On the sensitivity of food webs to multiple disturbances

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Data accessibility statement:

To do:

- ☐ Proposal for Ecology Letters Ideas and Perspectives
- ☒ 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 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?
- ☐ 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 thougth 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

Proposal letter

Cover letter and novelty statement

Letter

Documents joined

Reviewers

Proposed reviewers:

- Reviewer 1
- Reviewer 2
- Reviewer 3

Conflicts of interest:

- In-conflict individual and reason

Conflict of interest statement

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

1 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 explictely considering species interactions to properly capture the effects of multiple stressors and safeguard ecological communities against global changes.

2 Introduction

2.1 Context

- **Global changes, multiple stressors and food webs**
  - Global changes are resulting in increasingly intricate environmental stress exposure regimes (Halpern *et al.* 2015; Côté *et al.* 2016; Bowler *et al.* 2019). 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 (Darling & Côté 2008; Côté *et al.* 2016).
  - 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 (Crain *et al.* 2008; Darling & Côté 2008; Côté *et al.* 2016)
  - 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; Darling & Côté 2008; Côté *et al.* 2016).
  - 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 & 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

2.2 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.

- **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 & 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 & 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**

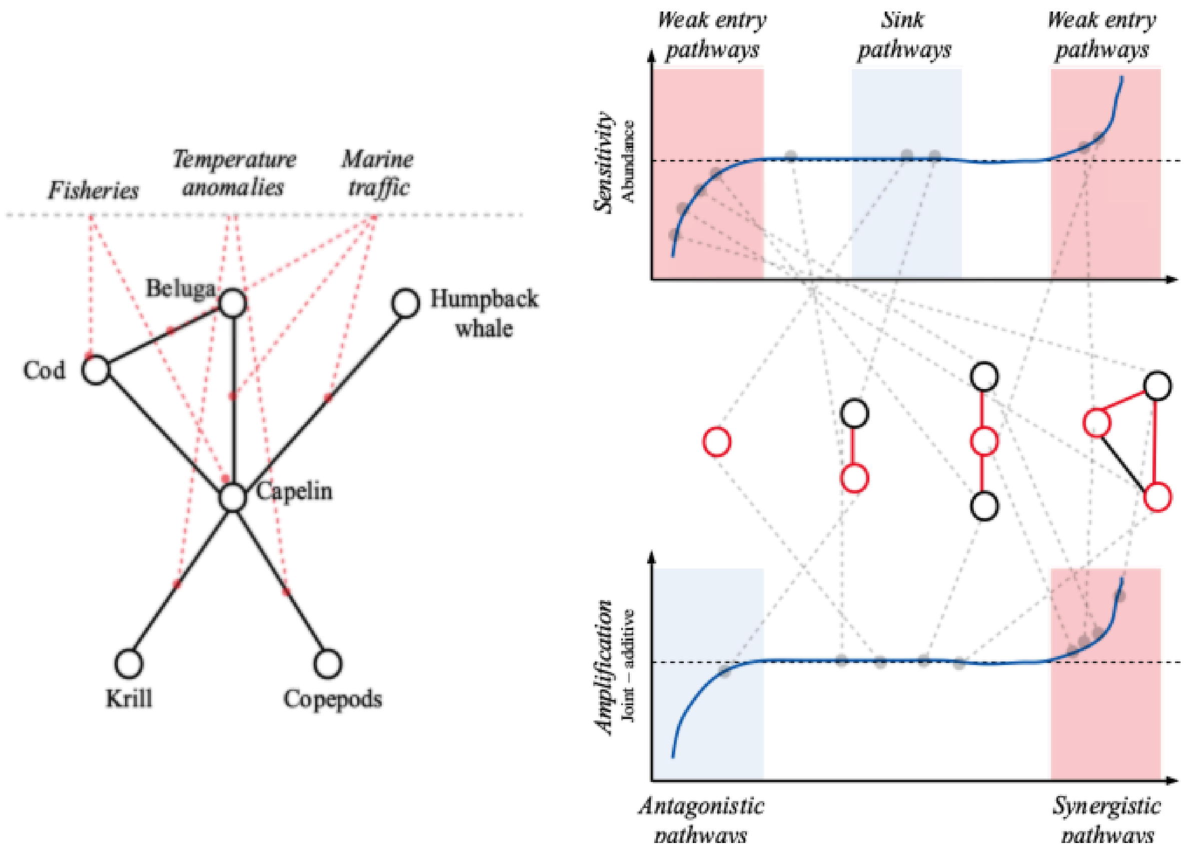

Figure 1: Conceptualize the effects of multiple disturbances on food webs

  - 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 ($D_{i,j} >> D_i + D_j$), antagonistic ($D_{i,j} << D_i + D_j$) or dominant ($D_{i,j} = D_i \veebar D_j$) 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:

3 Methodology

3.1 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 & 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.

3.2 Disturbances

For each motif, a 1% change in initial equilibria equations parameter values was applied to simulate negative disturbances through all possibile 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.

3.3 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.

3.4 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).

3.5 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

3.6 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.

