

1 On the sensitivity of food webs to multiple
2 disturbances

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

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

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

7 ³Department of Integrative Biology, University Of Guelph, Guelph, Ontario, Canada N1G
8 2W1

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

10

11 **Running title:**

12

13 **Keywords:**

14

15 **Type of article:** Ideas and Perspectives

16

17 **Abstract word count:**

18 **Main text word count:**

19 **Number of references:**

20 **Number of figures:**

21 **Number of tables:**

22 **Number of text boxes:**

23

24 **Correspondence:**

25 David Beauchesne

26 david.beauchesne@uqar.ca

27 1-514-553-4975

28

29 **Statement of authorship:**

30

31 **Data accessibility statement:**

32 **Literature to cite - or at least look at!**

- 33 • (???)
34 • (???)
35 • (???)
36 • (???)
37 • Crain *et al.* (2008)
38 • (???)
39 • (???)
40 • Galic *et al.* (2018) *
41 • Jackson *et al.* (2016)
42 • (???)
43 • (???)
44 • Piggott *et al.* (2015)
45 • Schäfer & Piggott (2018) *
46 • (???)
47 • (???)
48 • Thompson *et al.* (2018)
49 • (???)
50 • Montoya *et al.* (2009)
51 • Hodgson *et al.* (2019)
52 • Holt (1997)
53 • Stouffer *et al.* (2007)
54 • Stouffer & Bascompte (2010)
55 • Stouffer *et al.* (2012)
56 • (???)
57 • Wootton (1993)
58 • Wootton (2002)
59 • Yodzis (2000)
60 • (???)

61 To reread:

- 62 • De Laender (2018) for conceptual portion of my text, should aim for something similar.
63 • Montoya *et al.* (2009)
64 • Stouffer *et al.* (2007) for motifs, with (???)
65 • Stouffer & Bascompte (2010)
66 • Stouffer *et al.* (2012)
67 • thompson2018 Ecosphere
68 • gellner2016 introduction for motifs

69 **Latest:**

- 70 • Abdala-Roberts2019

- 71 • ogorman2010 -> intro on food webs
- 72 • ogorman2009
- 73 • yodzis2000
- 74 • bascompte2009a
- 75 • bascompte2009
- 76 • giakoumi2015
- 77 • hodgson2017
- 78 • hodgson2019
- 79 • hodgson2019a
- 80 • hale2018
- 81 • griffen2016
- 82 • klaise2017
- 83 • wootton2002
- 84 • menge1995
- 85 • kissling2015
- 86 • holt2017
- 87 • Tylianakis2017
- 88 • williams2000
- 89 • polis1996
- 90 • estes2011
- 91 • milo2004
- 92 • strogatz2001
- 93 • wootton2017
- 94 • guiden2019
- 95 • stouffer2007
- 96 • stouffer2010
- 97 • stouffer2012
- 98 • galic2018
- 99 • dempsey2017
- 100 • borrelli2015
- 101 • saterberg 2013
- 102 • Woodworth-Jefcoats 2019

103 Ecology Letters structure ideas - guiden2019 -

104 Conceptual description: - De Laender (2018)

105 Relevant for this paper: - letten2019: non-additive effects - guiden2019: disturbances

¹⁰⁶ **Notes**

¹⁰⁷ **Modelling disturbances on food webs**

- ¹⁰⁸ • (???)
¹⁰⁹ • Thompson *et al.* (2018)
¹¹⁰ • Galic *et al.* (2018)

¹¹¹ thompson2018: Trophic interations: synergistic effects due to supressed species compensation
¹¹² Species at higher trophic levels are more sensitive because of both direct and indirect
¹¹³ interacton mediated effects We find that this should also hold true for lower trophic level
¹¹⁴ species

¹¹⁵ **Points to make**

- ¹¹⁶ • Most empirical and theoretical exercises have focused on 2 or 3 sources of stress tops
¹¹⁷ – We provide the most comprehensive evaluation of simulated stressors ever published, testing all possible
¹¹⁸ – Slightly different definition of disturbances than what is usually used.
¹¹⁹ * We define disturbances as any single pathway of effect affected
¹²⁰ * In this sense we ignore that a single pathway of effect may be impacted by
¹²¹ multiple sources of stress
¹²² · While this may be critisized, this allows us to infer on the effects of
¹²³ multivariate pathways of effects and it provides a theoretical framework
¹²⁴ to test for combinations of stressors affecting the same pathways of effects.
¹²⁵
¹²⁶ • Variations in abundance (sensitivity) are consistently greater than variations in abundance due to amplification of the effects. Considering the additive effects will therefore capture most of the impacts observed, yet there may still be surprises creeping up depending on topology and the specific pathways of effects that are targetted by disturbances.

¹³¹ **Plan**

- ¹³² • **Abstract**
¹³³ • **Introduction**
¹³⁴ – Global changes and disturbances propagation through food webs
¹³⁵ – Uncertainty associated with multiple disturbances
¹³⁶ – Limits of *in situ* and experimental approaches to study multiple disturbances
¹³⁷ – Limited insights from null model testing

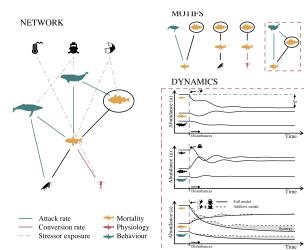
- Shift towards ecological modelling to better understand mechanisms
- Insights on the effects of disturbances on ecological communities from theoretical ecology
- Theoretical focus on single disturbances, coexistence and extinctions

• Objectives

- Investigate the role of species and their interactions in mediating the effects of multiple disturbances on food webs.
- Questions of particular significance to management:
 - 1) should interactions be considered in impact assessments?
 - 2) can the effects of stressors be evaluated separately or should they be considered in combination?
 - 3) which species are most sensitive to disturbances based on their trophic position?

• Of food webs and multiple disturbances

- [1] Food web dynamics
- [2] Indirect effects
- [3] Environmental pressures
- [4] Effects of disturbances on food webs
 - * What we know: robustness to extinctions, importance of indirect effects
- [5] Pathways of effects
- [6] Non-additive effects
- [7] Topology (trophic position and interaction types)
- [8] Motifs
 - * to understand how topology influences sensitivity to and amplification of disturbances
- [9] Archetypes
- [10] Subweb dynamics/insights (Holt 1997; Stouffer 2007)
- [11] Definitions - pathway, trophic (position), biotic (species)
 - * Weak entry points
 - * Sinks
 - * Buffers (cite Montoya et al. 2009)
 - * Multipliers



170 • Simulating multiple disturbances on food webs

171 – Method for simulations:

- 172 * Exhaustive investigation of how topology affects species abundance at
173 * equilibrium to univariate and multivariate pathways of effects

174 • Topology and sensitivity

175 – Method: Comparison between initial and disturbed abundance: trophic sensitiv-
176 ity

177 – Amplitude of effects is highly variable, and much higher for multivariate pathways
178 of effects

179 – Importance of considering species interactions

- 180 * Univariate pathways of effects simulations clearly show that interactions in-
181 fluence the amplitude of the effects of disturbances

- 182 * Complex interactions = greater variability

- 183 * Control motifs (disconnected &)

184 – Species position and interaction type leads to varying sensitivity

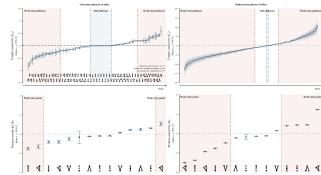
- 185 * Interactions generally amplify effects on species

- 186 * Control motifs largely unaffected

- 187 * Complex interactions more sensitive (i.e. tri-trophic food chain and omnivory)

- 188 * Competitive interactions (Competitive and apparent competition) less sensi-
189 tive

- 190 * Basal resources and top predators generally more sensitive



191 • Topology and amplification

192 – Method: Comparison between full models considering all pathways of effects si-
193 multaneously and additive models considering the sum of the effects of univariate
194 pathways of effect to identify antagonistic, additive and synergistic pathways of
195 effect: trophic amplification

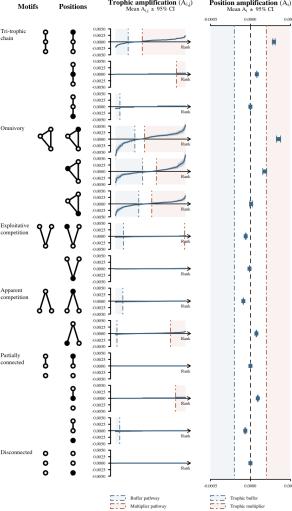
196 – Frequency and variability of non-additive effects more important for omnivory
197 and tri-trophic chain.

198 – Predator release for resources or meso-predators (positive effects)

199 – Limited non-additive effects for control motifs

200 – Competition: antagonism

201 – Complex interactions: more non-additive effects, dominated by synergistic effects
202 for consumers



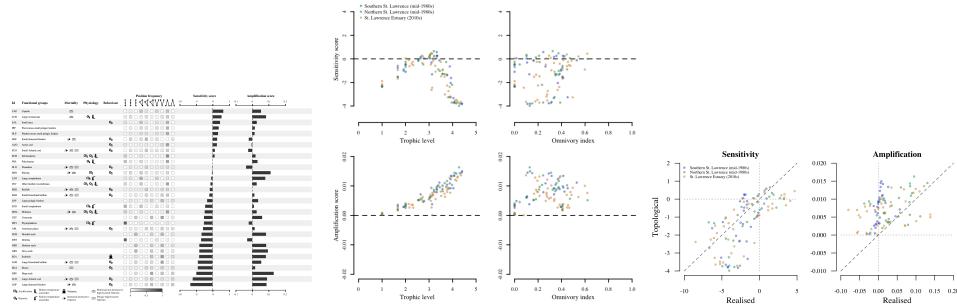
• Complex food webs

- Simulations provide theory informed heuristics that can be used to infer species sensitivity to and amplification of disturbances
- Method: Topological and realised sensitivity and amplification scores; expert opinion on effects of drivers on mortality, physiology and behaviour.
- Empirical food web: Northern Gulf of St. Lawrence, prior to the groundfish stock collapse in the 1990s
- Topological vs realised scores
 - * Interpret biplots
- Trophic level
 - * Realised sensitivity non-linear with trophic level. Lower and higher trophic levels have low sensitivity scores, while intermediate trophic levels have null or positive sensitivity scores
 - * Realised Amplification looks like a sinusoid, with antagonism at low trophic levels which increases to synergism towards intermediate trophic levels. It then drops to antagonisms again at intermediate trophic levels and then increases again towards synergisms for higher trophic levels.
- Food web:
 - * Few biotic sinks, more negative weak entry points
 - * Very few biotic buffers, many biotic multipliers
 - * A species does not have to be impacted directly to have large trophic sensitivity and amplification scores (e.g. seals and seabirds), and direct disturbances do not necessarily result in sensitivity or amplification.
 - * Groundfish collapse: decrease in groundfish species and increase in invertebrates, crustaceans and shrimp (economical shift ensued with fisheries now focused on those species)
 - Groundfish species are negative weak entry points and biotic multipliers
 - Large crustaceans positive weak entry point and biotic multiplier

- 231
- Shrimp biotic sink

232

 - Check up on capelin populations post stock collapse



• Conclusions

- Complex interactions = more sensitive and non-additive effects
- Meso-predator in complex interactions or resources in apparent competition = predator release
- Competitive interactions = less sensitive and more antagonism
- Mechanistic understanding
- Probabilities
- Management

241 Trame narrative :

242 **Intro:** - [1] Cumulative stressors and the problematics that arise from them - [2] Connaisances empiriques et théoriques limitées - [3] Some insights from theory - [4] Theory meets practice - [5] In a management context, we wish to know the effects before we begin to observe extinctions - [6] Objectives

246 **Food webs and multiple stressors:** - [1] Food web dynamics - [2] Indirect effects - [3] Environmental pressures - [4] Effects of disturbances on food webs - [5] Pathways of effects - [6] Non-additive effects - [7] Topology (trophic position and interaction types) - [8] Motifs - [9] Archetypes - [10] Subweb dynamics/insights (Holt 1997; Stouffer 2007) - [11] Definitions - pathway, trophic (position), biotic (species)

