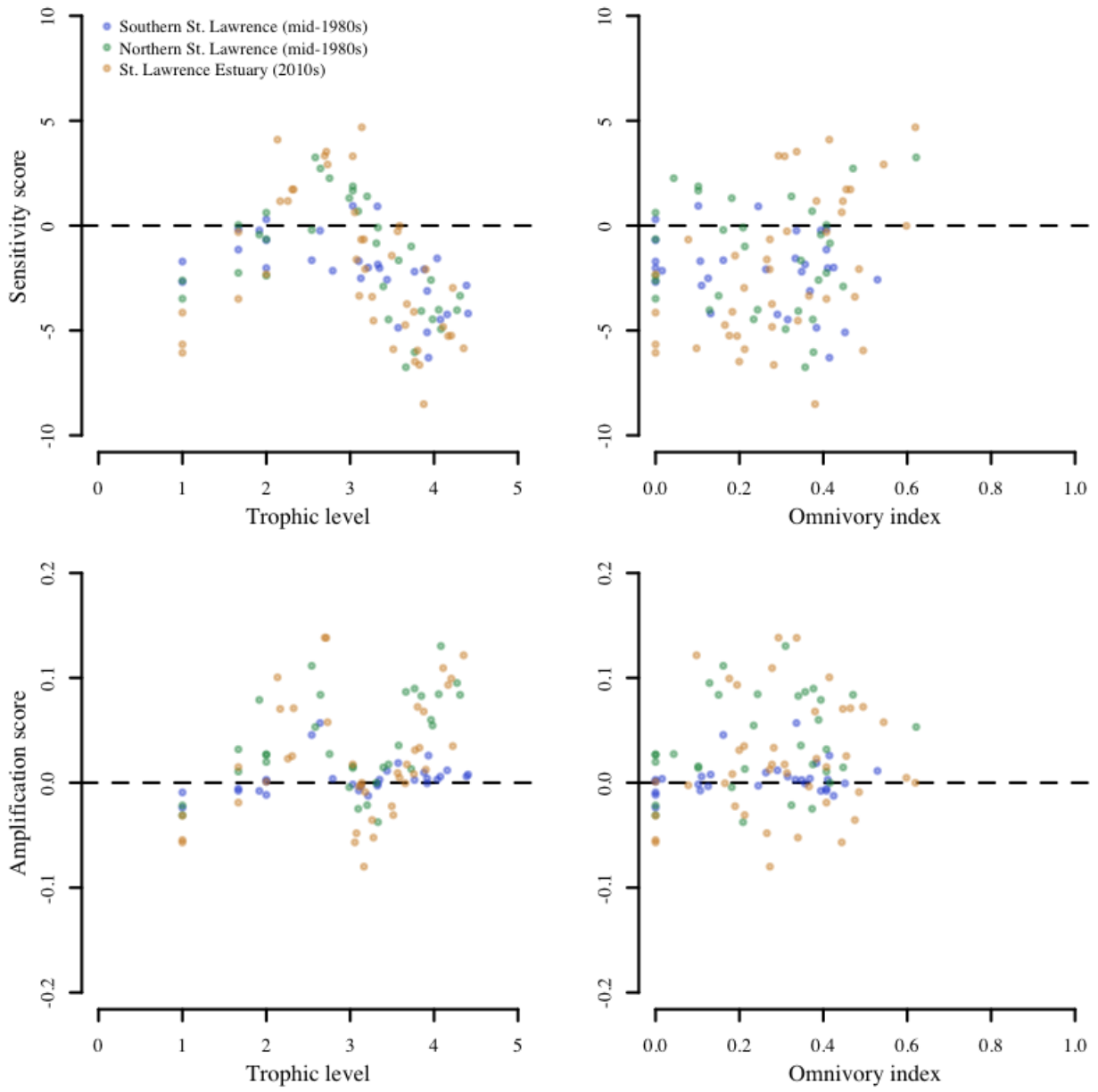


Figure 13: Impact scores as a function of trophic level and omnivory index

7 Supplementary Material

7.1 Models

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

Table 2: Systems of Lotka-Volterra equations used to model the effect of multiple disturbances