4 Results

4.1 Disturbances

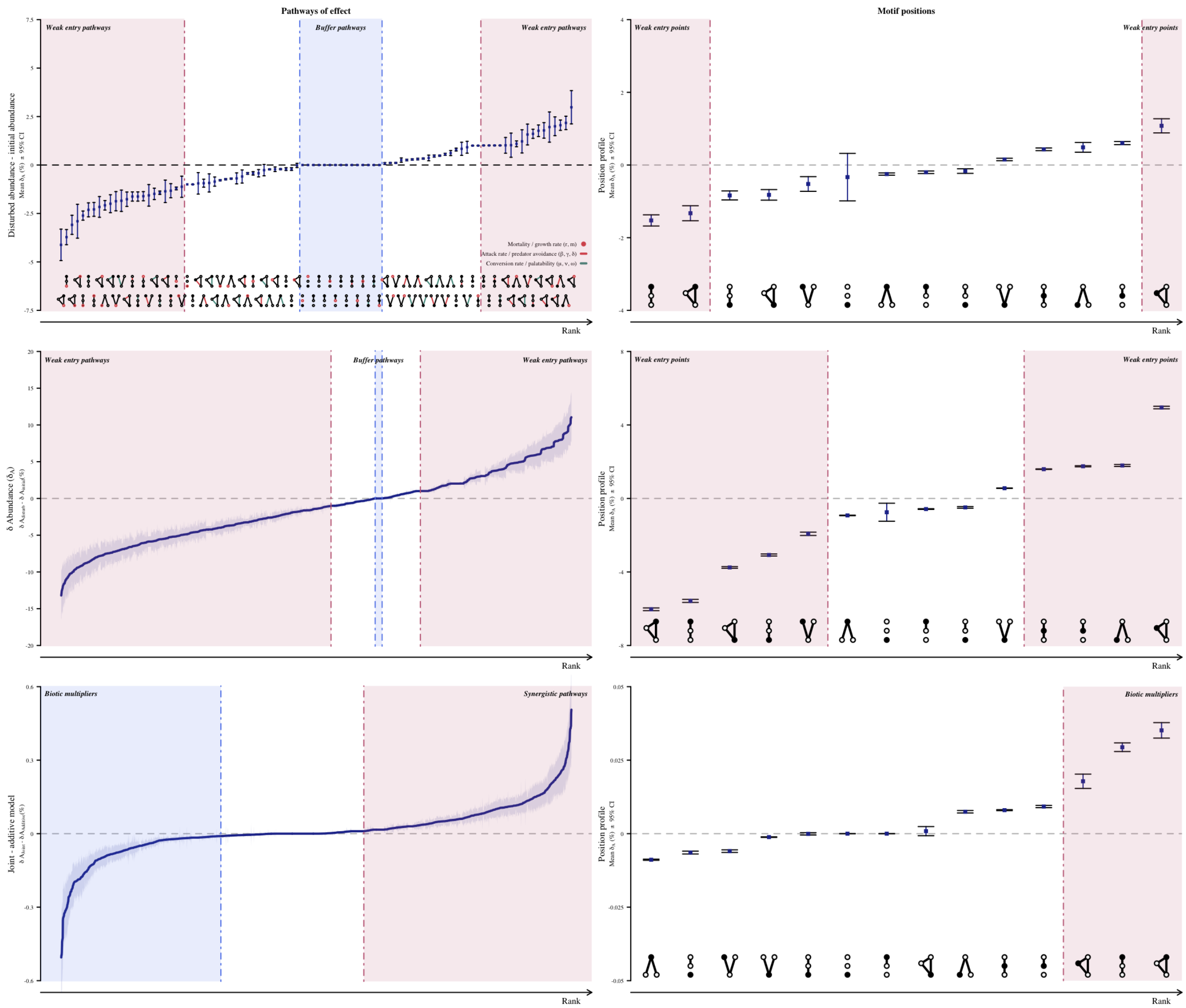

Figure 2: Disturbances. Line 1: Univariate disturbances; Line 2: Multivariate disturbances; Line 3: Joint - additive disturbances