251 **Simulated disturbances:** - [1] Models formulation - [2] Models parameterization - [3] Simulated disturbances

253 **Trophic sensitivity:** - [1] Measuring trophic sensitivity - [2] Main results: - Interactions amplify the effects of disturbances

- 255
- Amplitude of effects is highly variable, and much higher for multivariate pathways of effects

256

 - Importance of considering species interactions
 - Univariate pathways of effects simulations clearly show that interactions influence the amplitude of the effects of disturbances

- 260 – Complex interactions = greater variability
261 – Control motifs (disconnected &)
- 262 • Species position and interaction type leads to varying sensitivity
- 263 – Interactions generally amplify effects on species
264 – Control motifs largely unaffected
265 – Complex interactions more sensitive (i.e. tri-trophic food chain and omnivory)
266 – Competitive interactions (Competitive and apparent competition) less sensitive
267 – Basal resources and top predators generally more sensitive

268 **To do:**

- 269 Proposal for Ecology Letters Ideas and Perspectives
270 Check and adjust for unique pathways of effect (exploitative and apparent competition).
271 – They are all unique when you consider the position of the species, except for the disconnected motif.
- 272 Think on the best way to establish position profile. At the moment what is used is
273 the mean of individual pathways of effect per position, and I feel we could do better.
274 ***Perhaps with maximal positional scores.***
- 275 Integrate (Hodgson *et al.* 2019) in the introduction
- 276 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. ->
277 This will be discussed in this paper, and developed in the subsequent spatial paper
- 278 Figure out methodology to evaluate species profile through two indices: sensitivity score
279 and amplification score. These could be used to adjust Halpern's equation later on.
- 280 Cheung, W.W.L., Sarmiento, J.L., Dunne, J., Frolicher, T.L., Lam, V.W.Y., Palomares,
281 M.L.D., Watson, R., and Pauly, D. 2013. Shrinking of fishes exacerbates
282 impacts of global ocean changes on marine ecosystems. Nature Climate Change 3:
283 254-258.
- 284 Uniformiser les indices dans les équations de l'article
- 285 Modify the score for species using realised pathways of effects. I thought that this was
286 done, but since we are not using probabilities, I'm not sure what I should be doing
287 anymore with this. Ideally I would still use a probability and have a general function,
288 but we might still want to keep this for the 4th chapter of the thesis. -> in 4th chapter.
- 289 Verify all codes so that the proper equations are used
- 290 Update thresholds used
- 291 Give proper credit to icons and images used
- 292 Sensitivity and amplification ~ in- and out-degree
- 293 Figure ex. biotic multiplier ~ position
- 294 Evaluate realised score potential (maximum) for each position. Not all pathways could
295 be realised simultaneously, since when a multivariate pathway of effect exists, all of
296 its constituent pathways cannot exist anymore. We could therefore come up with a
297 maximal sensitivity and amplification score. We could then check the maximal possible
298 score for a species and see whether we are close to it or not. Since there can only be a
299 single realised pathway between 3 species, the maximum score would be the pathway
300 of effect with the highest sensitivity and the one with the higher amplification score.
- 301 Check whether the unsensitivity of resources in competitive exploitation is due to the
302 competitive parameters added to the models to get to equilibrium
- 303 If indirect effects are as important as direct effects, then it means that to better understand
304 the impacts of disturbances, it may be as important to look at species beyond
305 our focal species of interest.
- 306 ***Have to look into the importance of direct vs indirect effects***

³¹⁰ **Proposal letter**

³¹¹ **Instructions**

³¹² *Unsolicited proposals, which will be evaluated by the Ideas and Perspectives or*
³¹³ *Reviews and Syntheses Editors, in consultation with the Editorial Board and*
³¹⁴ *Editor-in-Chief, prior to a full submission. Proposals should be no more than*
³¹⁵ *300 words long, describe the nature and novelty of the work, the contribution*
³¹⁶ *of the proposed article to the discipline, and the qualifications of the author(s)*
³¹⁷ *who will write the manuscript. Proposals should be sent to the Editorial Office*
³¹⁸ *(ecolets@cefe.cnrs.fr).*

³¹⁹ **Notes**

- ³²⁰ • In it's current form, I believe that the contribution portion is not good enough
³²¹ • I wonder whether the qualitifications should be more in depth.
³²² • Right now, the letter is 43 words over the word limit.
³²³ • Also, this text might be better than the current abstract

³²⁴ **Letter**

³²⁵ Evaluating the effects of multiple sources of stress in natural environments has become an
³²⁶ increasingly important issue as the effects of intensifying global change and expanding hu-
³²⁷ man activities result in complex stress exposure regimes. Even though the non-additive
³²⁸ effects of multiple stressors have been investigated empirically for a few decades now, there
³²⁹ remains a general lack of theoretical understanding of their impacts on natural systems.
³³⁰ In particular, the role of species and their interactions in mediating the effects of multiple
³³¹ disturbances through ecological communities, although widely acknowledged, has yet to be
³³² formally explored. We propose the first such formal exploration by exhaustively simulating
³³³ the impacts of all possible pathways of effects on the dynamics of 3-species motifs using
³³⁴ Lotka-Volterra models. We uncover that interaction types and species position greatly influ-
³³⁵ ence sensitivity to and amplification of multiple disturbances and that indirect pathways of
³³⁶ effects are the main cause of non-additive effects. In particular, predators in food chain and
³³⁷ omnivory interactions act as both weak entry points (*i.e.* highly sensitive to disturbances)
³³⁸ and biotic amplifiers (*i.e.* affected synergistically by disturbances). We then use the simlu-
³³⁹ ated sensitivity and amplification scores as heuristics to infer trophic vulnerability of species
³⁴⁰ based on topology and realised pathways of effects in the food web of the Northern Gulf of
³⁴¹ St. Lawrence, Canada, prior to a groundfish stock collapse in the 1990s. We find that heavily
³⁴² exploited species appear to be the most vulnerable trophically, while fisheries transitioned
³⁴³ to insensitive or beneficiary species post-collapse. This contribution is significant and timely
³⁴⁴ theoretically as the first exploration of the effects of multiple disturbances on structural prop-
³⁴⁵ erties of food webs, as well as practically by answering questions crucial to management.
³⁴⁶ Our group of co-authors is singularly positioned to write this paper. D. Beauchesne and

³⁴⁷ P. Archambault both have strong backgrounds in environmental assessments in general and
³⁴⁸ cumulative impacts in particular. K. Cazelles and D. Gravel are both experts in theoretical
³⁴⁹ ecology with strong backgrounds and recognition in the field.

³⁵⁰ **Cover letter and novelty statement**

³⁵¹ **Letter**

³⁵² **Documents joined**

³⁵³ **Reviewers**

³⁵⁴ **Proposed reviewers:**

- ³⁵⁵ • Reviewer 1
- ³⁵⁶ • Reviewer 2
- ³⁵⁷ • Reviewer 3

³⁵⁸ **Conflicts of interest:**

- ³⁵⁹ • In-conflict individual and reason

³⁶⁰ **Conflict of interest statement**

³⁶¹ The authors declare that the submitted work was carried out in the absence of any personal,
³⁶² professional or financial relationships that could potentially be construed as a conflict of
³⁶³ interest.

³⁶⁴ **1 Abstract**

³⁶⁵ Global changes are resulting in increasingly intricate environmental stress exposure regimes.

³⁶⁶ These can in turn induce complex and unpredictable environmental effects permeating entire
³⁶⁷ ecological communities by way of species interactions.

³⁶⁸ The role of species and their interactions in mediating the effects of multiple disturbances
³⁶⁹ on food webs is however still understudied. Experimental and *in situ* approaches provide
³⁷⁰ limited insight, while theoretical approaches have yet to fully tackle the issue.

³⁷¹ Using Lotka-Volterra equilibria models of the 4 most common 3-species motifs in empirical
³⁷² food webs, we show that trophic position and interaction type influence the sensitivity to
³⁷³ and the amplification of the effects of multiple disturbances.

³⁷⁴ We then show that how species are embedded in complex food webs and the types of dis-
³⁷⁵ turbances they are exposed to dictates their sensitivity to multiple sources of stress.

³⁷⁶ Our results illustrate the importance of explicitly considering species interactions to properly
³⁷⁷ capture the effects of multiple stressors and safeguard ecological communities against global
³⁷⁸ changes.

³⁷⁹ Global changes are creating intricate stress exposure regimes that induce unpredictable en-
³⁸⁰ vironmental effects permeating entire ecological communities by way of species interactions.

³⁸¹ The role of species and their interactions in mediating the effects of multiple disturbances on
³⁸² food webs remains understudied. Experimental and *in situ* approaches provide contextual
³⁸³ insights, while theory has yet to fully tackle the issue. Using Lotka-Volterra models, we
³⁸⁴ show that topology (i.e. trophic position and interaction type) influences the sensitivity to
³⁸⁵ and the amplification of the effects of multiple disturbances.

³⁸⁶ We show that species position in complex food webs and the types and combinations of
³⁸⁷ disturbances they are exposed to dictates their sensitivity to multiple sources of stress. Our
³⁸⁸ results illustrate the importance of considering species interactions and non-additive effects

³⁸⁹ to capture the effects of multiple disturbances and safeguard ecological communities against
³⁹⁰ global changes.

³⁹¹ Contribution: we define multiple types of ecological outcomes from different pathways of
³⁹² effects, i.e. weak entry points, biotic sinks, biotic buffers and biotic amplifiers.

³⁹³ Surprises: non-additive effects Interactions: affects the amplitude of the predicted effects of
³⁹⁴ disturbances Explain why 2 disturbances make the situation more complex when considering
³⁹⁵ interactions

³⁹⁶ We provide theory-driven heuristics to inform the likely effects of multiple stressors based
³⁹⁷ on trophic knowledge (see Hodgson *et al.* 2019)

³⁹⁸ 2 Introduction 2

³⁹⁹ Global changes and human activities result in increasingly intricate environmental stress
⁴⁰⁰ exposure regimes that can induce complex and unpredictable effects (???: Côté *et al.* 2016;
⁴⁰¹ Bowler *et al.* 2019). This cocktail of environmental pressures impedes our ability to evaluate
⁴⁰² and partition the effects of interacting drivers in cumulative effects assessments (???: ???:
⁴⁰³ Jones 2016). This is in part due to the breadth and interaction potential of environmental
⁴⁰⁴ pressures operating on natural systems (Côté *et al.* 2016), compounding the pathways of
⁴⁰⁵ effects through which natural systems can be impacted. Another aspect is the potential
⁴⁰⁶ for non-additive affects, *i.e.* when the effect of multiple interacting drivers is greater (*i.e.*
⁴⁰⁷ synergism) or lower (*i.e.* antagonism) than the sum of their individual parts. These effects
⁴⁰⁸ seem to be the norm rather than the exception with the effects of multiple drivers (*e.g.*
⁴⁰⁹ Darling & Côté 2008; ???; Crain *et al.* 2008; Jackson *et al.* 2016).

⁴¹⁰ Common drivers of environmental stress include climate change, resource exploitation and
⁴¹¹ pollution (???: ???). Drivers have typically been described according to their effect on
⁴¹² habitats. For instance, fisheries can destroy habitats and extract biomass, while marine
⁴¹³ traffic affects noise levels. At the species scale, drivers may be more appropriately described
⁴¹⁴ as ecological modifiers, which we define as natural or anthropogenic processes that disturb a
⁴¹⁵ single or multiple ecological processes. Through this lens, fisheries may be a modifier of cod
⁴¹⁶ behaviour and mortality, and marine traffic a modifier of whale behaviour.

⁴¹⁷ Drivers can affect a variety of ecological processes such as behaviour (*e.g.* ???), reproduction
⁴¹⁸ (*e.g.* ???), physiology (*e.g.* ???), mortality (*e.g.* ???) and species interactions (*e.g.* ???).

