On the sensitivity of food webs to multiple disturbances

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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.

☐ Figure out methology 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?

2 INDEX

Kevin Cazelles Admettons qu'on est, for a given species:

$$P_{i,j} = P_{positioni,motif,i}$$

Then we can define the expected departure/deviance from the additive model, $\bar{D}_a$ as follows:

$$P_{i,j} = \sum_{i,j} D_{a,i,j} P_{positioni,motif,i}$$

where $D_{a,i,j}$ is the departure/deviance from the additive model in motif i at postilion j as defined elsewhere.

Tu peux faire ça pour les 2 différentes mesure. Mais ça implique d'avoir les probas! Ça se fait j'imagine, en tout cas on devrais être capable de le faire au moins en simulation.

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 mutliple 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 mecanisms underlying non-additive stressor effects (De Laender, 2018).

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

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

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- **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 seperately 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 seperately 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.

4

- **Transition to motifs**

  - ...?

- **Motif description and use**

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

- **Our focus**

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

- **Pathways of effect**

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

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

163   – Species can occupy different roles in these pathways of multiple effects. Inves-
164   tigating species profile (e.g.* Stouffer et al., 2012) could thus inform us on the
165   role played by individual species in buffering against or amplifying the effects of
166   multiple disturbances.
167   – We define 4 key roles in species propagating or buffering against multiple distur-
168   bances:

| Role	Description	Mathematically	Example
Weak entry point	Species directly or indirectly more affected than expected	Synergistic effect on focal species	S_i in $\Delta i \| D_{i,j} >> \Delta i \| D_i + \Delta i \| D_j$
Biotic multiplier	Species propagating disturbances	Peripheral species involved in synergistic effect	S_j in $\Delta i \| D_{i,j} >> \Delta i \| D_i + \Delta i \| D_j$
Biotic sink	Species directly or indirectly affected less than expected	Antagonistic effect on focal species	S_i in $\Delta i \| D_{i,j} << \Delta i \| D_i + \Delta i \| D_j$
Biotic buffer	Species blocking the propagation of disturbances	Peripheral species involved in antagonistic effect	S_j in $\Delta i \| D_{i,j} << \Delta i \| D_i + \Delta i \| D_j$
Biotic dominant	Species whose individual effect dictates the response of other species	Focal or peripheral species driving dominance effect	S_j in $\Delta i \| D_{i,j} = \Delta i \| D_j$
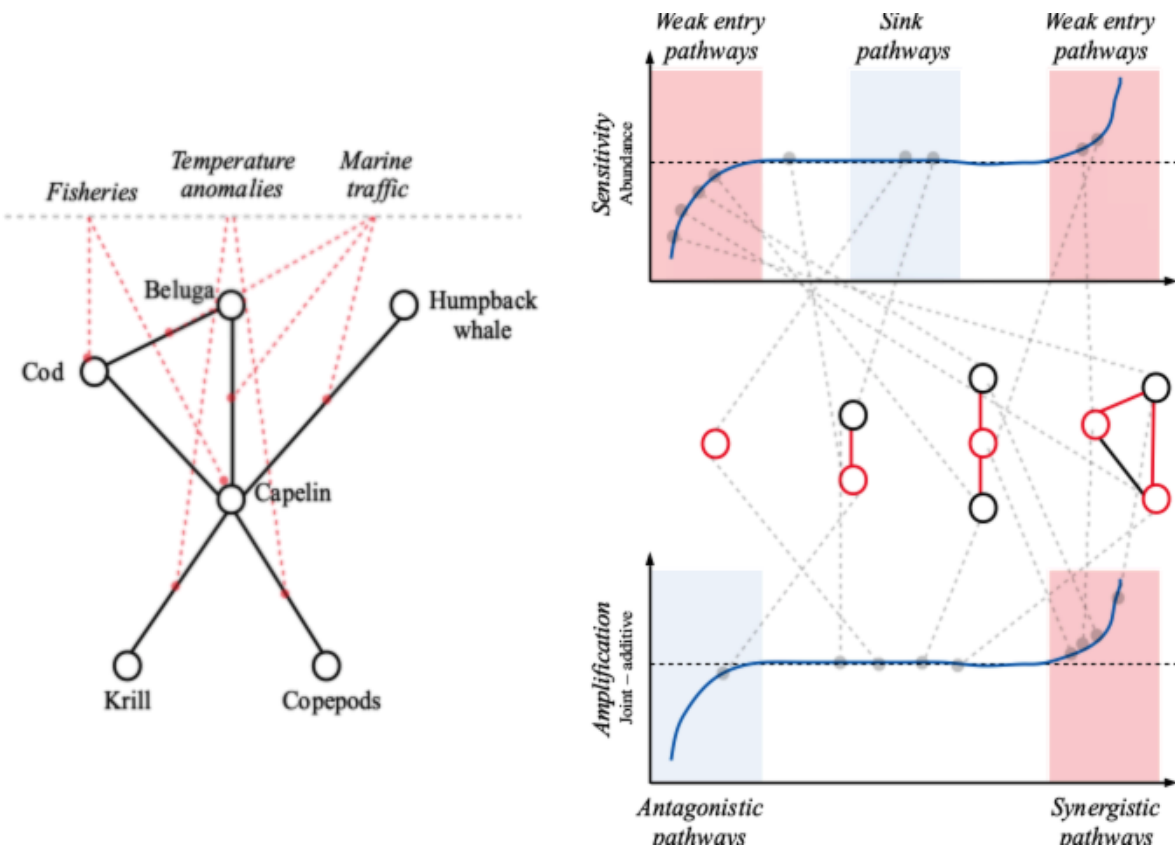
Figure 1: Conceptualize the effects of multiple disturbances on food webs