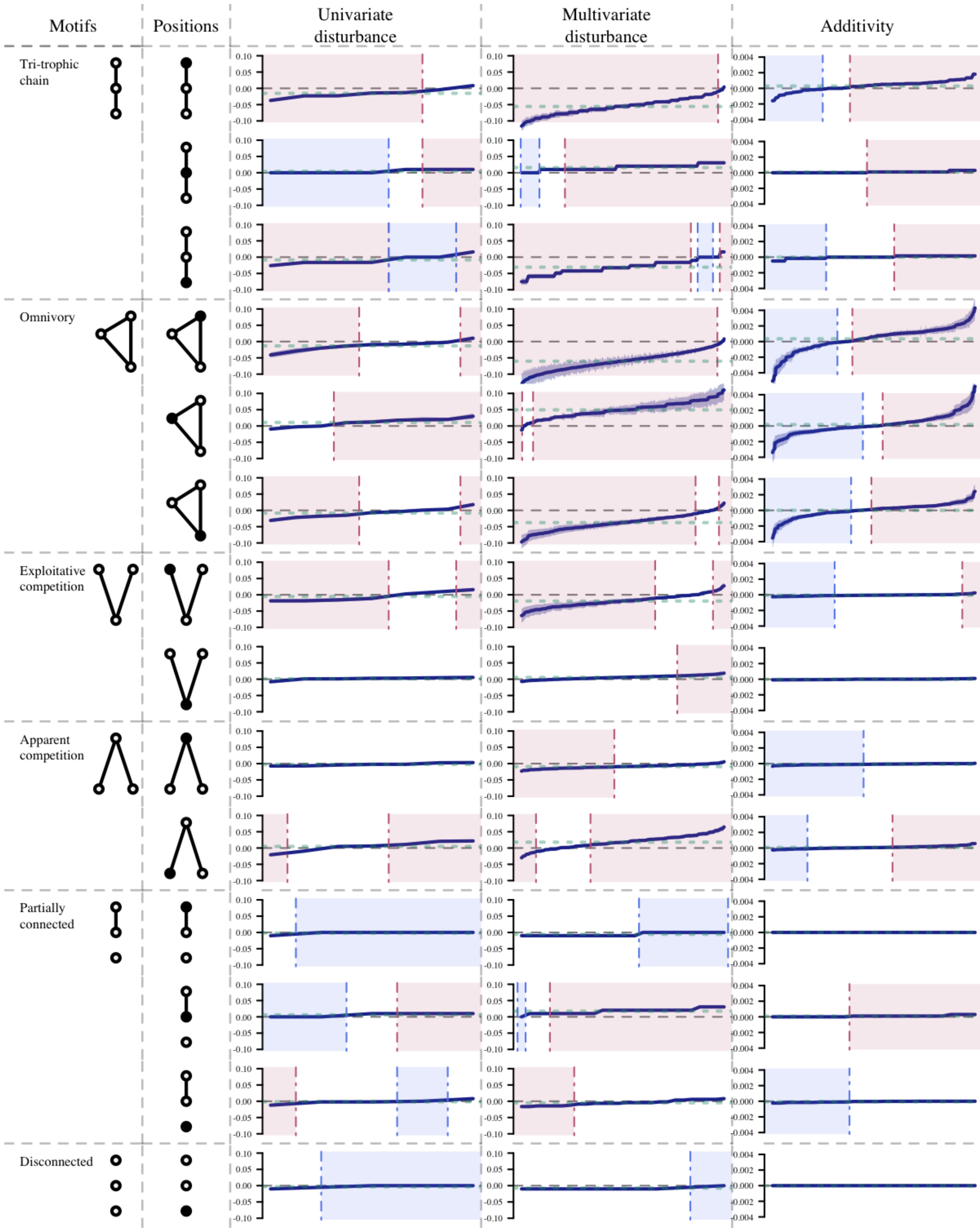

Figure 3: Morif positions and disturbances

Id	Functional groups	Mortality	Physiology	Behaviour

Figure 4: Species scores for the St. Lawrence

5 Supplementary Figures

5.1 Simulation figures

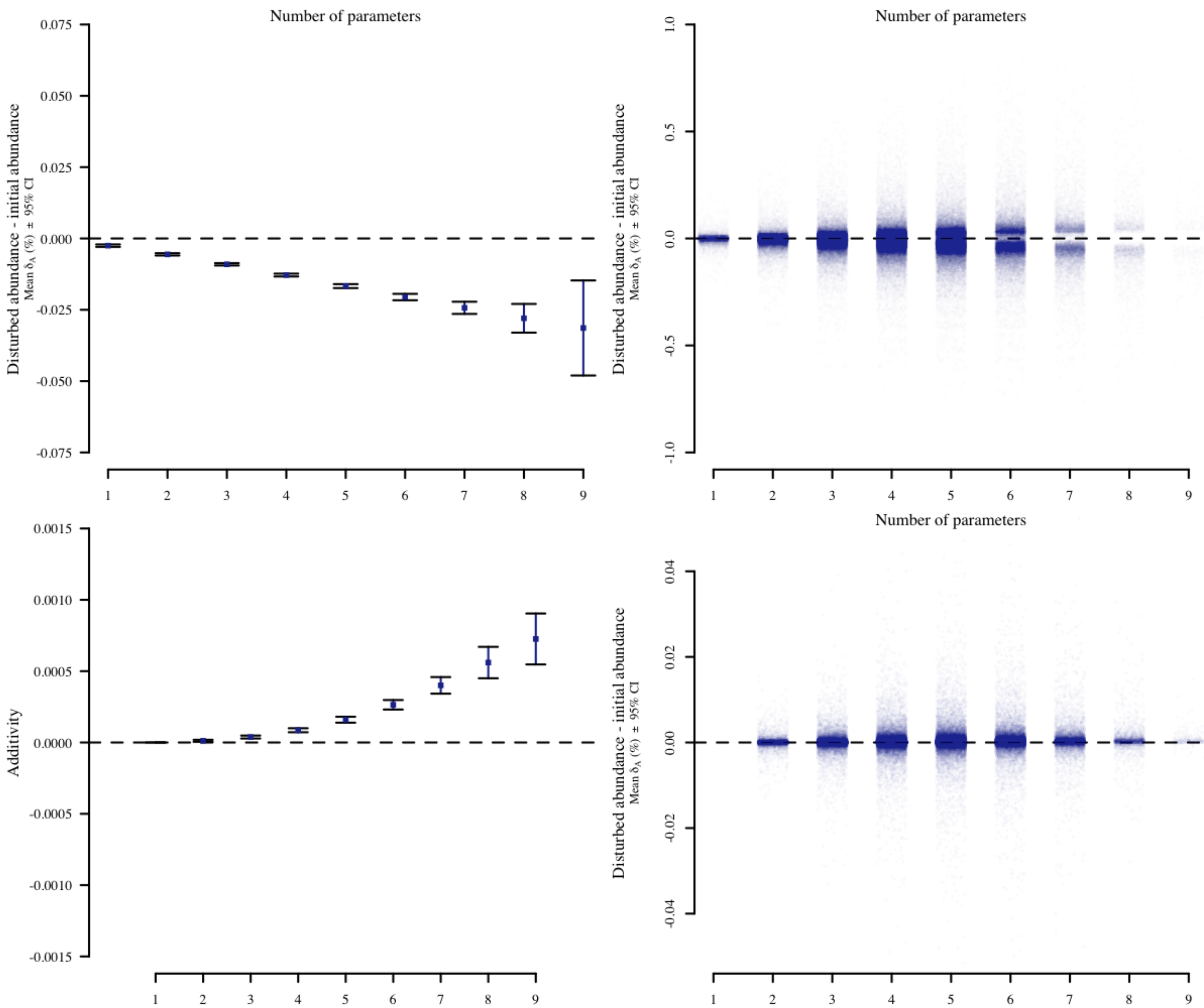

Figure 5: Mean delta abundance and difference between joint and additive models as a function of the number of parameters

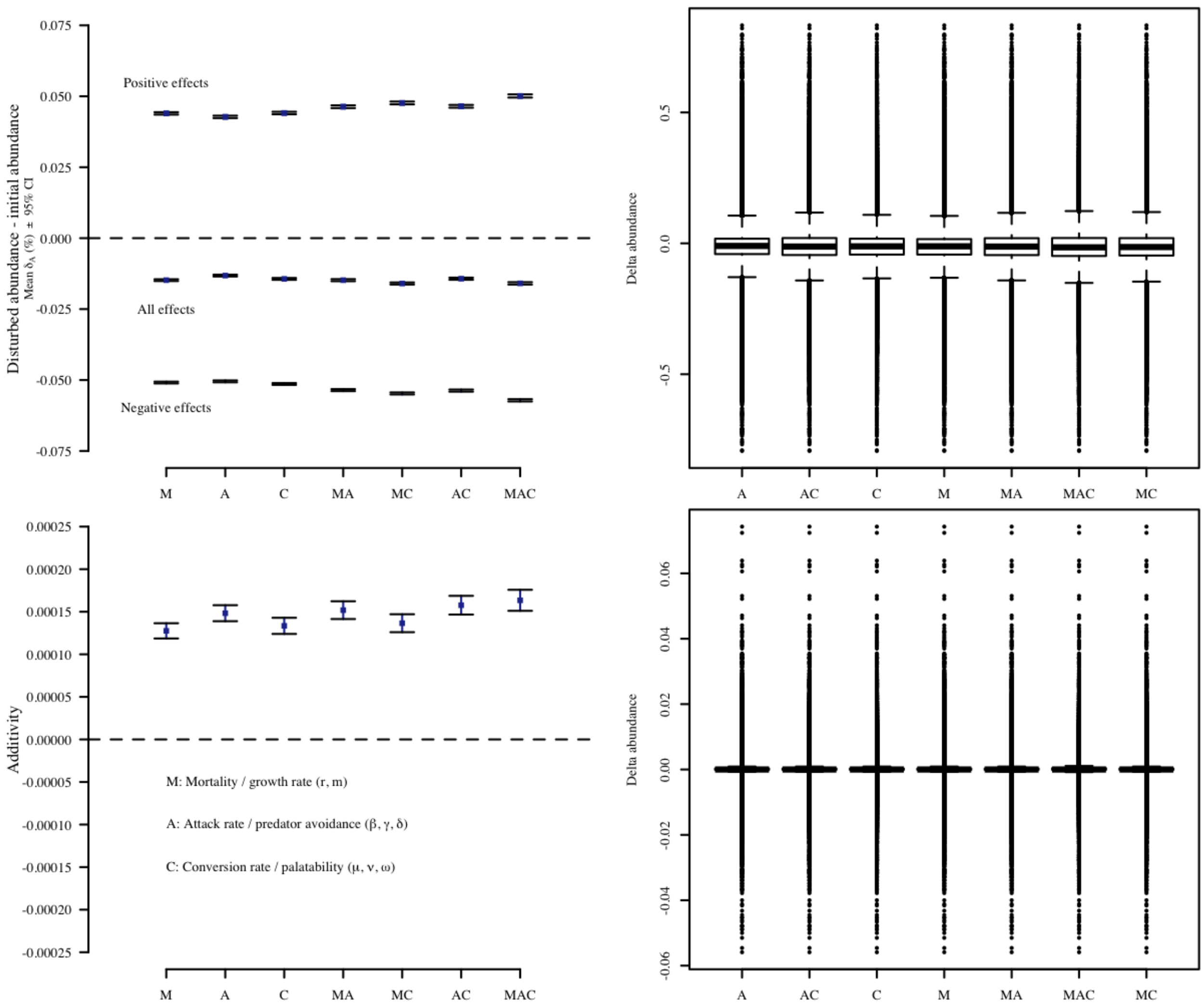

Figure 6: Mean delta abundance and difference between joint and additive models as a function of the types of parameters, i.e. growth/mortality rates, attack rates and conversion rates