⁴¹⁹ Species interactions are of particular interest, as they may serve as the indirect pathways
⁴²⁰ through which pressures permeate entire ecological communities (Wootton 2002; Bascompte
⁴²¹ 2009; Montoya *et al.* 2009; Thompson *et al.* 2018). Indirect effects, *i.e.* when two or more
⁴²² direct effects are linked by a single species involved in both effects, may be as important of,
⁴²³ and propagate faster than, direct effects (Wootton 1993, 2002; Menge 1995; Yodzis 2000). In

⁴²⁴ multi-species systems, where both direct and indirect effects are operating simultaneously, it
⁴²⁵ is expected that the effects of environmental pressures will be amplified or dampened through
⁴²⁶ biotic interactions (???: Wootton 2002; Thompson *et al.* 2018). Interaction strength and
⁴²⁷ type (*e.g.* omnivory vs apparent competition) have also been linked to enhanced or decreased
⁴²⁸ community persistence (???: ???: Allesina & Pascual 2008). How species are embedded in
⁴²⁹ complex communities is therefore likely to affect their sensitivity to and amplification of
⁴³⁰ single and multiple disturbances.

⁴³¹ This has not been done because it is complex. It however offers a mechanistic understanding
⁴³² that has thus far eluded studies on the effects of multiple stressors.

⁴³³ Current practice to identify the effects of multiple drivers has been relying on approaches
⁴³⁴ that provide little insight into the underlying ecological mechanisms (Griffen *et al.* 2016;
⁴³⁵ Jackson *et al.* 2016; De Laender 2018; Schäfer & Piggott 2018). There has been an upsurge
⁴³⁶ of theory-driven modelling approaches to address this lack of mechanistic understanding (*e.g.*
⁴³⁷ Hodgson *et al.* 2017; De Laender 2018; Galic *et al.* 2018; Thompson *et al.* 2018). These
⁴³⁸ approaches provide frameworks under which predictions can be tested against well-defined
⁴³⁹ underlying assumptions (De Laender 2018). Crucially, they also provide the ability to explore
⁴⁴⁰ the many different pathways of effects through which stressors can affect ecosystems across
⁴⁴¹ scales of biological organization (Galic *et al.* 2018; Guiden *et al.* 2019; Hodgson & Halpern
⁴⁴² 2019; Hodgson *et al.* 2019).

⁴⁴³ The complexity of empirical food webs is prohibitive when studying community dynamics.
⁴⁴⁴ Studying smaller subgraphs - community motifs or modules - has thus emerged as an alter-
⁴⁴⁵ native to gather insights into the dynamics and stability of complex ecological communities
⁴⁴⁶ (Holt 1997; Holt & Hochberg 2001). Motifs are collections of n -species that, when put
⁴⁴⁷ together, construct whole food webs (Milo *et al.* 2002; Stouffer *et al.* 2007). They form
⁴⁴⁸ the backbone of food webs and provide a mesoscale characterization of community struc-
⁴⁴⁹ ture (Bascompte & Melián 2005; Stouffer *et al.* 2007). Their dynamics has been studied

extensively to uncover how structural properties of food webs can benefit community persistence and stability (Allesina & Pascual 2008; Kondoh 2008; Stouffer & Bascompte 2010, 2011; Monteiro & Faria 2016) and to assess the structural roles of species within food webs (Stouffer *et al.* 2012; Cirtwill & Stouffer 2015).

Four 3-speciees motifs have received particular attention in theoretical and empirical studies due to their roles (???) and prevalance (Camacho *et al.* 2007; Stouffer & Bascompte 2010) in food webs: tri-trophic food chain, omnivory or intraguild predation, exploitative competition and apparent competition. -> Paragraph(s) on them, with some archetypes as examples

Meaningful insights for conservation are provided by investigations using motifs to study community stability and persistence. For example, results from Stouffer *et al.* (2012) suggests that species trophic benefits to community persistence could be a valuable conservation target, as role diversity does not directly correlate to species richness. In the context of the management of the effects of multiple stressors, additional insights could be gleaned from studying motifs at equilibrium, *i.e.* when the dynamics of the system is constrained by species coexistance. This is of particular relevance to managers using ecosystem-based approaches to manage and maintain exploited populations. Dynamic models of motifs could then help us in

Here, we investigate the role of species in mediating the effects of multiple disturbances on food webs. In doing so, we seek to answer questions of particular significance to management: 1) should species interactions be considered in impact assessments, 2) should the effects of stressors be evaluated seperately or in combination, and 3) which species are most sensitive to disturbances?

⁴⁷² **3 Introduction**

⁴⁷³ Global changes and human activities result in increasingly intricate environmental stress
⁴⁷⁴ exposure regimes that can induce complex and unpredictable effects (Halpern *et al.* 2015;
⁴⁷⁵ Côté *et al.* 2016; Bowler *et al.* 2019). Common drivers of stress include climate change,
⁴⁷⁶ resource exploitation and pollution (???). This cocktail of environmental pressures impedes
⁴⁷⁷ our ability to evaluate and partition the effects of interacting stressors in cumulative effects
⁴⁷⁸ assessments (??; ??; Jones 2016). This is in part due to the breadth of environmental
⁴⁷⁹ pressures operating on natural systems and their interaction potential (Côté *et al.* 2016),
⁴⁸⁰ effectively constraining *in situ* and experimental approaches to simplified and contextual
⁴⁸¹ conclusions.

⁴⁸² Thus far, much of the evidence gathered on the cumulative effects of multiple stressors has
⁴⁸³ focused on identifying the prevalence of non-additive effects.

⁴⁸⁴ Non-additive effects are...

⁴⁸⁵ This is of particular relevance to management, as single-driver assessments are still over-
⁴⁸⁶ whelmingly applied (???) even though evidence suggests that non-additive effects are the
⁴⁸⁷ norm rather than the exception when dealing with the effects of multiple stressors (*e.g.*
⁴⁸⁸ Darling & Côté 2008; ???; Crain *et al.* 2008; Jackson *et al.* 2016).

⁴⁸⁹ Current practice to identify the effects of multiple stressors has been relying on approaches
⁴⁹⁰ that provide little insight into the mechanisms underlying the effects of multiple stressors
⁴⁹¹ (Griffen *et al.* 2016; Jackson *et al.* 2016; De Laender 2018; Schäfer & Piggott 2018). There
⁴⁹² has been an upsurge of theory-driven modelling approaches to address this lack of mechanistic
⁴⁹³ understanding (*e.g.* Hodgson *et al.* 2017; De Laender 2018; Galic *et al.* 2018; Thompson
⁴⁹⁴ *et al.* 2018). These approaches provide frameworks under which predictions can be tested
⁴⁹⁵ against well-defined underlying assumptions (De Laender 2018). Crucially, they also provide
⁴⁹⁶ the ability to explore the many different pathways of effects through which stressors can
⁴⁹⁷ affect ecosystems across scales of biological organization (Galic *et al.* 2018; Guiden *et al.*

498 2019; Hodgson & Halpern 2019; Hodgson *et al.* 2019).

499 Stressors can affect numerous biological processes such as behaviour (*e.g.* ???), reproduction
500 (*e.g.* ???), physiology (*e.g.* ???), mortality (*e.g.* ???) and species interactions (*e.g.*
501 ???). Species interactions are of particular interest for the evaluation of the effects of single
502 and multiple stressors, as they may serve as the indirect pathway through which pressures
503 permeate entire ecological communities (Wootton 2002; Bascompte 2009; Montoya *et al.*
504 2009; Thompson *et al.* 2018). Indirect effects, *i.e.* when two or more direct effects are
505 linked by a single species involved in both effects, may be as important of, and propagate
506 faster than, direct effects (Wootton 1993, 2002; Menge 1995; Yodzis 2000). In multi-species
507 systems, where both direct and indirect effects are operating simultaneously, it is expected
508 that the effects of environmental pressures will be amplified or dampened through biotic
509 interactions (???; Wootton 2002; Thompson *et al.* 2018). How species are embedded in
510 complex communities is therefore likely to affect its sensitivity to and amplification of single
511 and multiple stressors.

512 Here, we investigate the

513 Here, we investigate the role of species in mediating the effects of multiple disturbances on
514 food webs. In doing so, we seek to answer questions of particular significance to management:
515 1) should species interactions be considered in impact assessments, 2) should the effects of
516 stressors be evaluated separately or in combination, and 3) which species are most sensitive
517 to disturbances?

518 4 Of food webs and multiple disturbances

519 Food web structure Stressors and how they penetrate food webs (act as factors modifying
520 community dynamics) Simplifying community dynamics through motifs Studying motif dy-
521 namics to better understand how interaction type and position (*i.e.* topology) influences

522 sensitivity to and amplification of disturbances Definitions that we provide in the paper

523 Sprinkle examples throughout

524 drivers are biotic modifiers

525 The complexity of empirical food webs is prohibitive when studying community dynamics.

526 Studying smaller subgraphs - community motifs or modules - has thus emerged as an alter-

527 native to gather insights into the dynamics and stability of complex ecological communities

528 (Holt 1997; Holt & Hochberg 2001). Motifs are collections of n -species that, when put

529 together, construct whole food webs (Milo *et al.* 2002; Stouffer *et al.* 2007). They form

530 the backbone of food webs and provide a mesoscale characterization of community struc-

531 ture (Bascompte & Melián 2005; Stouffer *et al.* 2007). Their dynamics has been studied

532 extensively to uncover how structural properties of food webs can benefit community per-

533 sistence and stability (Allesina & Pascual 2008; Kondoh 2008; Stouffer & Bascompte 2010,

534 2011; Monteiro & Faria 2016) and to assess the structural roles of species within food webs

535 (Stouffer *et al.* 2012; Cirtwill & Stouffer 2015).

536 Four 3-speciees motifs have received particular attention in theoretical and empirical studies

537 due to their roles (???) and prevalance (Camacho *et al.* 2007; Stouffer & Bascompte 2010) in

538 food webs: tri-trophic food chain, omnivory or intraguild predation, exploitative competition

539 and apparent competition. -> Paragraph(s) on them, with some archetypes as examples

540 Meaningful insights for conservation are provided by investigations using motifs to study

541 community stability and persistence. For example, results from Stouffer *et al.* (2012) sug-

542 gests that species trophic benefits to community persistence could be a valuable conservation

543 target, as role diversity does not directly correlate to species richness. In the context of the

544 management of the effects of multiple stressors, additional insights could be gleaned from

545 studying motifs at equilibrium, *i.e.* when the dynamics of the system is constrained to

546 the space in which all species coexist. This is of particular relevance to managers using

547 ecosystem-based approaches to manage and maintain exploited populations. Dynamic mod-

548 els of motifs could then help us in

549 De Laender (2018) discusses how the effects of multiple stressors could affect the coexistence
550 of two species competing for shared resources through different pathways of effects.

551 insights for management, whose interest focuses on what happens between persistence and
552 extinction.

- 553 • *The ecological role of a species in a network is a direct result of its interactions with*
554 *other species (Luczkovich 2003; Olesen 2007; Allesina 2009) (in Stouffer 2012)*

555 For amplification, reread and cite Thompson's article.

556 • Weak entry points

557 • Sinks

558 • Buffers (cite Montoya et al. 2009)

559 • Multipliers

560 [1] Food web dynamics - The dynamics of multi-species systems is governed by species
561 interactions. - Trophic interactions in particular are essential to energy and nutrient flows
562 in complex systems.

563 [2] Indirect effects - Through these interactions arise indirect effects, *i.e.* two or more direct
564 effects linked by a single species involved in both effects (Wootton (1993); Wootton (2002)).
565 - For example, [...] - Indirect effects may be as important of, and propagate faster than,
566 direct effects (Menge (1995); Wootton (2002)). - In multi-species systems, both direct and
567 indirect effects are expected to operate simultaneously, with the potential to amplify or
568 dampen their individual effects (Wootton (2002))

569 [3] Environmental pressures - Density-mediated effects as well as effects affecting species
570 interactions, which gathers the different types of indirect effects discussed by wooton2002. -

571 Consequently, it is expected that the effects of environmental pressures will also be amplified
572 or dampened through biotic interactions as a function of their configuration and strength
573 (Wootton (2002); (??)).