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-Voltera 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 resource and a predator and a prey interaction, and a fully disconnected motif with three independent species modelled as resources.

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 and predators were modeled with 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. e is a scaling parameter of the attack rate which cannot exceed 1, since 1 unit of resource biomass cannot be transformed into more than 1 unit of consumer biomass.

Models were solved at equilibrium since we wished to study the dynamics of the motifs in the context of persistent food webs, which is closer to reality. As no equilibrium exists for the exploitative competition motif with Lotka-Voltera models of these 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 and obtain equilibrium solutions. Sage (**???**) was used to solve all equation systems at equilibrium. All other analyses were performed using R (**???**). All code and data used to perform the simulations and analyses are available at [...].

Initial model parameter values for intrinsic growth (r) and resource density-dependence (α_{ii}) parameters were fixed to 1 and 0.001, respectively, to bound all 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.

4.2 Disturbances

Parameters selected to simulate disturbances were those related to population growth (r and m) and interaction rates (e and α_{ij}). Disturbances were simulated by applying a 1% variation on all combinations of selected model parameters to simulate all possible unique pathways of univariate and multivariate effects. Parameter variation were only applied as a simulation of stress, hence mortality rates were increased, while all other parameters were decreased by 1%.

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Parameter combinations resulted in between 7 (disconnected) and 511 (omnivory possible pathways of effect, for a total of 930 unique pathways of effects (*to check, I may be multiplying the number of unique pathways for exploitative and apparent competition*).

The sensitivity to disturbances was measured as percent change between the analytical abundance after parameter variation and the initial abundance, for each species and each pathway of effect. The amplication potential of pathways of multiple effects was measured as percent difference between the analytical abundance of the multivariate disturbance model and the sum of the univariate disturbance models. A value of 0 equals a null or additive effect, a value below 0 is a dominant or antagonistic effect, and a value over 0 is a synergistic effect.

4.3   Sensitivity and amplification scores

4.3.1   Pathways of effects

Sensitivity and amplification scores for individual pathways of effects, motif positions and motifs were evaluated by [. . .]

4.3.2   Motif positions

The sensitiivity score was calculated for each motif position by taking the mean absolute value of the percent abundance change between initial and disturbed models for all pathways of effect. This means that a value of 1 is a percent change in abundance equal to the percent change in parameter value to simulate a disturbance, a value below 1 is a percent abundance change lower than the simulated disturbance, and a value above 1 is a percent abundance change greater than the percent parameter change.

Similarly, the amplification score was measure by adding 1 to the difference between the joint model and the additive model, so that antagonistic and synergistic effects are centered on 1 rather than 0.

4.3.3   Food web

Single species sensitivity and amplification profiles were evaluated by multiplying the frequency at which they appear in each motif position by the sensitivity and amplification scores.