5.2 Species position frequency

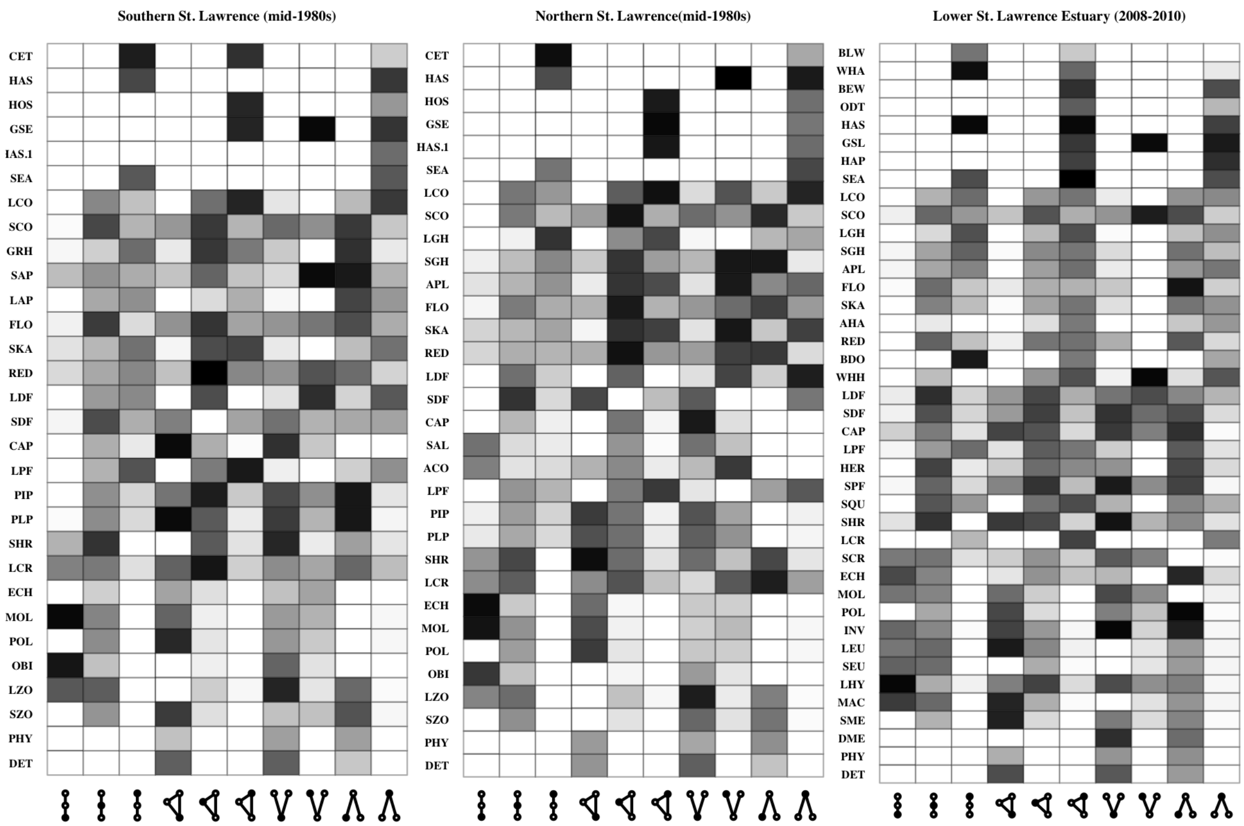

Figure 7: Frequency in which each species of three empirical food webs are found in each motif position.

5.3 Food web sensitivity and amplification scores

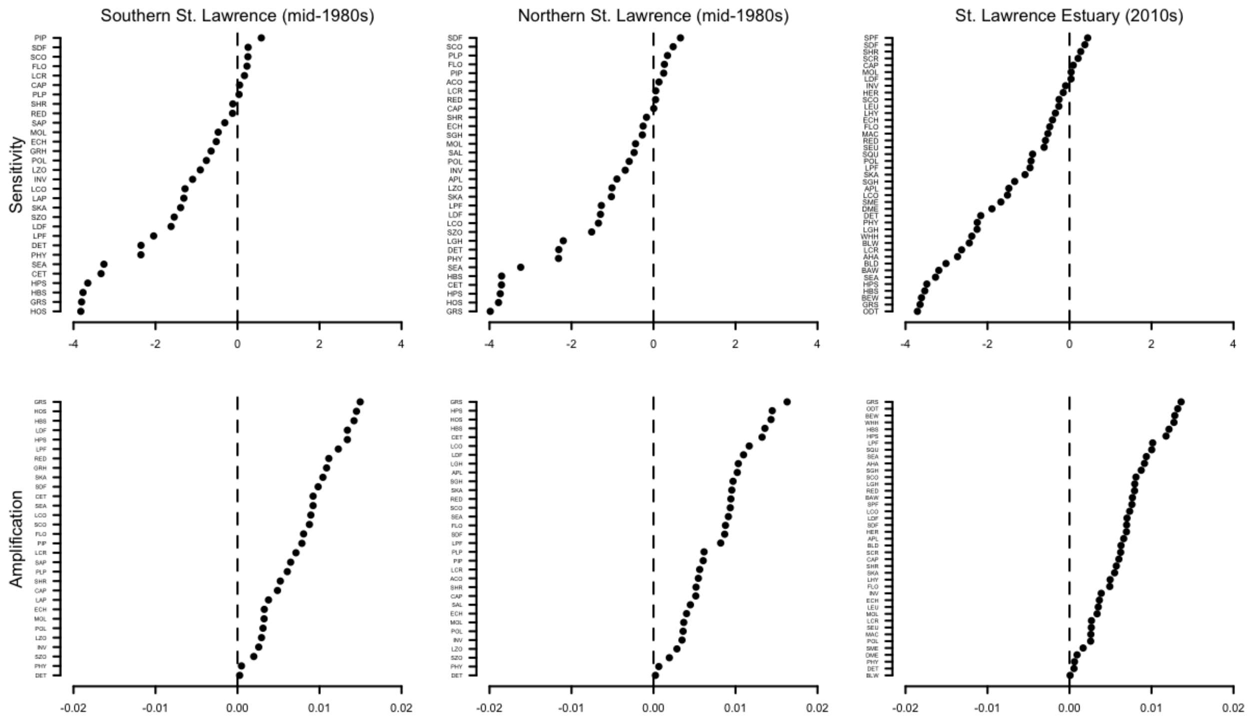

Figure 8: Sensitivity scores for species in the food webs of the southern St. Lawrence, northern St. Lawrence, and the estuary of St. Lawrence