- 574 • Different types of interactions will lead to different overall effects (???).
- 575 – Different sensitivity for species involved in different types of interactions (segway
576 to motifs) -> concept
- 577 • [1] Food web dynamics
- 578 – Energy flow in complex systems is dependent on species trophic interactions
- 579 – Importance of species interactions
- 580 – Energy flow in complex systems
- 581 – indirect effects can be as important as direct effects, and may propagate through
582 food webs faster than food webs by affecting pathways that may be impacted
583 instantaneously (wootton2002; menge1995)
- 584 – suggesting that species co-tolerance must be taken into account (vinebrooke2004)
- 585 * If we break down the complexity of the trophic position of a species, we can
586 evaluate the total sensitivity of a species as the sum of all the interaction
587 types it is involved i
- 588 • [2] Indirect effects
- 589 – Multiplies the number of pathways of effects ((??))
- 590 – We focus on density-mediated indirect effects (see wooton2002 and menge1995)
- 591 – In complex multi-species communities, multiple direct and indirect pathways are
592 likely to be operating simultaneously, potentially reinforcing or cancelling each
593 other's overall effects ((??))

594 – the role of biotic interactions in transmitting environmental variation may be
595 either amplified or dampened, depending on the configuration and strength of
596 direct and indirect effects ((??); (??))

597 – Infinitely more indirect than direct pathways ((??))

598 • [3] Environmental pressures

599 – Global changes and direct human activities -> environmental pressures / drivers
600 / disturbances

601 – In a food web context, it depends on species tolerance and co-tolerance to drivers

602 – Species tolerance ((??))

603 – Multiple

604 • Global changes and human activities impose environmental pressures on ecological
605 communities.

606 – For example

607 •

608 • These pressures may penetrate food webs via many direct and indirect pathways of
609 effects.

610 – For example

611 • Species co-tolerance

612 – Species interactions play a role in mediating non-linear effects of environmental
613 stressors (thompson2018 Ecography)

614 – Importance of ecological novelties and how they can induce non-additive effects
615 through predator-prey interactions (Guiden *et al.* (2019))

- 616 • [4] Effects of disturbances on food webs
- 617 – What we know: robustness to extinctions, importance of indirect effects
- 618 • [5] Pathways of effects
- 619 • [6] Non-additive effects
- 620 • [7] Topology (trophic position and interaction types)
- 621 – Position of species in complex food webs affects their benefits to community
- 622 persistence (Stouffer *et al.* (2012))
- 623 • [8] Motifs
- 624 – to understand how topology influences sensitivity to and amplification of disturbances
- 625
- 626 • [9] Archetypes
- 627 • [10] Subweb dynamics/insights (Holt 1997; Stouffer 2007)
- 628 • [11] Definitions - pathway, trophic (position), biotic (species)
- 629 – Weak entry points
- 630 – Sinks
- 631 – Buffers (cite Montoya et al. 2009)
- 632 – Multipliers
- 633 • Species are linked
- 634 • Disturbing one means that you will likely disturb another one
- 635 • The position and types of interactions a species is involved in will affect its sensitivity to multiple disturbances
- 636

- 637 • In real systems, food webs are threatened by many environmental pressures that can
638 penetrate them in many different ways.

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

643 **4.1 Other thoughts, clean up**

644 • **Motif description and use**

- 645 – A food web can be decomposed into a set of smaller n -species subgraphs called
646 motifs (???: Stouffer *et al.* 2007). For example, there are 13 distinct 3-species
647 motifs composed of 30 unique positions (Stouffer *et al.* 2007, 2012). Motifs are
648 the backbone of food webs and their study has unearthed valuable insights on
649 community dynamics such as [...].
- 650 – Their type and frequency has been linked to food web stability and persistence
651 (???)
- 652 – Like many disturbance studies in theoretical ecology, however, these have focused
653 less on the dynamics of population abundances and more on the resistance of food
654 webs to extinctions.
- 655 – Motifs have been used to investigate the persistence of food web to species ex-
656 tinctions (Stouffer & Bascompte 2010) and the benefit associated to each species
657 in food web persistence (Stouffer *et al.* 2012).
- 658 – *The ecological role of a species in a network is a direct rest if its interactions with*
659 *other species (Luczkovich 2003; Olesen 2007; Allesina 2009) (in Stouffer 2012)*
- 660 – *The number and types of motifs that make up a food web are known to directly*
661 *affect the web’s stability and persistence (Neutel 2002; Kondoh 2008; Allesina*

662 2008; García-Domingo 2008; Stouffer 2010; in Stouffer 2012)

663 • Our focus

- 664 – Here we focus on the most abundant types of interactions: omnivory, tri-trophic
665 food chain, exploitative competition and apparent competition (Camacho *et al.*
666 2007; Stouffer & Bascompte 2010)
- 667 – Two additional motifs, *i.e.* partially connected and disconnected were also consid-
668 ered in order to evaluate whether interactions in food webs are truly more likely
669 to be characterized by non-linear effects.
- 670 – To study the effects of multiple stressors in a trophic context, we rather focus on
671 the resulting disturbances following different pathways of effect rather than on
672 the disturbances themselves. This means that we will not investigate the effects
673 of multiple stressors applied to a single species in the food web. This precludes us
674 from investigating the sensitivity of species to each individual stressor. Rather, we
675 investigate the effects of disturbances to multiple species simultaneously. But see
676 Thompson *et al.* (2018) and (???) for a description of a modelling approach-
677 incorporating multiple sources of stress in a food web model.
- 678 – We are interested in pathways that affect the trophic dynamic of food webs, *i.e.*
679 those that target population growth (*i.e.* birth and death rates) and the rates at
680 which species interact (*i.e.* attack and conversion rates).

681 • Terminology for types of pathways and position profile

- 682 – Species can occupy different roles in these pathways of multiple effects. Inves-
683 tigating species profile (e.g.* Stouffer *et al.* 2012) could thus inform us on the
684 role played by individual species in buffering against or amplifying the effects of
685 multiple disturbances.
- 686 – We define 4 key roles in species propagating or buffering against multiple distur-
687 bances:

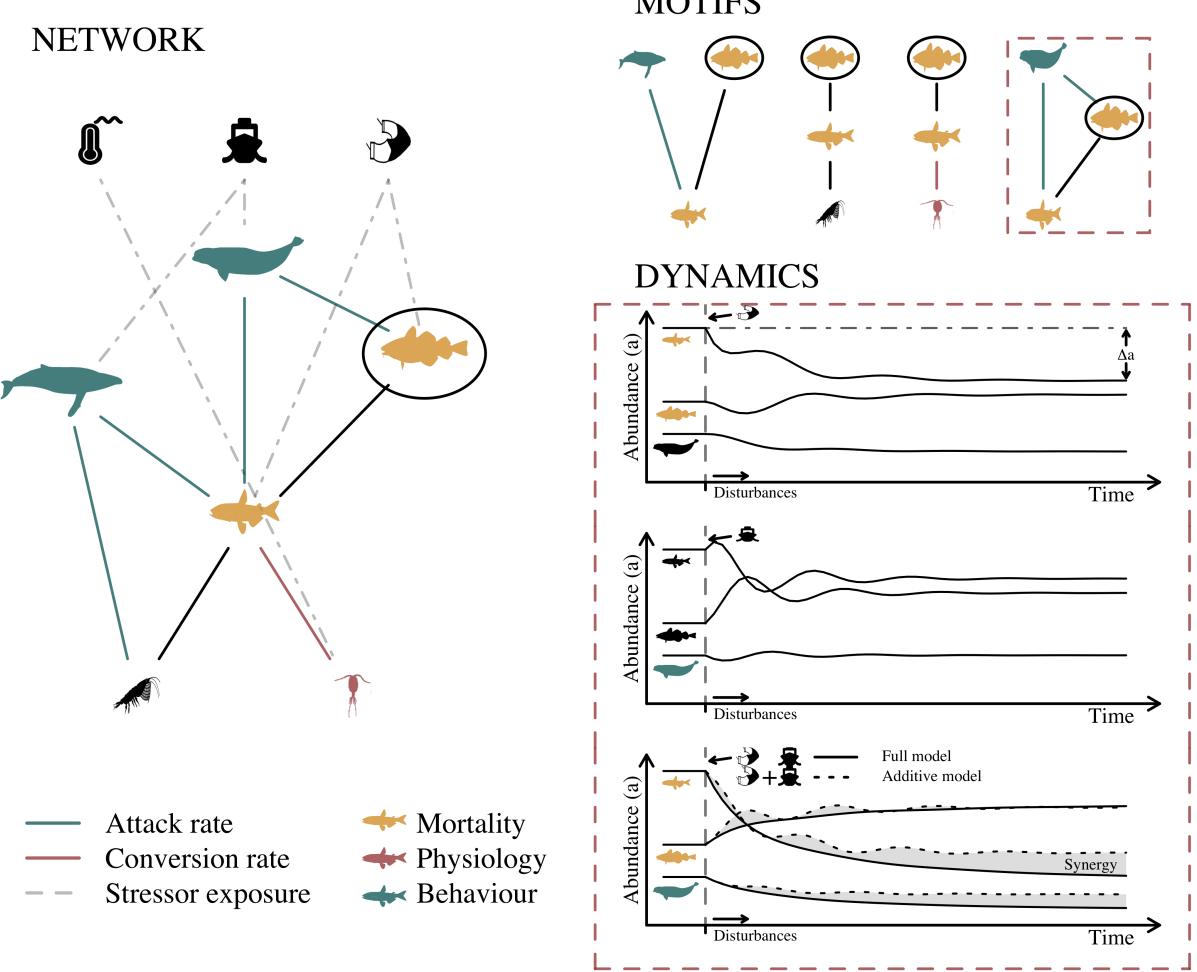


Figure 2: Conceptualize the effects of multiple disturbances on food webs

688 **5 Sumulating disturbances on food webs**

689 **5.1 Models**

690 The dynamics of the four most abundant 3-species motifs (*i.e.* tri-trophic food chain, om-
691 nivory, exploitative and apparent competition) in empirical food webs (Stouffer & Bascompte
692 2010) were modeled using Lotka-Volterra equation systems (Table S1). Two additional motifs
693 were included to serve as controls to test the importance of considering species interactions
694 when evaluating environmental effects, *i.e.* a partially connected motifs with a disconnected
695 species and a predator-prey interaction, and a fully disconnected motif with three indepen-
696 dent species.

697 Resources were modeled using logistic growth equations of the form

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

698 ,

699 where X are species, i is the resource, j are the consumers, r_i is the intrinsic resource growth
700 rate, α_{ii} is the density-dependent effect of the resource on itself and α_{ij} is the rate at which
701 consumer j affects resource i , *i.e.* the attack rate.

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

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

703 ,

704 where m is the mortality rate and e is the rate at which resource biomass is transformed
705 into consumer biomass, *i.e.* the conversion rate, and is a scaling parameter of the attack
706 rate which cannot exceed 1.

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

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

710 were included in the consumer models to constrain their growth.

711 5.2 Disturbances

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

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

726 6 Trophic sensitivity

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

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

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

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

735 We define *weak entry pathways* and *sink pathways* as those pathways whose effect on the
736 abundance of a motif position exceeds 1% ($S_{i,j} < -1\%$ or $S_{i,j} > 1\%$) and is null (*i.e.*
737 $S_{i,j} = 0$), respectively (2).