$$Score_{species} = Frequency * Sensititivity * Amplification$$

4.4   Empirical food webs

We used 5 food webs from the Estuary and Gulf of St. Lawrence
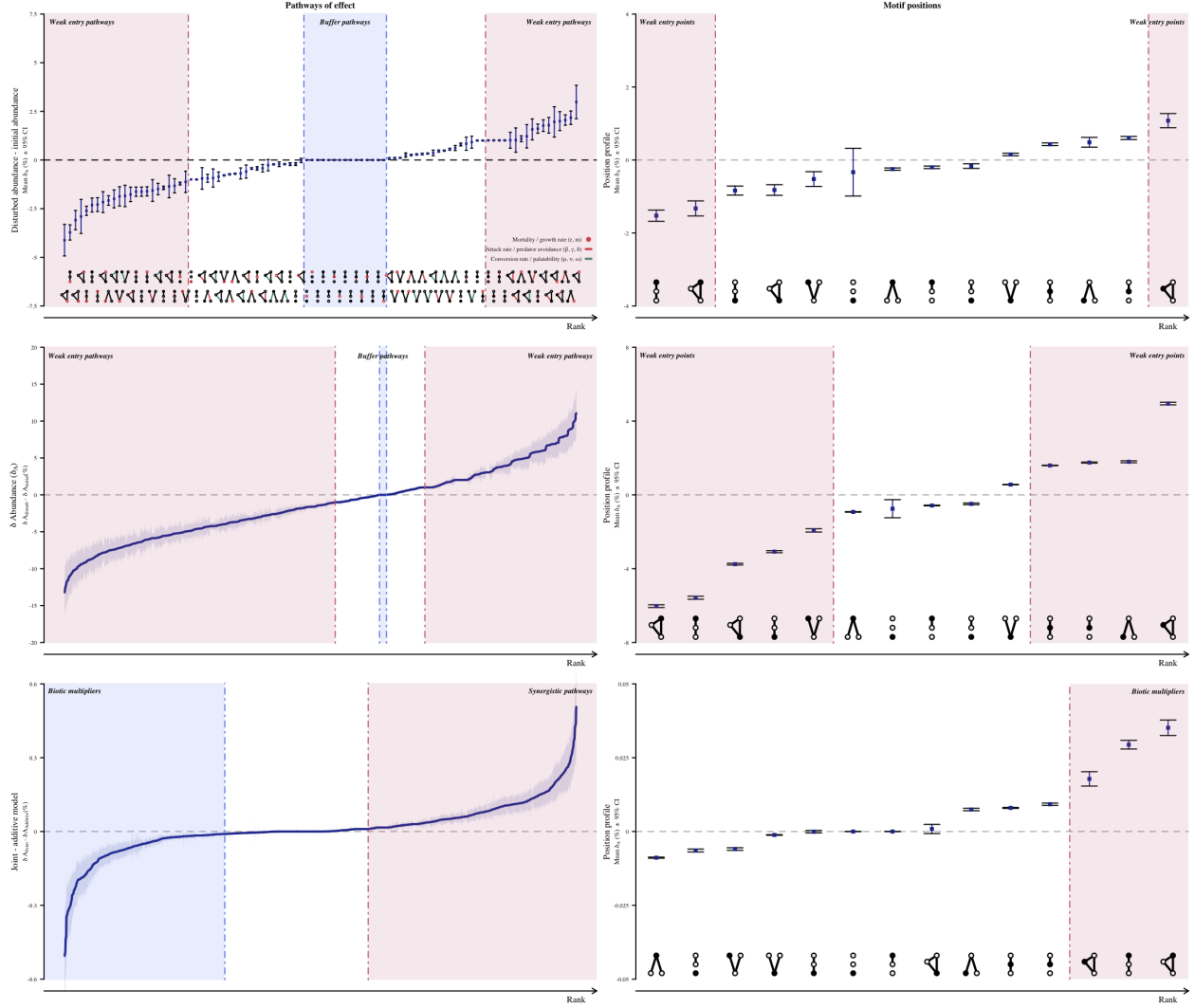
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5 Results