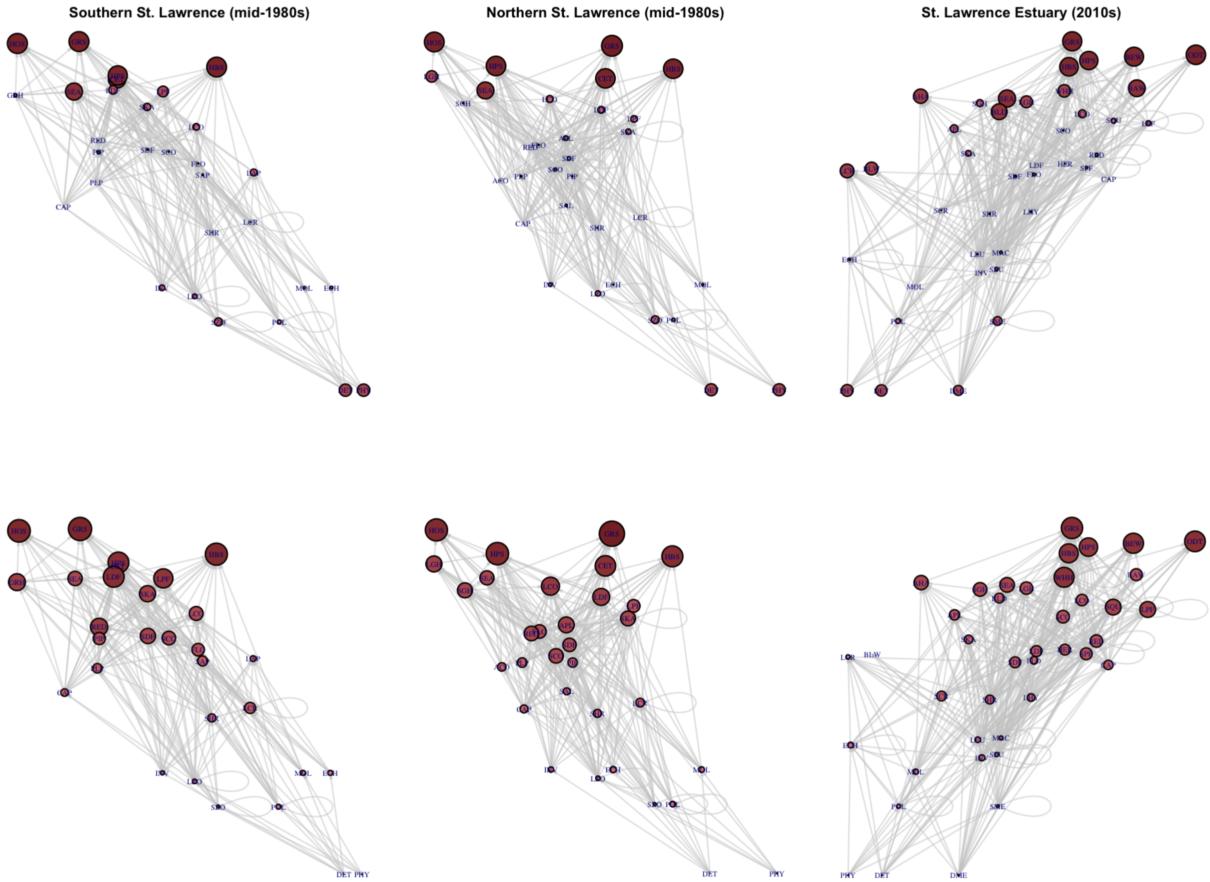

Figure 9: Sensitivity scores for species in the food webs of the southern St. Lawrence, northern St. Lawrence, and the estuary of St. Lawrence