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

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

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

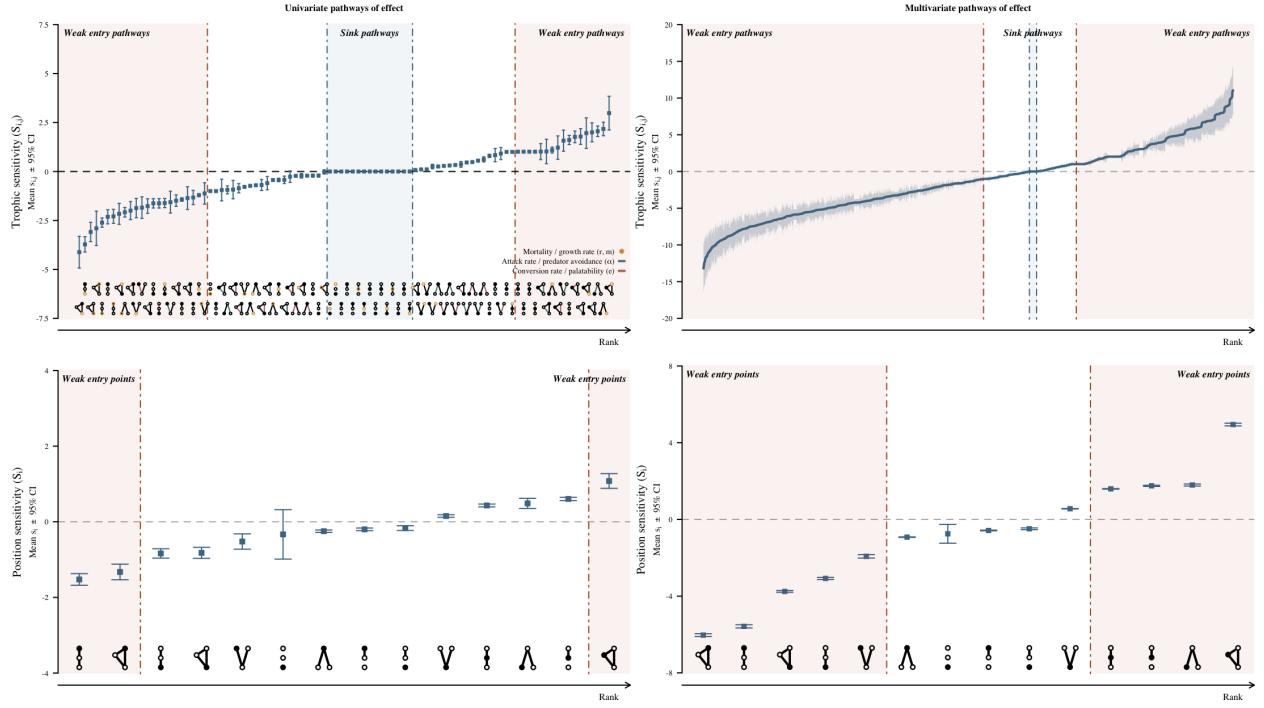


Figure 3: Disturbances. Line 1: Univariate disturbances; Line 2: Multivariate disturbances

742 7 Trophic amplification

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

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

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

747 where K_j is a multivariate pathway of effect j and k_j are unitary pathways of effect compo-
 748 sition j . The amplification score evaluates the deviance of a multivariate pathway of effect
 749 and the sum of the univariate effects composing the pathway of effect, *i.e.* the additive
 750 model. Thus, a value of 0 identifies a null of additive effect, a value below 0 identifies an

⁷⁵¹ antagonistic effect, and a value over 0 identifies synergistic effects.

⁷⁵² We define *antagonistic pathways* and *synergistic pathways* as those pathways whose effect on
⁷⁵³ the abundance of a motif position is significantly different than the additive model, while
⁷⁵⁴ *additive pathways* are those pathways whose effect is not significantly different than the
⁷⁵⁵ additive model (2).

⁷⁵⁶ A score of position amplification (A_i) was evaluated using the mean of the set of all possible
⁷⁵⁷ pathways of effect (K^i) for a give position i :

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

⁷⁵⁸ We define *biotic buffers* and *biotic multipliers* as positions whose amplification score is sig-
⁷⁵⁹ nificantly different than 0, while *biotic invariants* are positions whose amplification score is
⁷⁶⁰ not significantly different than 0 (2).

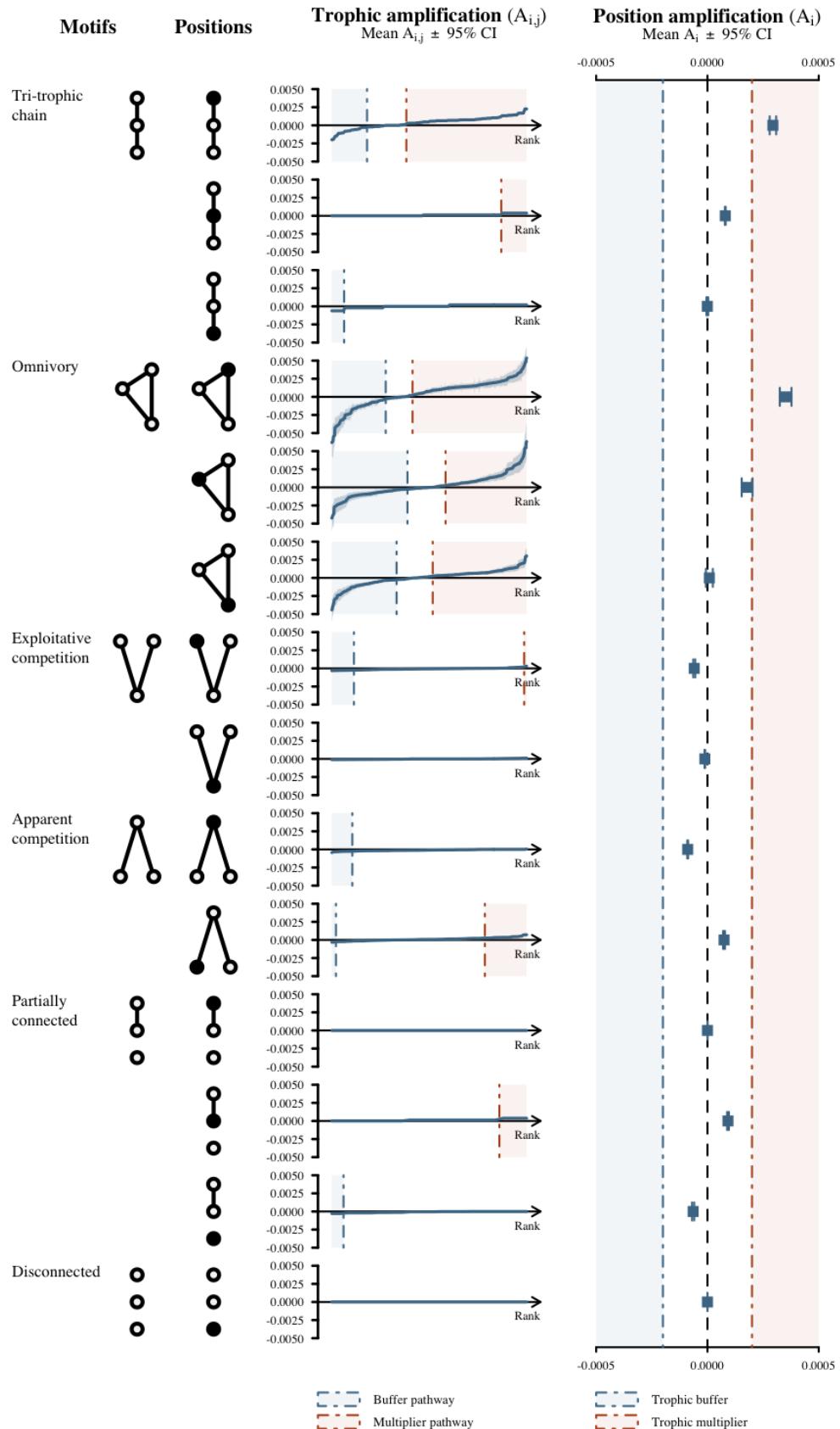


Figure 4: Motif positions and disturbances
34

761 **8 Species role to food web sensitivity to multiple dis-**
762 **turbances**

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

$$S_m = \sum_i f_m i S_i$$

$$A_m = \sum_i f_m i A_i$$

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

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

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

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

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

₇₇₃ **8.1 Empirical food webs**

₇₇₄ We used empirical food web data from the Estuary and Gulf of St. Lawrence, in eastern
₇₇₅ Canada, to evaluate the sensitivity and amplification scores of its constituent species. The
₇₇₆ food webs come from different regions of the St. Lawrence and different time periods, and
₇₇₇ contain different yet overlapping functional groups. The Northern (???) and Southern (???)
₇₇₈ St. Lawrence food webs were for the mid-1980s, prior to the groundfish stock collapses of
₇₇₉ the early 1990s, and contain the same functional groups. The Estuary food web, mean-
₇₈₀ while, contains more functional groups and represents the beginning of the 2010s (???). See
₇₈₁ supplementary materials for a description of the food webs used for this analysis.