5.1 Disturbances

Figure 2: Disturbances. Line 1: Univariate disturbances; Line 2: Multivariate disturbances; Line 3: Joint - additive disturbances
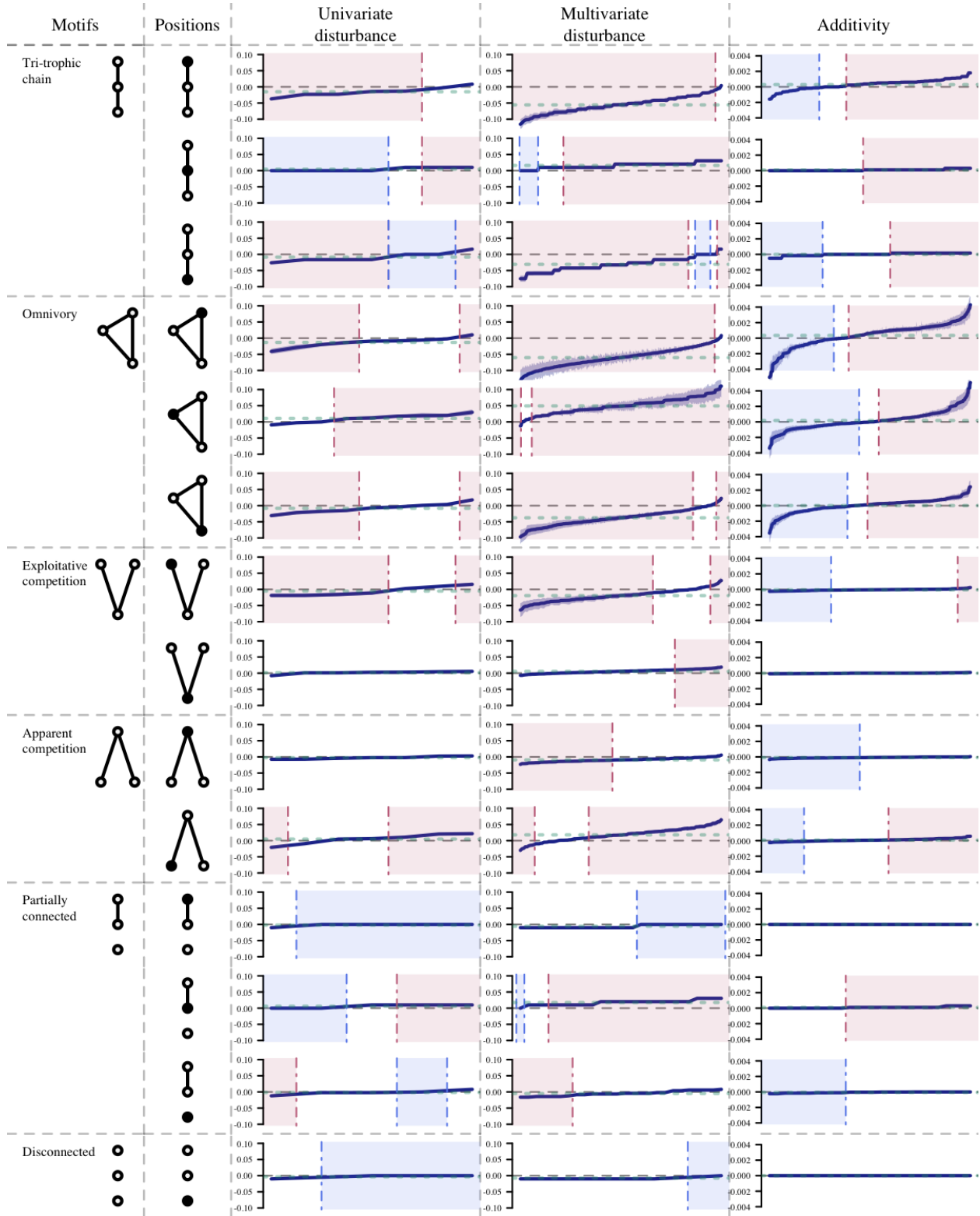
Figure 3: Morif positions and disturbances
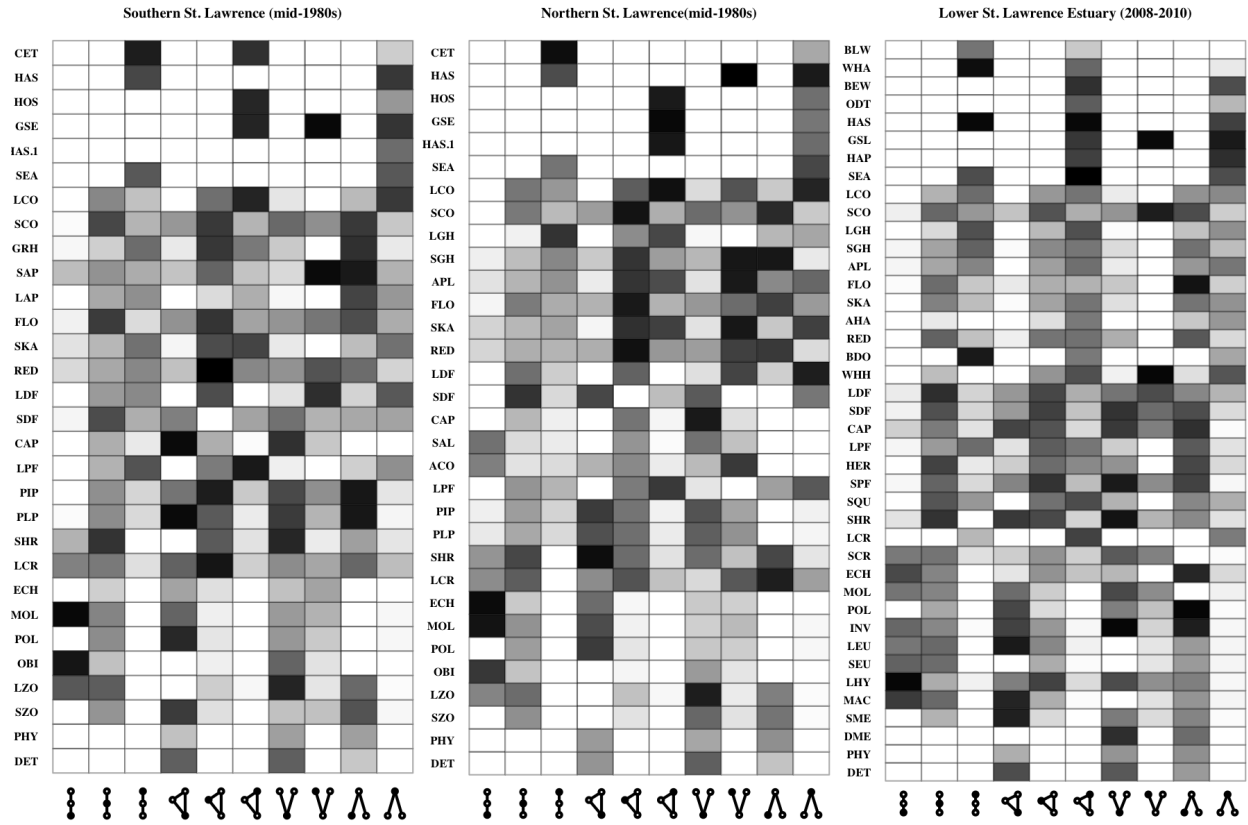
5.2 Empirical food webs