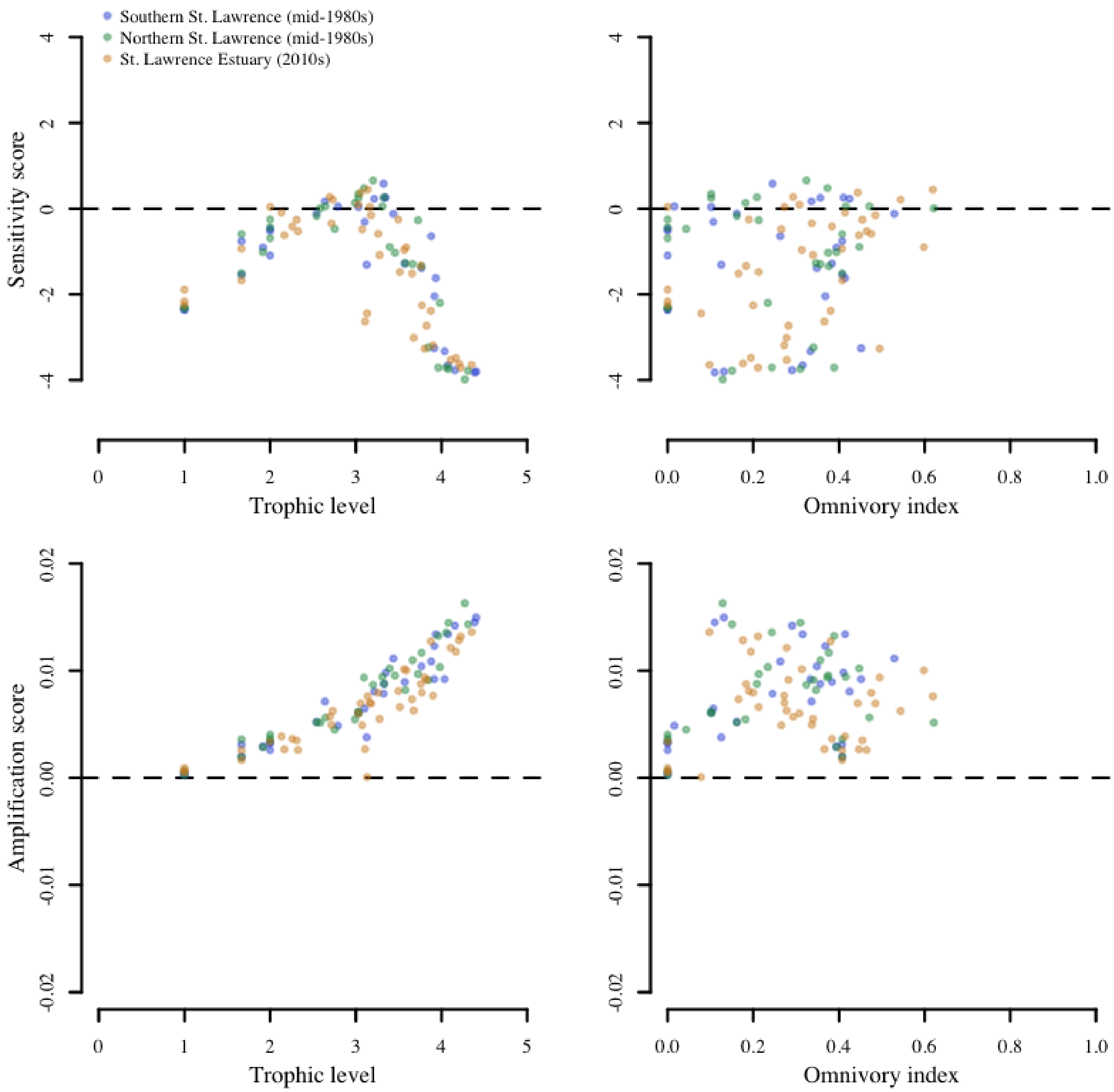

Figure 10: Sensitivity scores as a function of trophic level and omnivory index

5.4 Realised food web sensitivity and amplification scores

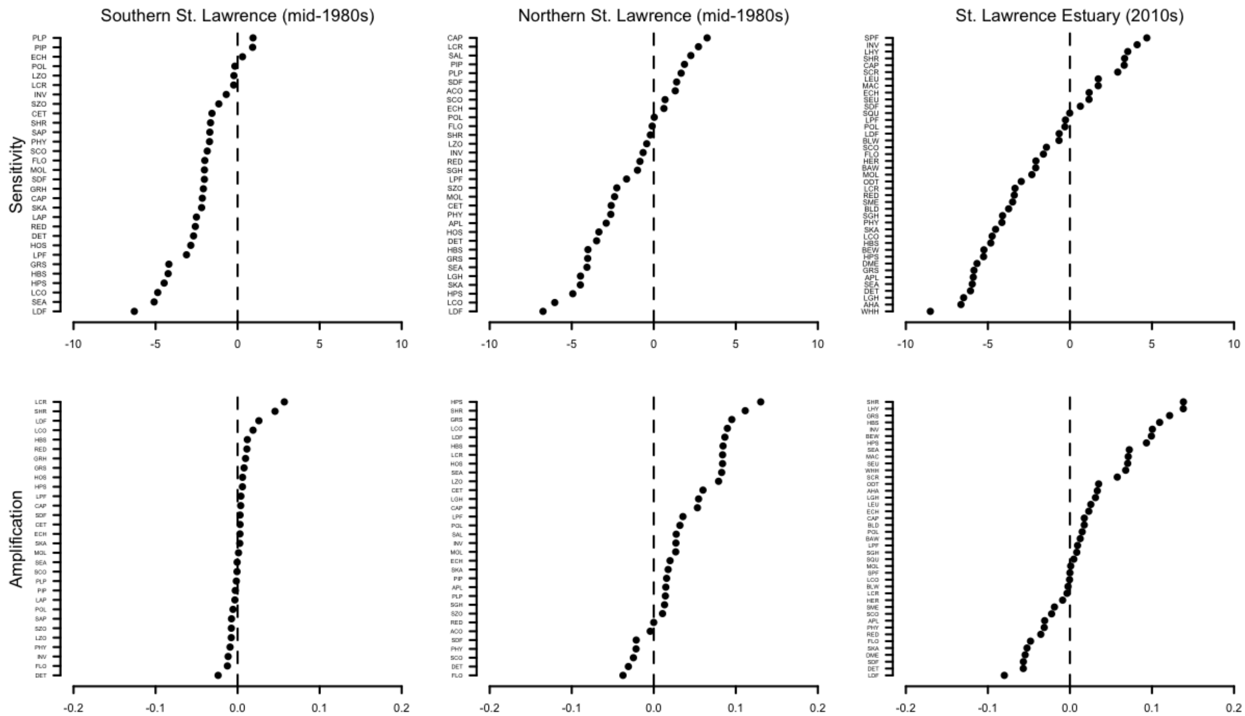

Figure 11: Impact scores for species in the food webs of the southern St. Lawrence, northern St. Lawrence, and the estuary of St. Lawrence