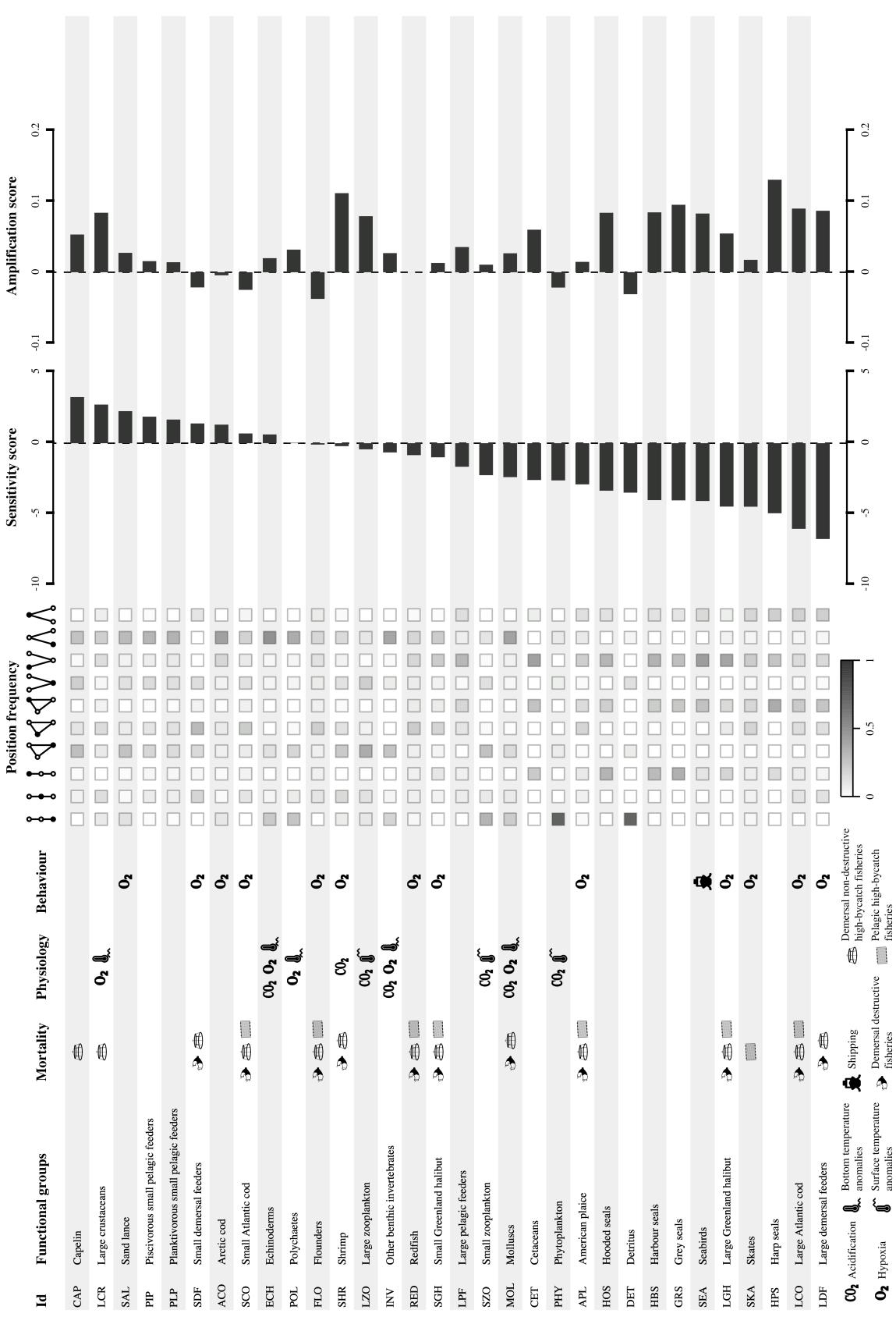


Figure 5: Species scores for the St. Lawrence

782 9 Supplementary Figures

783 9.1 Simulation figures

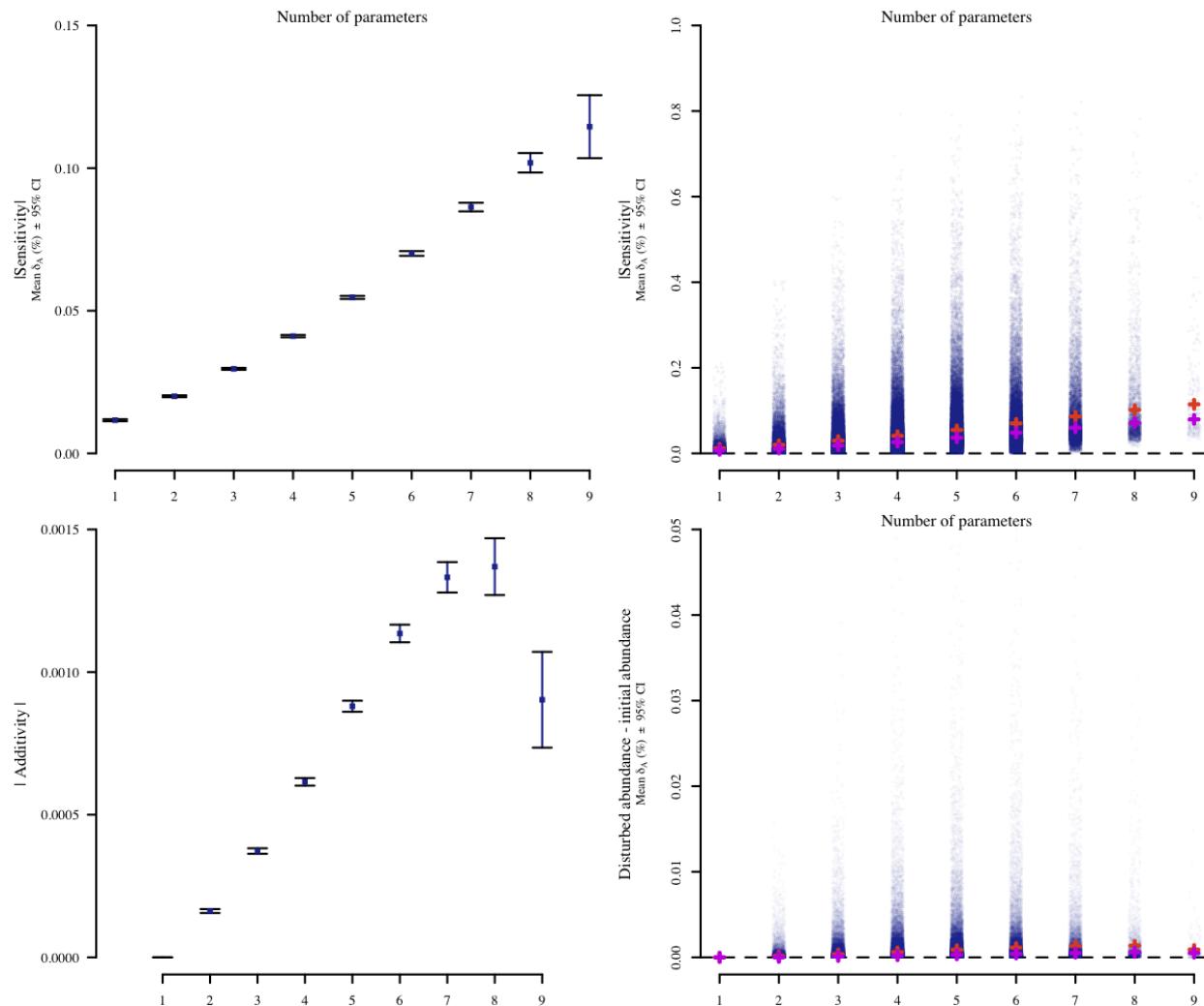


Figure 6: Mean delta abundance and difference between joint and additive models as a function of the number of parameters

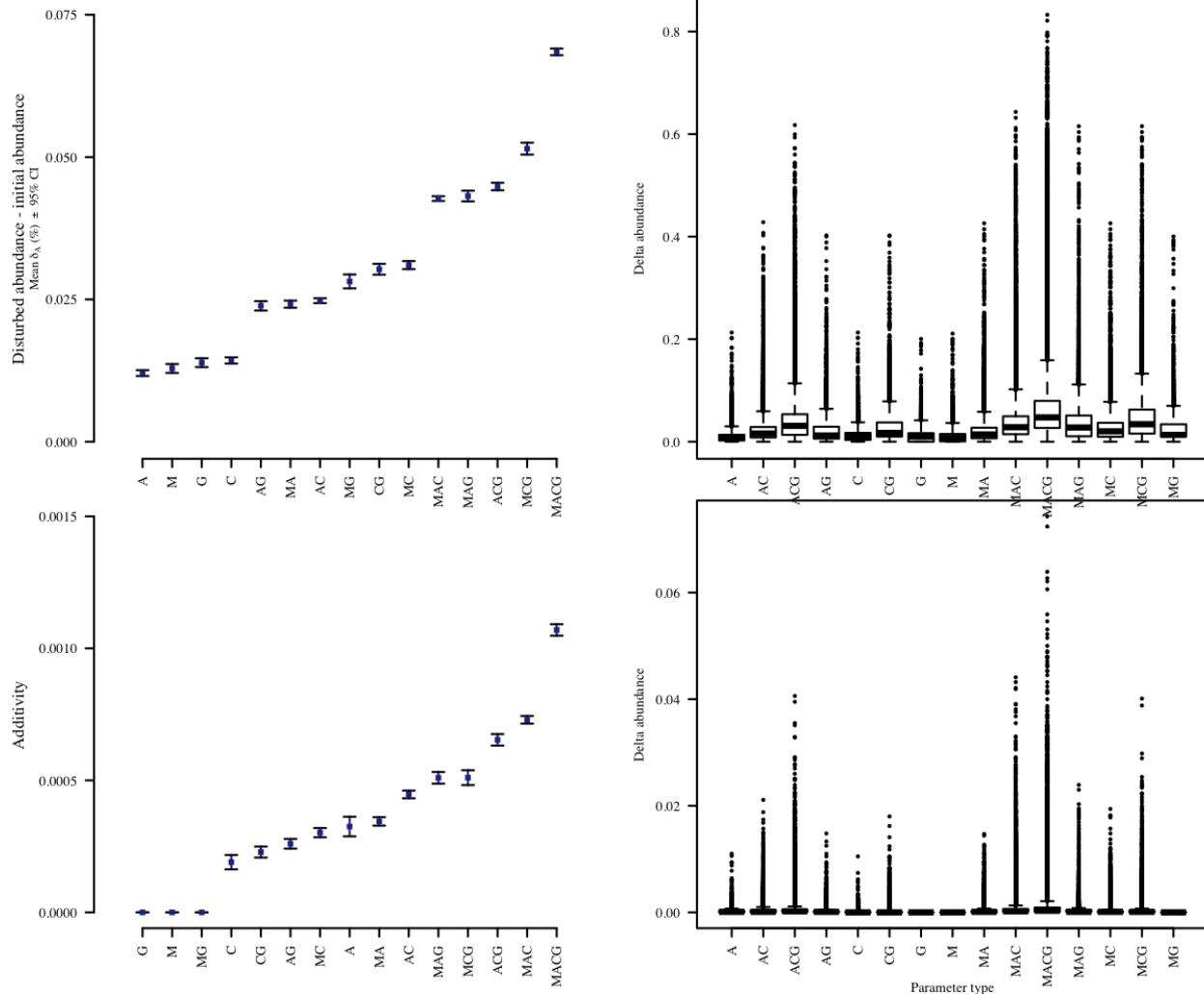


Figure 7: Mean delta abundance and difference between joint and additive models as a function of the types of parameters, i.e. growth/mortality rates, attack rates and conversion rates