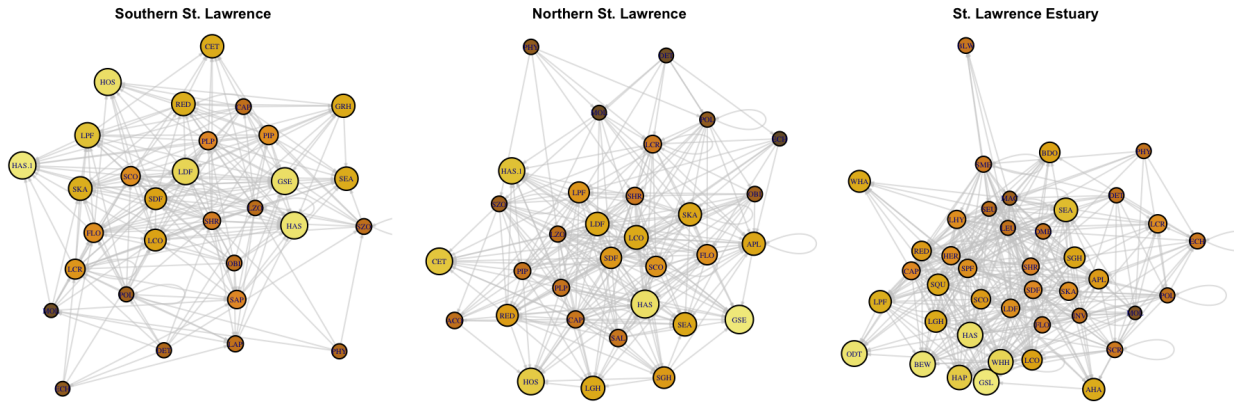Figure 4: Frequency in which each species of three empirical food webs are found in each motif position.

Figure 5: Sensitivity scores for species in the food webs of the southern St. Lawrence, northern St. Lawrence, and the estuary of St. Lawrence
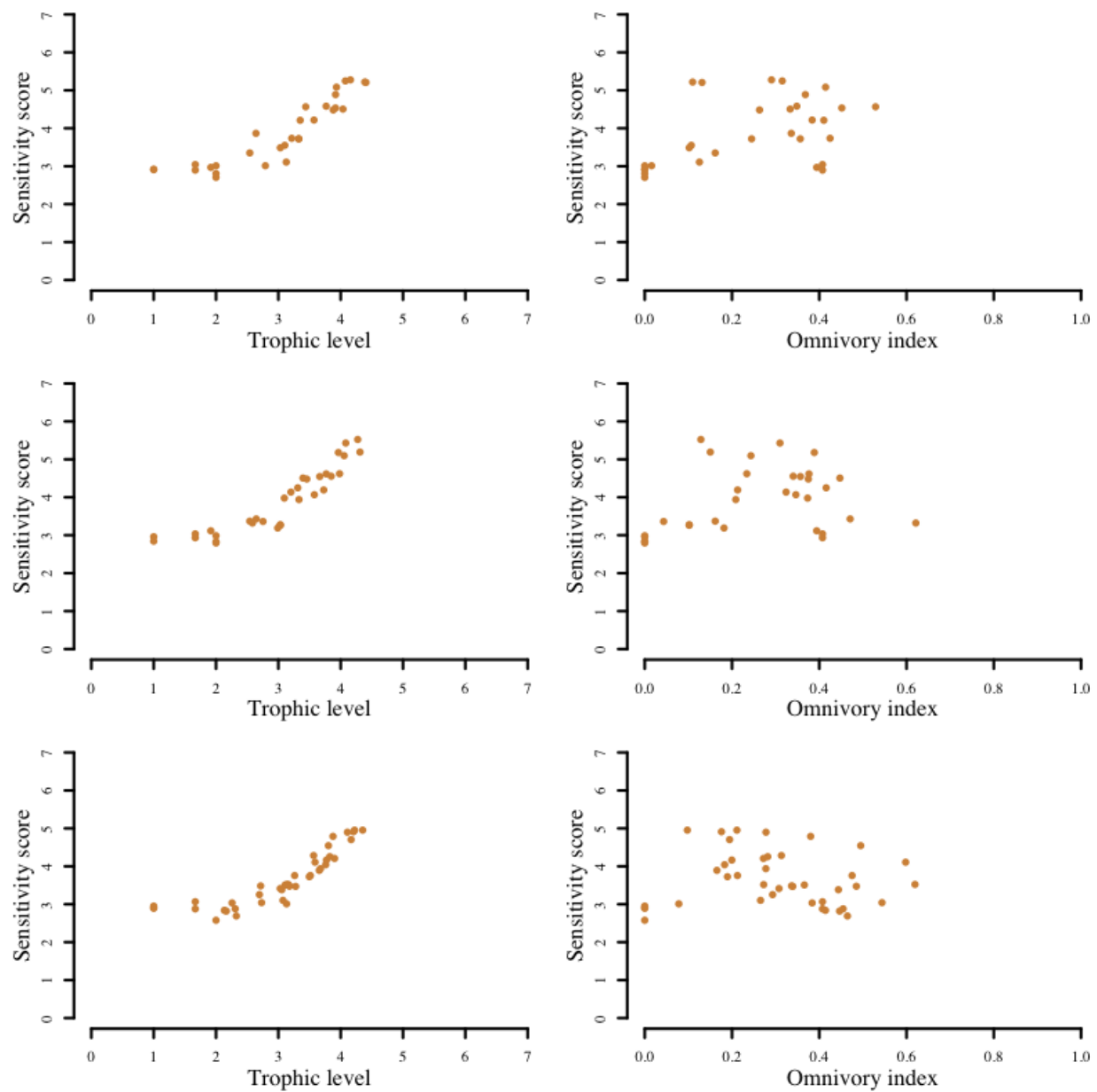
Figure 6: Sensitivity scores as a function of trophic level and omnivory index