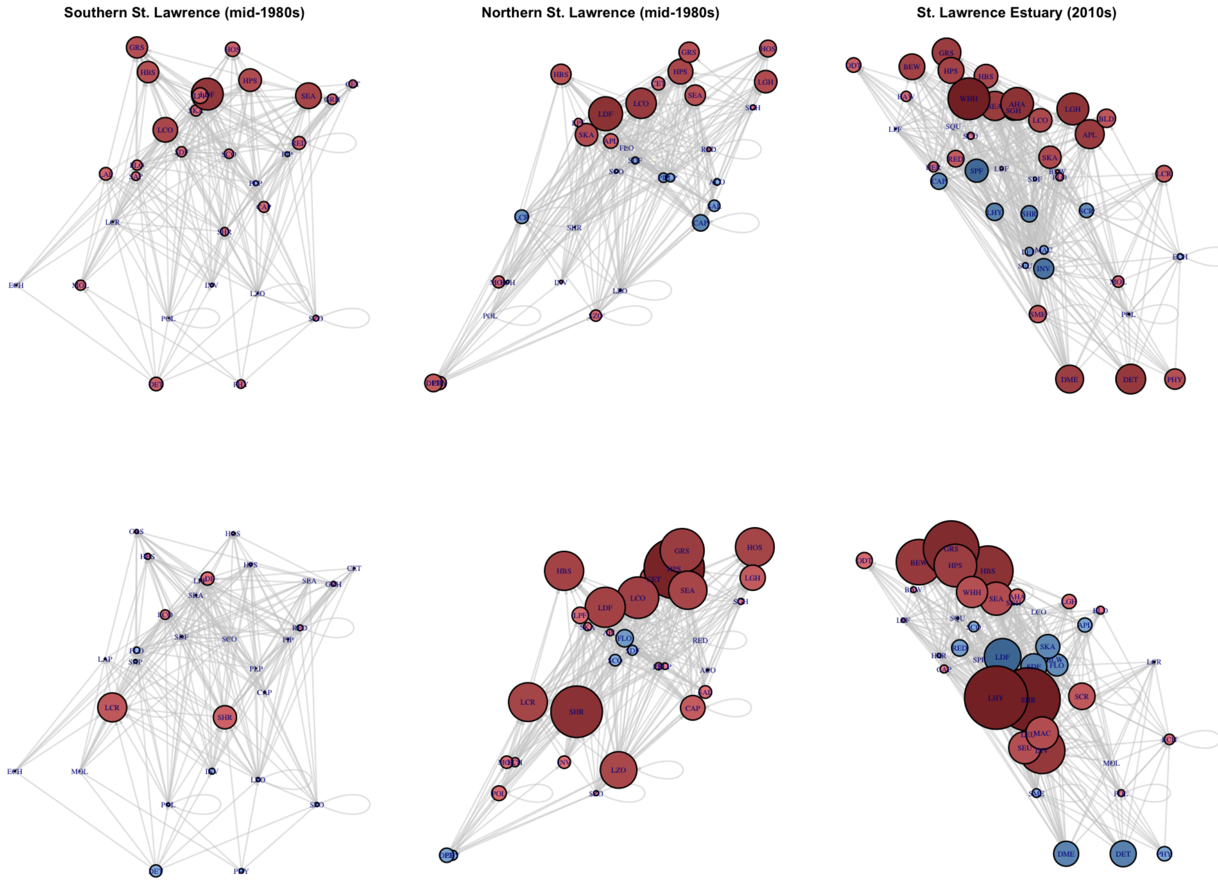

Figure 12: Sensitivity scores for species in the food webs of the southern St. Lawrence, northern St. Lawrence, and the estuary of St. Lawrence

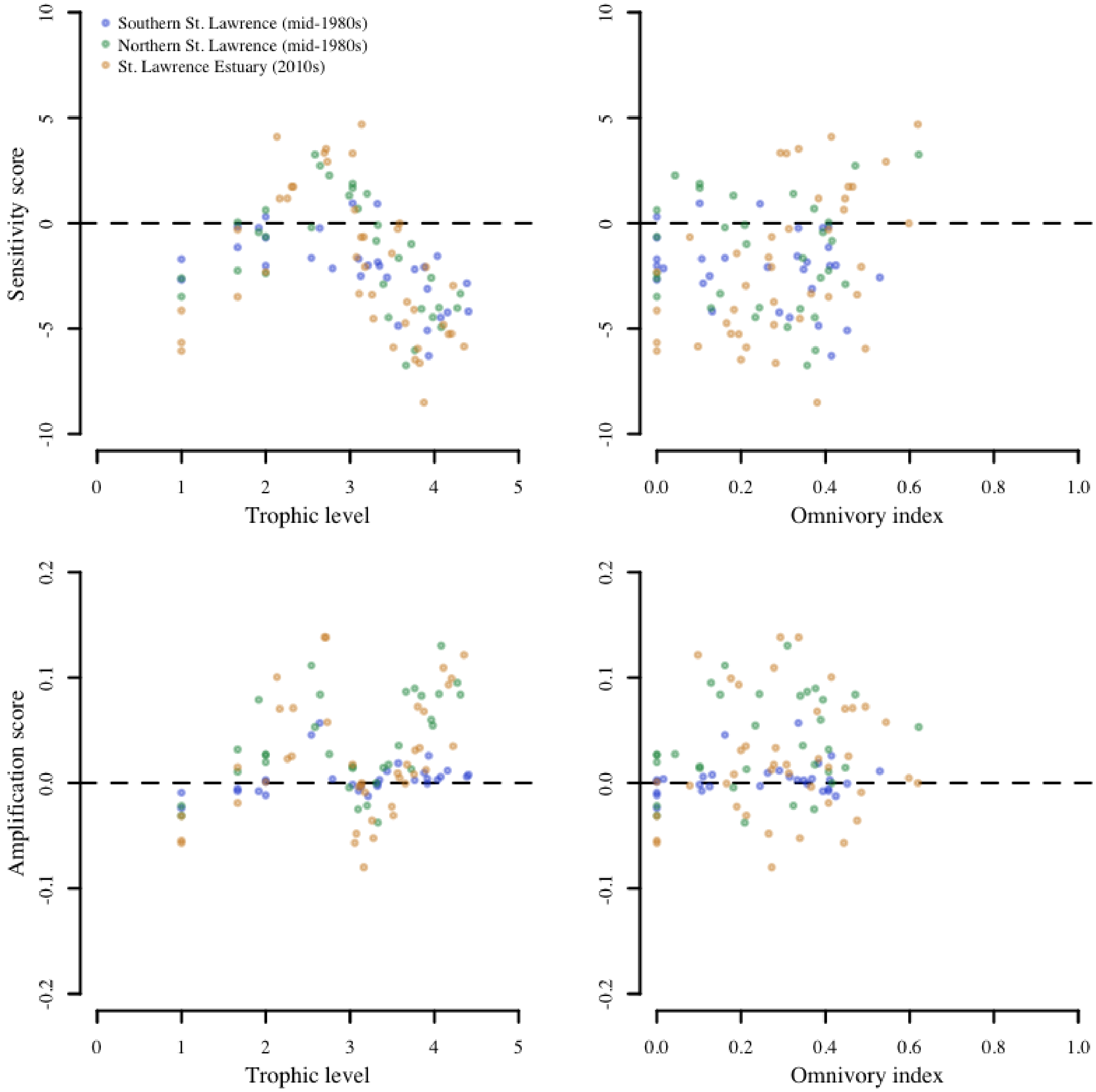

Figure 13: Impact scores as a function of trophic level and omnivory index

6 Supplementary Material

6.1 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

7 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

8 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?

9 Interesting points

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

10 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 & Piggott (2018) *
- Segner *et al.* (2014)
- Thompson *et al.* (2018a)
- Thompson *et al.* (2018b)
- Vinebrooke *et al.* (2004)

11 References

12 Ecology Letters formatting and submission

12.1 Latex files

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

12.2 Formatting

- Numbered pages
- Text:
  - Double-spaced
  - No hyphenation
  - No automatic wordwrap
- Tables
  - As MS Excel or MS Word or equivalent
  - Cited consecutively in the text
  - Numbered with Arabic numerals
  - Grouped together at the end od the paper or in a separate file
  - Titles and typed double-spaced on a separate sheet
  - Clearly indicate units for each entries in the table
  - Footnotes to tables hsould be identified by the sumbols * † ‡ § ¶ (in that order) and placed at the bottom of the table.
  - No vertical rules should be used
- Figures
  - Cited consecutively in the text
  - Numbered with Arabic numerals
  - Grouped together at the end od the paper or in a separate file
  - Titles and typed double-spaced on a separate sheet
  - Line and combination figures should preferably be submitted in vector graphics format (e.g. either embedded as vector graphics in a Word document or saved separately in PDF or eps format). If this is not possible, they should be saved separately as pixel-based graphics at 600 dpi at the required print size, and they should be saved in TIFF (not jpg) format or embedded as such in Word.