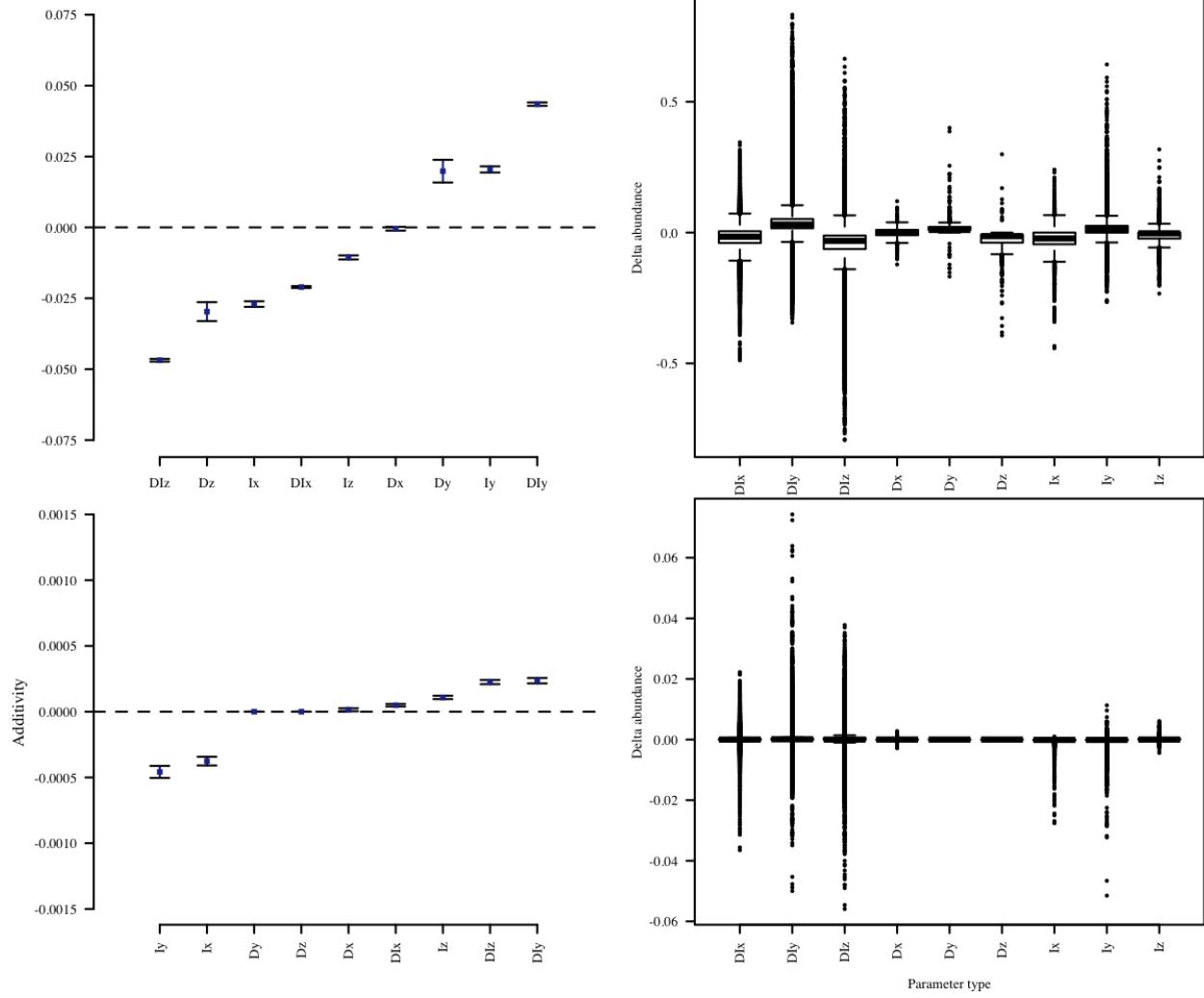


Figure 8: Direct vs indirect effects

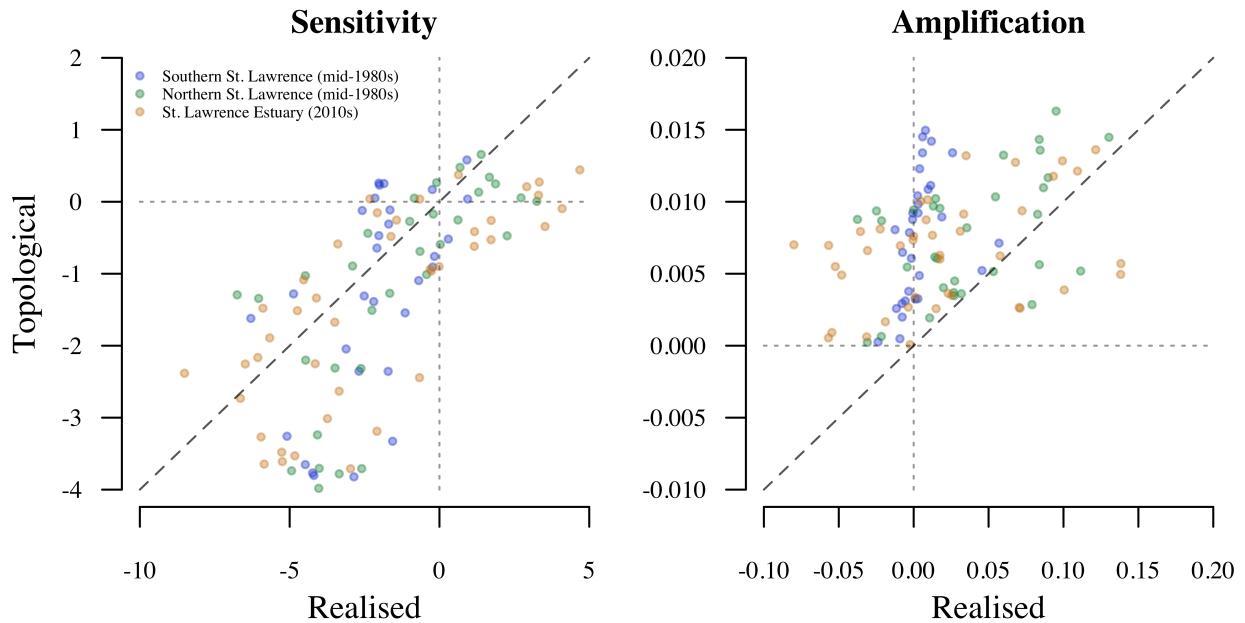


Figure 9: Realised vs topological scores

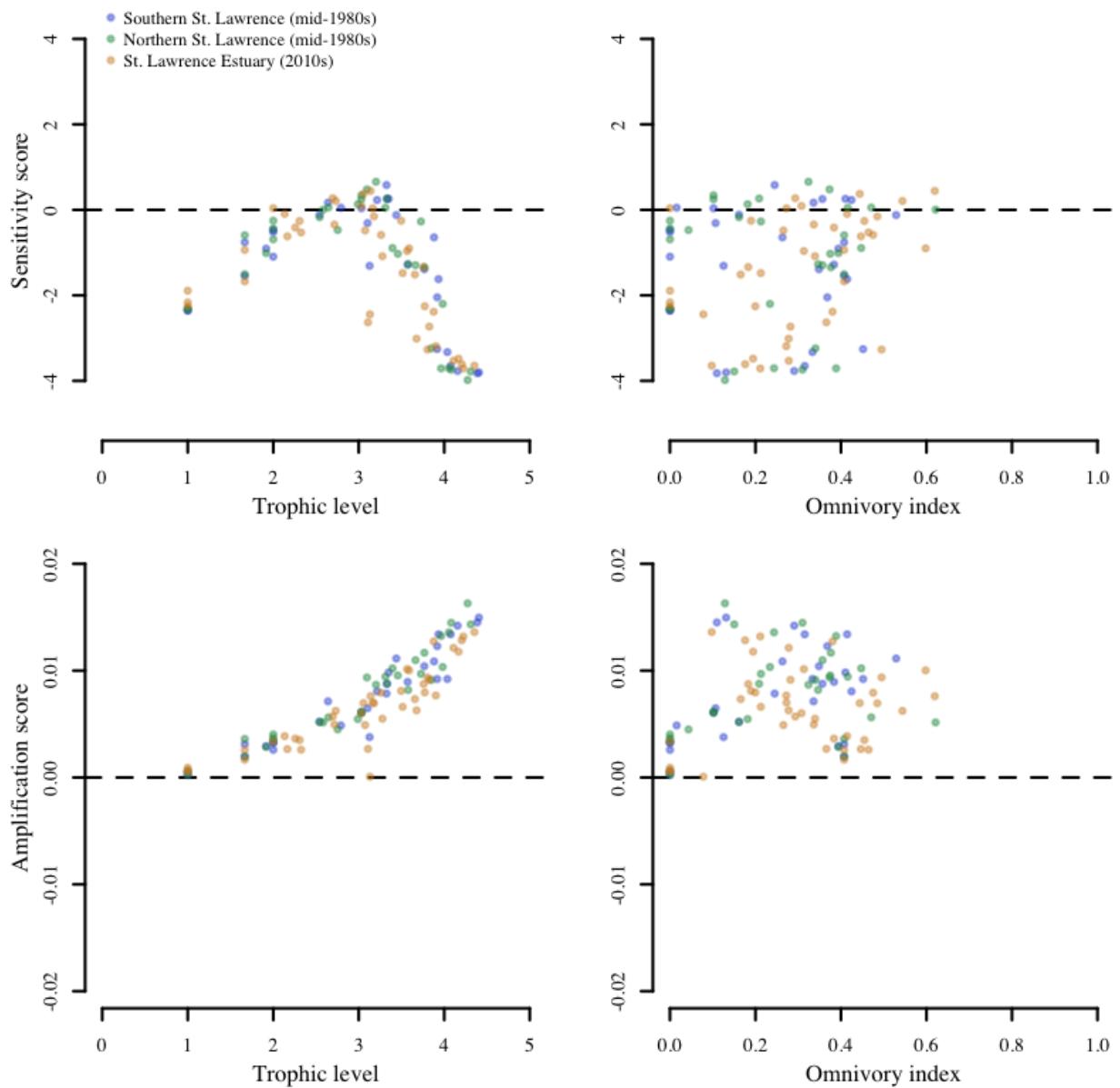


Figure 10: Sensitivity scores as a function of trophic level and omnivory index

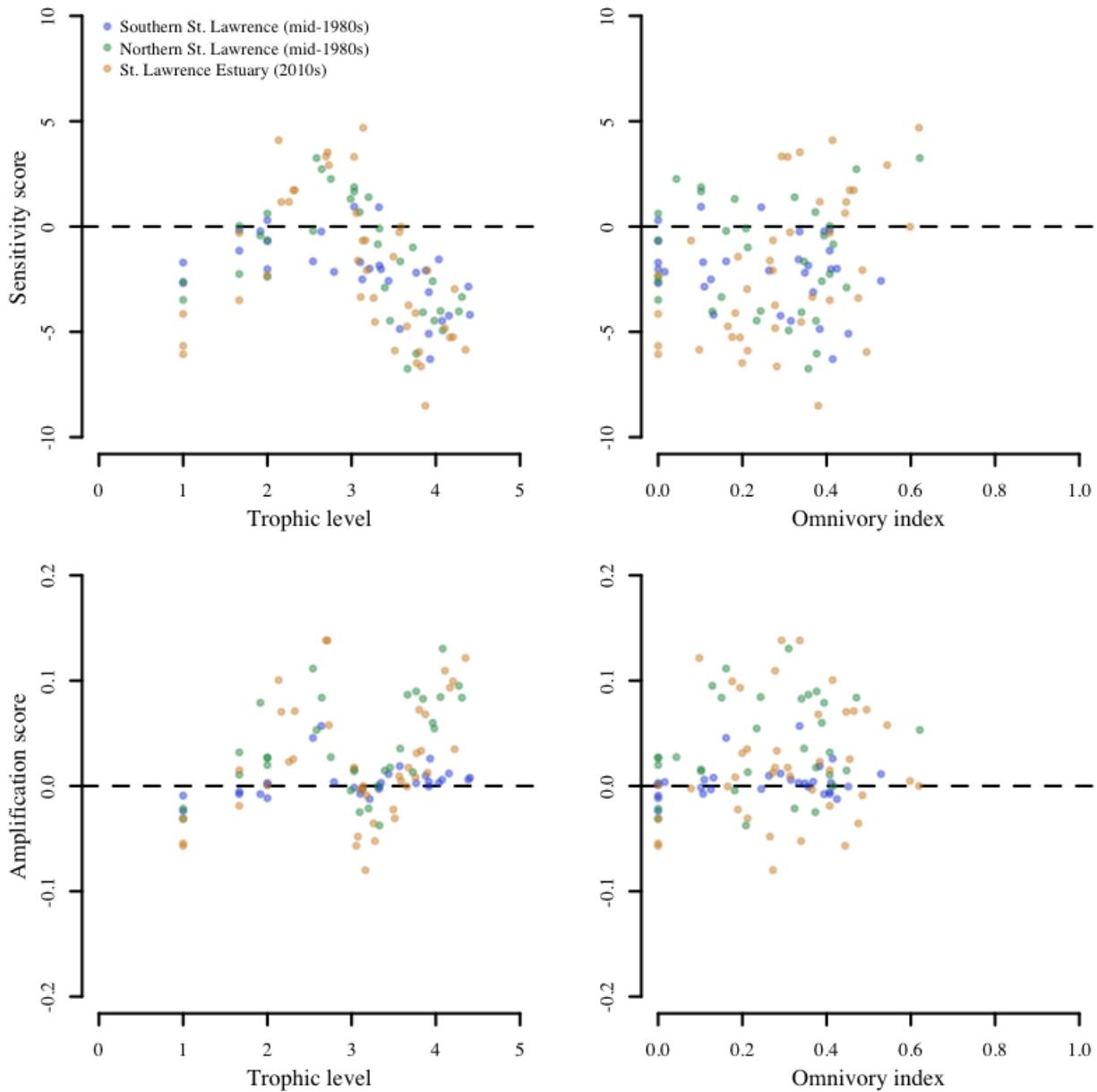


Figure 11: Impact scores as a function of trophic level and omnivory index

784 10 Supplementary Material

785 10.1 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

786 **11 Next points**

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

793 **12 Notes - to explore**

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

798 **13 Interesting points**

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

801 **14 Ecology Letters formatting and submission**

802 **14.1 Latex files**

803 **Instructions:** *Ecology Letters* does not have a standard LaTex style file. Manuscripts sub-
804 mitted using LaTeX should be accompanied by a PDF version of the paper. Upon final accep-

805 *tance for publication, authors will be requested to send their LaTeX source files accompanied*
806 *by all figures in EPS or TIFF format and also any non-standard LaTeX style files used in*
807 *the manuscript preparation.*

808 14.2 Formatting

- 809 • Numbered pages
- 810 • Text:
 - 811 – Double-spaced
 - 812 – No hyphenation
 - 813 – No automatic wordwrap
- 814 • Tables
 - 815 – As MS Excel or MS Word or equivalent
 - 816 – Cited consecutively in the text
 - 817 – Numbered with Arabic numerals
 - 818 – Grouped together at the end od the paper or in a separate file
 - 819 – Titles and typed double-spaced on a separate sheet
 - 820 – Clearly indicate units for each entries in the table
 - 821 – Footnotes to tables hsould be identified by the symbols * † ‡ § ¶ (in that order)
822 and placed at the bottom of the table.
 - 823 – No vertical rules should be used
- 824 • Figures
 - 825 – Cited consecutively in the text
 - 826 – Numbered with Arabic numerals
 - 827 – Grouped together at the end od the paper or in a separate file

- 828 – Titles and typed double-spaced on a separate sheet
- 829 – Line and combination figures should preferably be submitted in vector graphics
- 830 format (e.g. either embedded as vector graphics in a Word document or saved
- 831 separately in PDF or eps format). If this is not possible, they should be saved
- 832 separately as pixel-based graphics at 600 dpi at the required print size, and they
- 833 should be saved in TIFF (not jpg) format or embedded as such in Word.
- 834 – Photographic figures should be saved at 300 dpi in TIFF format, or jpg format
- 835 with low compression
- 836 – Figures should be drawn/submitted at their smallest practicable size (to fit a
- 837 single column (82 mm), two-thirds page width (110 mm) or full page width (173
- 838 mm)). Over-sized figures will be reduced by the Production Editor. If figures are
- 839 drawn larger than reproduction size, component parts such as symbols and text
- 840 must be large enough to allow for the necessary reduction. For full instructions on
- 841 preparing your figures, see our Electronic Artwork Information for Authors page
- 842 and the electronic artwork guidelines.