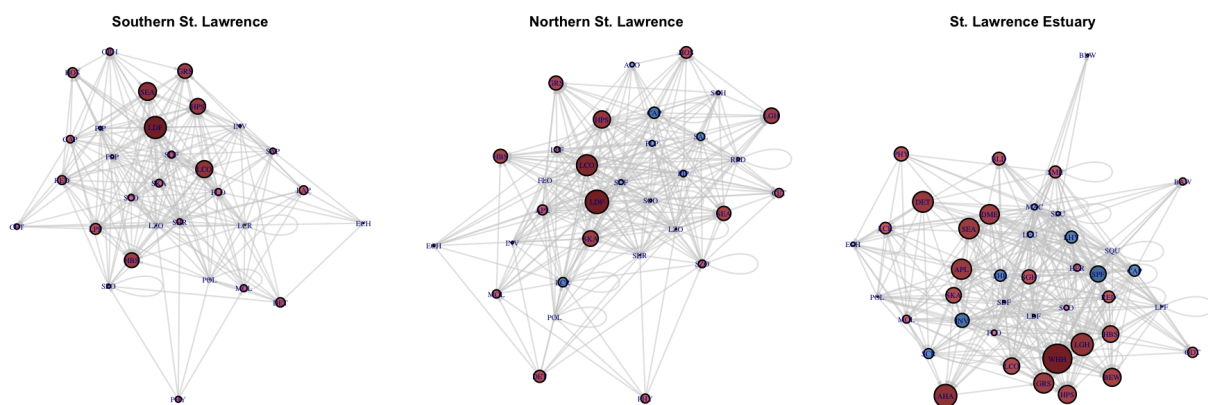## 5.3 Empirical food webs impact scores

Figure 7: Impact scores for species in the food webs of the southern St. Lawrence, northern St. Lawrence, and the estuary of St. Lawrence