  - Photographic figures should be saved at 300 dpi in TIFF format, or jpg format with low compression
  - Figures should be drawn/submitted at their smallest practicable size (to fit a single column (82 mm), two-thirds page width (110 mm) or full page width (173 mm). Over-sized figures will be reduced by the Production Editor. If figures are drawn larger than reproduction size, component parts such as symbols and text must be large enough to allow for the necessary reduction. For full instructions on preparing your figures, see our Electronic Artwork Information for Authors page and the electronic artwork guidelines.

- Text boxes

  - Text boxes may be used for standalone definitions, equations, necessary explanations of concepts, a glossary (if needed only), and other items that disrupt the flow of the manuscript or where repeated reference to them is necessary. Text boxes can include equations and references (included in the main reference list), but not tables, figures or footnotes. Text boxes are limited to 750 words including a title. Items in text boxes that are not logically separate from the main text of the manuscript should be incorporated into the main text. A glossary should only be given if the language is complex enough that it may not be understood by the general readership of the journal or if requested by an editor for the journal. Text boxes should be cited consecutively using Arabic numerals (e.g., Box 1, Box 2). Text for text boxes should be given after figures at the end of the manuscript and the text should begin with a short descriptive title, for instance "Box 1: Calculation of a trophic complexity index."

- Scientific names

  - The Latin names of each species should be given in full. Scientific names should be given priority in the text, with colloquial names in parentheses if desired. Please make sure that the identity of species used in your paper can be verified, unless these are very well known (e.g., Homo sapiens, Drosophila melanogaster, Escherichia coli). If the data came from another paper where the species was identified, it must be cited. If fresh data are presented, the name of the taxonomist who identified the specimens should be given, as well as the name of the company or provider of the organisms (e.g., a culture collection or seed company) and/or the reference work used to make the identification. Lodgement of voucher specimens in a recognized museum is desirable, especially for taxa which are poorly known, and should be stated in the manuscript.

- Mathematics

  - Wherever possible, mathematical equations and symbols should be typed in-line by keyboard entry (using Symbol font for Greek characters, and superscript and subscript options where applicable). Do not embed equations or symbols using Equation Editor or Math Type or equivalents, when simple in-line, keyboard entry is possible. Equation softwares should only be used for displayed, multi-line equations and equations and symbols that cannot be typed. LaTex files are supported, but if submitting in this format authors should also provide an identical PDF file.

12.2.1 Title page

- Article title
- full name(s), affiliation(s) and e-mail address(es) of all author(s)
- a short running title (abbreviated form of title) of less than 45 characters including spaces
- up to 10 keywords for indexing purposes. It is very important that the keywords be chosen carefully
- the type of article (Ideas and Perspectives, Letters, Reviews and Syntheses, or Technical Comments)
- the number of words in the abstract, the number of words in the main text (excluding abstract, acknowledgements, references, table and figure legends), and the number of words in each text box
- the number of references
- the number of figures, tables, and text boxes
- the name and complete mailing address (including telephone and fax numbers and e-mail address) of the person to whom correspondence should be sent
- Statement of authorship: Contributions by authors should be listed on the title page and will be printed at the end of the manuscript. This statement should be appropriate to the study described in the manuscript and should clarify who designed the study, who performed the research, who provided new methods or materials, and who wrote the manuscript. We encourage concise statements such as "JW performed phylogenetic analyses, MH collected data, performed modeling work and analyzed output data, and PK performed the meta-analysis. MH wrote the first draft of the manuscript, and all authors contributed substantially to revisions."
- Data accessibility statement: The statement must confirm that, should the manuscript be accepted, the data supporting the results will be archived in an appropriate public repository such as Dryad or Figshare and the data DOI will be included at the end of the article.

12.2.2 Abstract

- The abstract page should contain a short summary not exceeding 200 words for Ideas and Perspectives and Reviews and Syntheses.

12.2.3 Main text

- (a)Introduction. The introduction should summarize briefly the background and aims, 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.

- (d) Discussion. The Discussion section should be separate from the Results section. It allows authors to propose their interpretation of the results, and to suggest what they might mean in a wider context in general and relative to published literature. It should end with a clear statement of the main conclusions of the research, and a clear explanation of their importance and relevance.

- (e) Acknowledgements. Acknowledgements should be brief and concise.

- (f) References. See below for detailed information to in-text citations and Reference list.

12.2.4 In-text citations

- Chronological order
- Fully, except if >2 authors

12.2.5 Reference list

- All authors, up to 6 authors • Journal articles Last name, Initials. et al. (Year). Full title of article. Abbreviated journal title (standard abbreviations), Volume number, page range. • Books Last name, Initials. et al. (Year). Full title of book. Edition (only include this if not the first edition). Publisher, place (cities only except for USA and UK), pp. (page range) • Chapters in books Last name, Initials. et al. (Year). Full title of chapter. In: (Full title of book), Edition (only include this if not the first edition) { [ed(s).] [Editors(s) last name, initials] }. Publisher, City (Include state and country for USA and UK), pp. (page range). • Data Last name, Initials. et al. (Year). Data from: (Title of article). Dryad Digital Repository. Available at: http://dx.doi.org/10.5061/dryad.585t4. • Websites Authorship or Source. (Year). Title of web document or web page. Available at: [URL]. Last accessed DD MONTH YYYY. References to material available on the World Wide Web can be given only if the information is available on an official site and without charge to readers. Authors may provide electronic copies of the cited material for inclusion on the Ecology Letters Homepage at the discretion of the Editors.

12.2.6 Unpublished works

• “In press”: nly permissible for papers that have been accepted for publication (documentary evidence of acceptance must be provided). Example: Vázquez, D.P. & Simberloff, D. (2003). Changes in interaction biodiversity induced by an introduced ungulate. Ecol. Lett., in press (accepted). • “Personal communication”: Citation must be accompanied by the names of all persons concerned. Any person cited as the source of a ’ personal communication’ must have approved the reference.

12.2.7 Data archiving

- Data are important products of scientific enterprise, and they should be preserved and remain usable in future decades. Ecology Letters requires, as a condition for publication, that the data supporting the results in the paper will be archived in an appropriate public repository such as Dryad or Figshare. Whenever possible the scripts and other artefacts used to generate the analyses presented in the paper should also be publicly archived. Exceptions may be granted at the discretion of the Editor-in-Chief, especially for sensitive information such as human subject data or the location of endangered species. Authors will be required to complete a data accessibility statement for all accepted papers.

12.2.8 Online supplementary information

Supporting Information should be cited within the article text, and a descriptive legend should be included in each Supporting Information file. It is published as supplied by the author, and a proof is not made available prior to publication; for these reasons, authors should provide any Supporting Information in the desired final format. - Include sensitivity and amplification score data?

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