843 • Text boxes

- 844 – Text boxes may be used for standalone definitions, equations, necessary explana-
- 845 tions of concepts, a glossary (if needed only), and other items that disrupt the
- 846 flow of the manuscript or where repeated reference to them is necessary. Text
- 847 boxes can include equations and references (included in the main reference list),
- 848 but not tables, figures or footnotes. Text boxes are limited to 750 words including
- 849 a title. Items in text boxes that are not logically separate from the main text of
- 850 the manuscript should be incorporated into the main text. A glossary should
- 851 only be given if the language is complex enough that it may not be understood
- 852 by the general readership of the journal or if requested by an editor for the jour-
- 853 nal. Text boxes should be cited consecutively using Arabic numerals (e.g., Box

854 1, Box 2). Text for text boxes should be given after figures at the end of the
855 manuscript and the text should begin with a short descriptive title, for instance
856 “Box 1: Calculation of a trophic complexity index.”

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

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

878 **14.2.1 Title page**

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

905 the article.

906 **14.2.2 Abstract**

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

909 **14.2.3 Main text**

- 910 • (a) Introduction. The introduction should summarize briefly the background and aims,
911 and end with a very brief statement of what has been achieved by the work.
- 912 • (b) Material and methods. This section should contain sufficient detail so that all
913 procedures can be repeated (in conjunction with cited references). A checklist
914 is provided so that authors can check that their methods report details which
915 our editors regard as essential (please refer to the Checklist). Where specific
916 equipment and materials are named, the manufacturer's name, city and country
917 should be given (generally in parentheses after first mention).
- 918 • (c) Results. The Results section should present the experiments that support the
919 conclusions to be drawn later in the Discussion. The Results section should con-
920 form to a high standard of rigour. Extended lines of inference, arguments or
921 speculations should not be placed in the Results.
- 922 • (d) Discussion. The Discussion section should be separate from the Results section.
923 It allows authors to propose their interpretation of the results, and to suggest
924 what they might mean in a wider context in general and relative to published
925 literature. It should end with a clear statement of the main conclusions of the
926 research, and a clear explanation of their importance and relevance.
- 927 • (e) Acknowledgements. Acknowledgements should be brief and concise.

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

930 **14.2.4 In-text citations**

- 931 • Chronological order
932 • Fully, except if > 2 authors

933 **14.2.5 Reference list**

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

949 **14.2.6 Unpublished works**

- 950 • “In press”: only permissible for papers that have been accepted for publication (documentary evidence of acceptance must be provided). Example: Vázquez, D.P. & Simberloff, D.
951 (2003). Changes in interaction biodiversity induced by an introduced ungulate. Ecol. Lett.,
952 in press (accepted). • “Personal communication”: Citation must be accompanied by the
953 names of all persons concerned. Any person cited as the source of a ‘personal communica-
954 tion’ must have approved the reference.

956 **14.2.7 Data archiving**

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

966 **14.2.8 Online supplementary information**

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

972 15 References

- 973 Allesina, S. & Pascual, M. (2008). Network structure, predatorPrey modules, and stability
974 in large food webs. *Theoretical Ecology*, 1, 55–64.
- 975 Bascompte, J. (2009). Disentangling the Web of Life. *Science*, 325, 416–419.
- 976 Bascompte, J. & Melián, C.J. (2005). Simple Trophic Modules for Complex Food Webs.
977 *Ecology*, 86, 2868–2873.
- 978 Bowler, D., Bjorkmann, A., Dornelas, M., Myers-Smith, I., Navarro, L. & Niamir, A. *et al.*
979 (2019). The geography of the Anthropocene differs between the land and the sea. *bioRxiv*.
- 980 Camacho, J., Stouffer, D.B. & Amaral, L.A.N. (2007). Quantitative analysis of the local
981 structure of food webs. *Journal of Theoretical Biology*, 246, 260–268.
- 982 Cirtwill, A.R. & Stouffer, D.B. (2015). Concomitant predation on parasites is highly variable
983 but constrains the ways in which parasites contribute to food web structure. *The Journal
984 of Animal Ecology*, 84, 734–744.
- 985 Côté, I.M., Darling, E.S. & Brown, C.J. (2016). Interactions among ecosystem stressors and
986 their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*,
987 283, 20152592.
- 988 Crain, C.M., Kroeker, K. & Halpern, B.S. (2008). Interactive and cumulative effects of
989 multiple human stressors in marine systems. *Ecology Letters*, 11, 1304–1315.
- 990 Darling, E.S. & Côté, I.M. (2008). Quantifying the evidence for ecological synergies. *Ecology
991 Letters*, 11, 1278–1286.
- 992 De Laender, F. (2018). Community-and ecosystem-level effects of multiple environmental
993 change drivers: Beyond null model testing. *Global change biology*, 24, 5021–5030.
- 994 Galic, N., Sullivan, L.L., Grimm, V. & Forbes, V.E. (2018). When things don't add up:
995 Quantifying impacts of multiple stressors from individual metabolism to ecosystem process-

- 996 ing. *Ecology Letters*, 21, 568–577.
- 997 Griffen, B.D., Belgrad, B.A., Cannizzo, Z.J., Knotts, E.R. & Hancock, E.R. (2016). Re-
998 thinking our approach to multiple stressor studies in marine environments. *Marine Ecology
999 Progress Series*, 543, 273–281.
- 1000 Guiden, P.W., Bartel, S.L., Byer, N.W., Shipley, A.A. & Orrock, J.L. (2019). Predator-
1001 Prey Interactions in the Anthropocene: Reconciling Multiple Aspects of Novelty. *Trends in
1002 Ecology & Evolution*, 34, 616–627.
- 1003 Halpern, B.S., Frazier, M., Potapenko, J., Casey, K.S., Koenig, K. & Longo, C. *et al.* (2015).
1004 Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature
1005 Communications*, 6.
- 1006 Hodgson, E.E., Essington, T.E. & Halpern, B.S. (2017). Density dependence governs when
1007 population responses to multiple stressors are magnified or mitigated. *Ecology*, 98, 2673–
1008 2683.
- 1009 Hodgson, E.E. & Halpern, B.S. (2019). Investigating cumulative effects across ecological
1010 scales. *Conservation Biology*, 33, 22–32.
- 1011 Hodgson, E.E., Halpern, B.S. & Essington, T.E. (2019). Moving Beyond Silos in Cumulative
1012 Effects Assessment. *Frontiers in Ecology and Evolution*, 7.
- 1013 Holt, R.D. (1997). Community modules. In: *Multitrophic Interactions in Terrestrial Ecosys-
1014 tems, 36th Symposium of the British Ecological Society* (eds. Grange, A.C. & Brown, V.K.).
1015 Blackwell Science, Oxford, pp. 333–349.
- 1016 Holt, R.D. & Hochberg, M.E. (2001). Indirect interactions, community modules and bio-
1017 logical control: A theoretical perspective. *Evaluating indirect ecological effects of biological
1018 control*, 13–37.
- 1019 Jackson, M.C., Loewen, C.J.G., Vinebrooke, R.D. & Chimimba, C.T. (2016). Net effects
1020 of multiple stressors in freshwater ecosystems: A meta-analysis. *Global Change Biology*, 22,

- 1021 180–189.
- 1022 Jones, F.C. (2016). Cumulative effects assessment: Theoretical underpinnings and big prob-
1023 lems. *Environmental Reviews*, 24, 187–204.
- 1024 Kondoh, M. (2008). Building trophic modules into a persistent food web. *Proceedings of the*
1025 *National Academy of Sciences*, 105, 16631–16635.
- 1026 Menge, B.A. (1995). Indirect Effects in Marine Rocky Intertidal Interaction Webs: Patterns
1027 and Importance. *Ecological Monographs*, 65, 21–74.
- 1028 Milo, R., Shen-Orr, S., Itzkovitz, S., Kashtan, N., Chklovskii, D. & Alon, U. (2002). Network
1029 Motifs: Simple Building Blocks of Complex Networks. *Science*, 298, 824–827.
- 1030 Monteiro, A.B. & Faria, L.D.B. (2016). The interplay between population stability and food-
1031 web topology predicts the occurrence of motifs in complex food-webs. *Journal of theoretical*
1032 *biology*, 409, 165–171.
- 1033 Montoya, J., Woodward, G., Emmerson, M.C. & Solé, R.V. (2009). Press perturbations and
1034 indirect effects in real food webs. *Ecology*, 90, 2426–2433.
- 1035 Piggott, J.J., Townsend, C.R. & Mattheei, C.D. (2015). Reconceptualizing synergism and
1036 antagonism among multiple stressors. *Ecology and Evolution*, 5, 1538–1547.
- 1037 Schäfer, R.B. & Piggott, J.J. (2018). Advancing understanding and prediction in multiple
1038 stressor research through a mechanistic basis for null models. *Global Change Biology*, 24,
1039 1817–1826.
- 1040 Stouffer, D.B. & Bascompte, J. (2010). Understanding food-web persistence from local to
1041 global scales. *Ecology Letters*, 13, 154–161.
- 1042 Stouffer, D.B. & Bascompte, J. (2011). Compartmentalization increases food-web persis-
1043 tence. *Proceedings of the National Academy of Sciences*, 108, 3648–3652.
- 1044 Stouffer, D.B., Camacho, J., Jiang, W. & Nunes Amaral, L.A. (2007). Evidence for the
1045 existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society*

- ¹⁰⁴⁶ *B: Biological Sciences*, 274, 1931–1940.
- ¹⁰⁴⁷ Stouffer, D.B., Sales-Pardo, M., Sirer, M.I. & Bascompte, J. (2012). Evolutionary Conservation of Species' Roles in Food Webs. *Science*, 335, 1489–1492.
- ¹⁰⁴⁹ Thompson, P.L., MacLennan, M.M. & Vinebrooke, R.D. (2018). Species interactions cause non-additive effects of multiple environmental stressors on communities. *Ecosphere*, 9,
¹⁰⁵⁰ e02518.
- ¹⁰⁵² Wootton, J.T. (1993). Indirect Effects and Habitat Use in an Intertidal Community: Inter-
¹⁰⁵³ action Chains and Interaction Modifications. *The American Naturalist*, 141, 71–89.
- ¹⁰⁵⁴ Wootton, J.T. (2002). Indirect effects in complex ecosystems: Recent progress and future
¹⁰⁵⁵ challenges. *Journal of Sea Research*, Structuring Factors of Shallow Marine Coastal Com-
¹⁰⁵⁶ munities, Part I, 48, 157–172.
- ¹⁰⁵⁷ Yodzis, P. (2000). Diffuse Effects in Food Webs. *Ecology*, 81, 261–266.