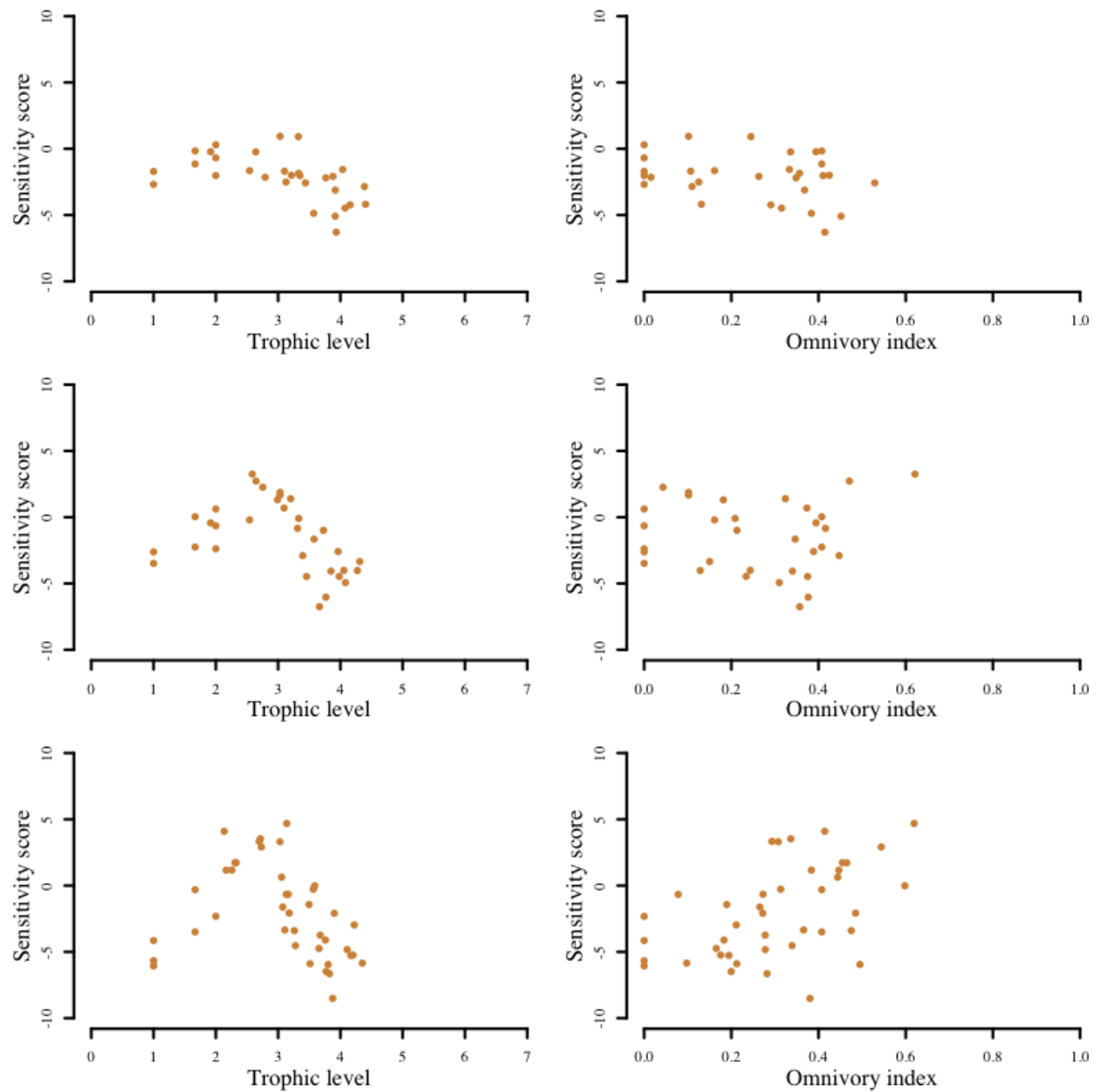
Figure 8: Impact scores as a function of trophic level and omnivory index
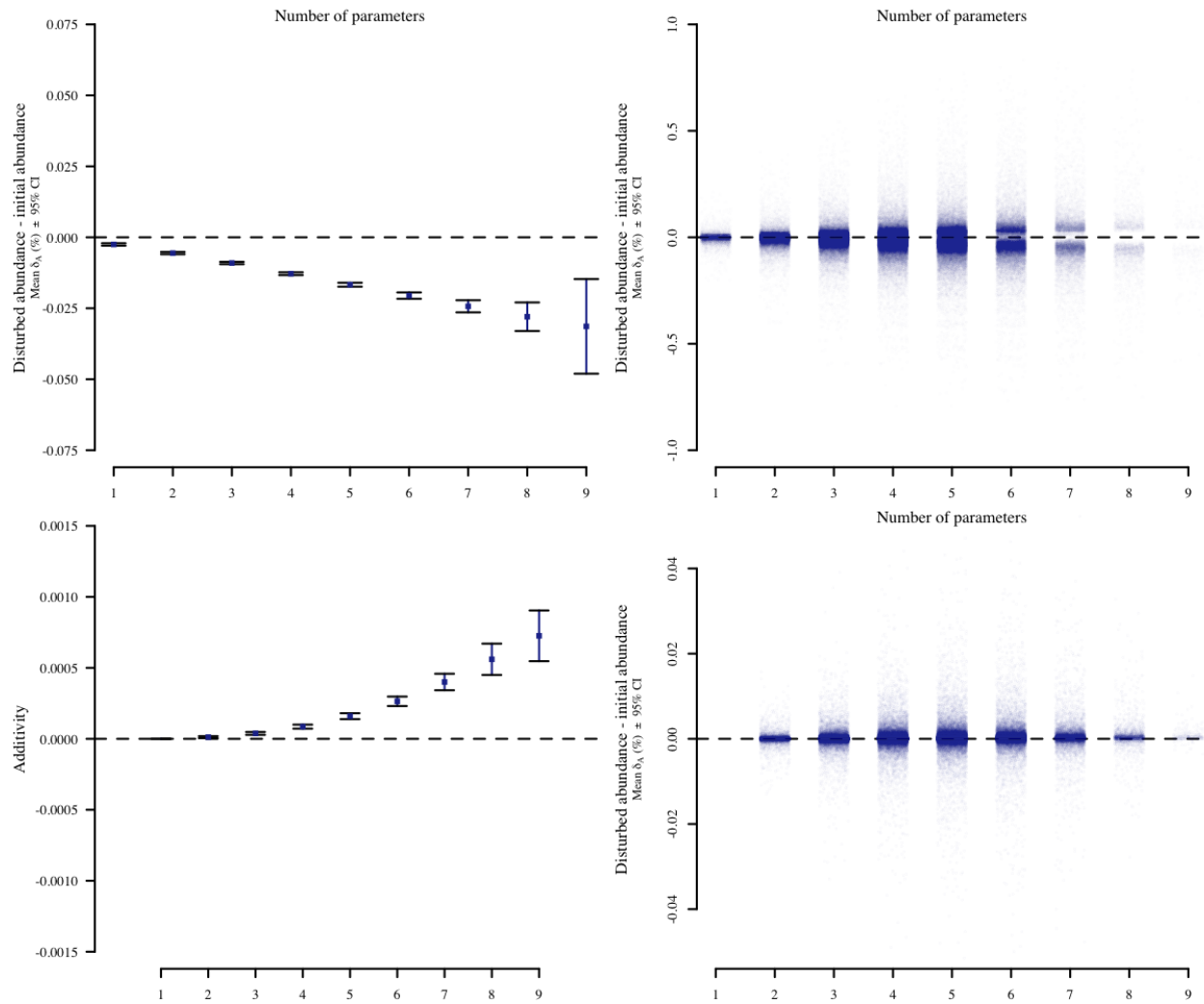
6 Supplementary Figures