8 Next points

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

9 Notes - to explore

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

10 Interesting points

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

11 Literature to cite - or at least look at!

- Adams (2005)
- Brown et al. (2013)
- Brown et al. (2014)
- Christensen et al. (2006)
- Crain et al. (2008)
- Darling et al. (2013)
- Folt et al. (1999)
- Galic et al. (2018) *
- Jackson et al. (2016)
- Kath et al. (2018)
- Lange et al. (2018)
- Piggott et al. (2015)
- Schäfer and Piggott (2018) *
- Segner et al. (2014)
- Thompson et al. (2018a)
- Thompson et al. (2018b)
- Vinebrooke et al. (2004)

12 References

- Adams, S. M. (2005). Assessing cause and effect of multiple stressors on marine systems. *Marine Pollution Bulletin* 51, 649–657.
- Bascompte, J. (2009). Disentangling the Web of Life. *Science* 325, 416–419. doi:10.1126/science.1170749.
- Bowler, D., Bjorkmann, A., Dornelas, M., Myers-Smith, I., Navarro, L., Niamir, A., et al. (2019). The geography of the Anthropocene differs between the land and the sea. *bioRxiv*. doi:10.1101/432880.
- Brown, C. J., Saunders, M. I., Possingham, H. P., and Richardson, A. J. (2013). Managing for interactions between local and global stressors of ecosystems. *PloS one* 8, e65765.
- Brown, C. J., Saunders, M. I., Possingham, H. P., and Richardson, A. J. (2014). Interactions between global and local stressors of ecosystems determine management effectiveness in cumulative impact mapping. *Diversity and Distributions* 20, 538–546. doi:10.1111/ddi.12159.
- Camacho, J., Stouffer, D. B., and Amaral, L. A. N. (2007). Quantitative analysis of the local structure of food webs. *Journal of Theoretical Biology* 246, 260–268. doi:10.1016/j.jtbi.2006.12.036.
- Christensen, M. R., Graham, M. D., Vinebrooke, R. D., Findlay, D. L., Paterson, M. J., and Turner, M. A. (2006). Multiple anthropogenic stressors cause ecological surprises in boreal lakes. *Global Change Biology* 12, 2316–2322.
- Côté, I. M., Darling, E. S., and Brown, C. J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences* 283, 20152592. doi:10.1098/rspb.2015.2592.
- Crain, C. M., Kroeker, K., and Halpern, B. S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters* 11, 1304–1315. doi:10.1111/j.1461-0248.2008.01253.x.
- Darling, E. S., and Côté, I. M. (2008). Quantifying the evidence for ecological synergies. *Ecology Letters* 11, 1278–1286. doi:10.1111/j.1461-0248.2008.01243.x.
- Darling, E. S., McClanahan, T. R., and Côté, I. M. (2013). Life histories predict coral community disassembly under multiple stressors. *Global Change Biology* 19, 1930–1940. doi:10.1111/gcb.12191.
- De Laender, F. (2018). Community-and ecosystem-level effects of multiple environmental change drivers: Beyond null model testing. *Global change biology* 24, 5021–5030.
- Folt, C. L., Chen, C. Y., Moore, M. V., and Burnaford, J. (1999). Synergism and antagonism among multiple stressors. *Limnology and oceanography* 44, 864–877.
- Galic, N., Sullivan, L. L., Grimm, V., and Forbes, V. E. (2018). When things don’t add up: Quantifying impacts of multiple stressors from individual metabolism to ecosystem processing. *Ecology Letters* 21, 568–577. doi:10.1111/ele.12923.

- Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., et al. (2015). Spatial and temporal changes in cumulative human impacts on the world’s ocean. *Nature Communications* 6. doi:10.1038/ncomms8615.
- Hodgson, E. E., Halpern, B. S., and Essington, T. E. (2019). Moving Beyond Silos in Cumulative Effects Assessment. *Frontiers in Ecology and Evolution* 7. doi:10.3389/fevo.2019.00211.
- Jackson, M. C., Loewen, C. J. G., Vinebrooke, R. D., and Chimimba, C. T. (2016). Net effects of multiple stressors in freshwater ecosystems: A meta-analysis. *Global Change Biology* 22, 180–189. doi:10.1111/gcb.13028.
- Kath, J., Thomson, J. R., Thompson, R. M., Kefford, B. J., Dyer, F. J., and Mac Nally, R. (2018). Interactions among stressors may be weak: Implications for management of freshwater macroinvertebrate communities. *Diversity and Distributions* 24, 939–950.
- Lange, K., Bruder, A., Matthaei, C. D., Brodersen, J., and Paterson, R. A. (2018). Multiple-stressor effects on freshwater fish: Importance of taxonomy and life stage. *Fish and Fisheries* 19, 974–983.
- Milo, R., Itzkovitz, S., Kashtan, N., Levitt, R., Shen-Orr, S., Ayzenshtat, I., et al. (2004). Superfamilies of Evolved and Designed Networks. *Science* 303, 1538–1542. doi:10.1126/science.1089167.
- Montoya, J., Woodward, G., Emmerson, M. C., and Solé, R. V. (2009). Press perturbations and indirect effects in real food webs. *Ecology* 90, 2426–2433. doi:10.1890/08-0657.1.
- O’Brien, A. L., Dafforn, K. A., Chariton, A. A., Johnston, E. L., and Mayer-Pinto, M. (2019). After decades of stressor research in urban estuarine ecosystems the focus is still on single stressors: A systematic literature review and meta-analysis. *Science of The Total Environment*. doi:10.1016/j.scitotenv.2019.02.131.
- Piggott, J. J., Townsend, C. R., and Matthaei, C. D. (2015). Reconceptualizing synergism and antagonism among multiple stressors. *Ecology and Evolution* 5, 1538–1547. doi:10.1002/ece3.1465.
- Schäfer, R. B., and Piggott, J. J. (2018). Advancing understanding and prediction in multiple stressor research through a mechanistic basis for null models. *Global Change Biology* 24, 1817–1826. doi:10.1111/gcb.14073.
- Segner, H., Schmitt-Jansen, M., and Sabater, S. (2014). *Assessing the impact of multiple stressors on aquatic biota: The receptor’s side matters*. ACS Publications.
- Stouffer, D. B., and Bascompte, J. (2010). Understanding food-web persistence from local to global scales. *Ecology Letters* 13, 154–161. doi:10.1111/j.1461-0248.2009.01407.x.
- Stouffer, D. B., Camacho, J., Jiang, W., and Nunes Amaral, L. A. (2007). Evidence for the existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences* 274, 1931–1940. doi:10.1098/rspb.2007.0571.
- Stouffer, D. B., Sales-Pardo, M., Sirer, M. I., and Bascompte, J. (2012). Evolutionary Conservation of Species’ Roles in Food Webs. *Science* 335, 1489–1492. doi:10.1126/science.1216556.

400 Thompson, P. L., MacLennan, M. M., and Vinebrooke, R. D. (2018a). An improved null
401 model for assessing the net effects of multiple stressors on communities. *Global change biology*
402 24, 517–525.

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

406 Vinebrooke, R. D., Cottingham, K. L., Scheffer, J. N., Marten, Dodson, S. I., Maberly,
407 S. C., and Sommer, U. (2004). Impacts of multiple stressors on biodiversity and ecosys-
408 tem functioning: The role of species co-tolerance. *Oikos* 104, 451–457. doi:10.1111/j.0030-
409 1299.2004.13255.x.

410 Wootton, J. T. (1993). Indirect Effects and Habitat Use in an Intertidal Community:
411 Interaction Chains and Interaction Modifications. *The American Naturalist* 141, 71–89.
412 doi:10.1086/285461.

413 Wootton, J. T. (2002). Indirect effects in complex ecosystems: Recent progress and future
414 challenges. *Journal of Sea Research* 48, 157–172. doi:10.1016/S1385-1101(02)00149-1.

415 Yodzis, P. (2000). Diffuse Effects in Food Webs. *Ecology* 81, 261–266. doi:10.1890/0012-
416 9658(2000)081[0261:DEIFW]2.0.CO;2.