Figure 9: Mean delta abundance and difference between joint and additive models as a function of the number of parameters
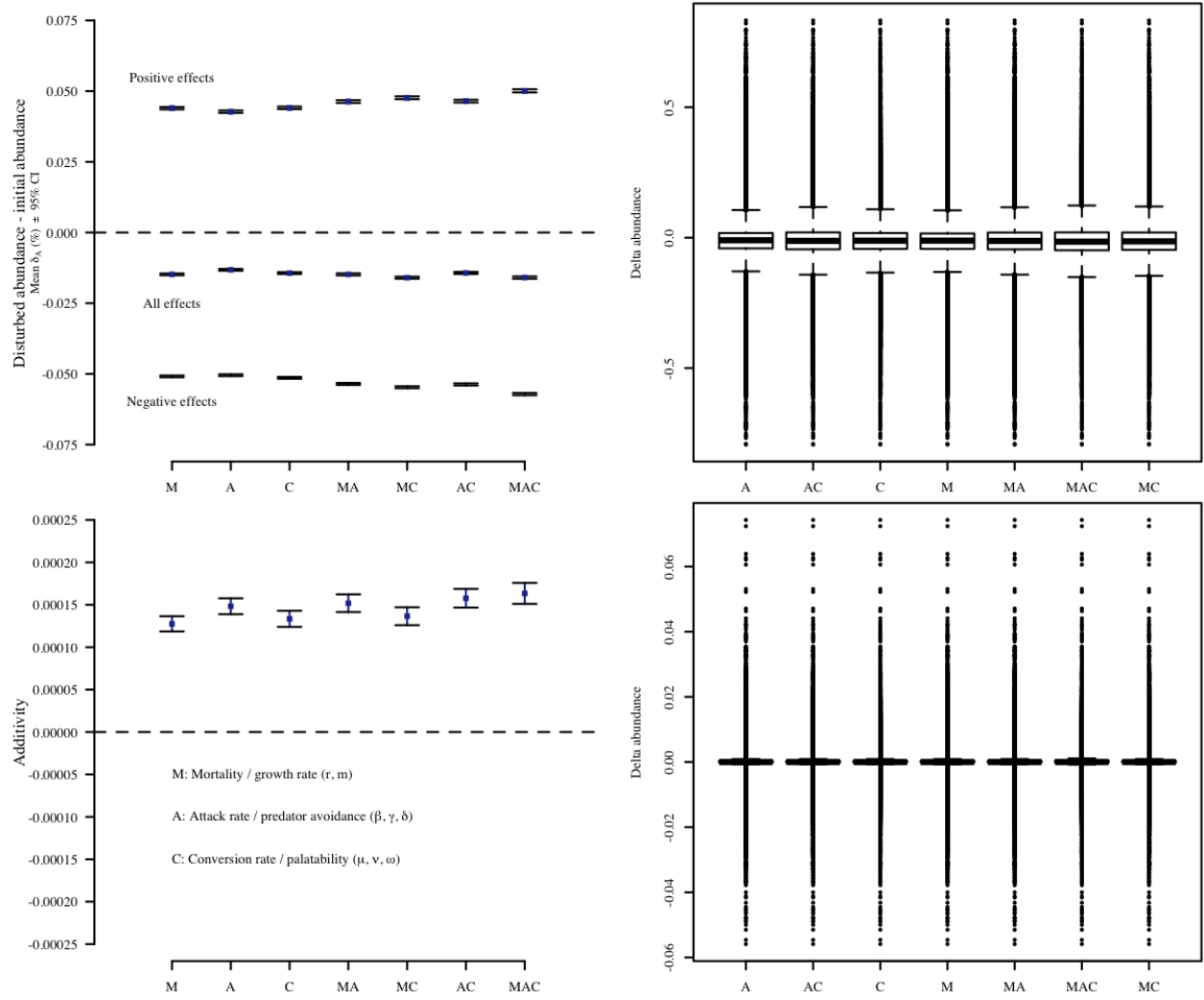
Figure 10: Mean delta abundance and difference between joint and additive models as a function of the types of parameters, i.e. growth/mortality rates, attack rates and conversion rates

7 Supplementary Material

7.1 Models

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

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)

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