On the sensitivity of food webs to multiple disturbances

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32 Proposal letter

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Notes \mathbf{Notes}

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

46 Letter

Evaluating the effects of multiple sources of stress in natural environments has become an increasingly important issue as the effects of intensifying global change and expanding human activities result in complex stress exposure regimes. Even though the non-additive effects of multiple stressors have been investigated empirically for a few decades now, there remains a general lack of theoretical understanding of their impacts on natural systems. 51 In particular, the role of species and their interactions in mediating the effects of multiple disturbances through ecological eommunities networks, although widely acknowledged, has yet to be formally explored. We propose the first such formal exploration by exhaustively simulating the impacts of all possible pathways of effects on the dynamics of 3-species mo-55 tifs using Lotka-Volterra models. We uncover that interaction types and species position greatly influence sensitivity to and amplification of multiple disturbances and that indirect 57 pathways of effects are the main cause of non-additive effects. In particular, predators in food chain and omnivory interactions act as both weak entry points (i.e. highly sensitive to 59 disturbances) and biotic amplifiers (i.e. affected synergistically by disturbances). We then use the simulated sensitivity and amplification scores as heuristics to infer trophic vulnera-61 bility of species based on topology and realized pathways of effects in the food web of the Northern Gulf of St. Lawrence, Canada, prior to a groundfish stock collapse in the 1990s. We find that heavily exploited species appear to be the most vulnerable trophically, while fisheries transitioned to insensitive or beneficiary species post-collapse. This contribution is significant and timely for two main reasons. First, from a theory stand point, this is the first exhaustive exploration of mitigation and amplification of multiple disturbances via trophic motifs. Second, we provide a clear link between theory and management by illustrating how

- our framework can be applied to detect most sensitive species in a real food web exposed to various stressors. Our group of co-authors is singularly positioned to write this paper.
- D. Beauchesne and P. Archambault both have strong backgrounds in environmental assess-
- ments in general and cumulative impacts in particular. K. Cazelles and D. Gravel are both
- experts in theoretical ecology with strong backgrounds and recognition in the field.

4 1 Abstract

Evaluating the effects of multiple sources of stress in natural environments has become an increasingly important issue as the effects of intensifying global change and expanding human activities result in complex stress exposure regimes. Even though the non-additive effects of multiple stressors have been investigated empirically for a few decades now, there remains a general lack of theoretical understanding of their impacts on natural systems. In particular, the role of species and their interactions in mediating the effects of multiple disturbances through ecological communities, although widely acknowledged, has yet to be formally explored. We propose the first such formal exploration by exhaustively simulating trophic impacts through all possible pathways of effects on the dynamics of 3-species motifs using 83 Lotka-Volterra models. We uncover that interaction types and species position greatly influence sensitivity to and amplification of multiple disturbances and that indirect pathways of 85 effects are the main source of non-additive effects. In particular, predators in food chain and 86 omnivory interactions act as both weak entry points (i.e. highly sensitive to disturbances) 87 and biotic amplifiers (i.e. affected synergistically by disturbances). We then use the simulations results as heuristics to infer trophic vulnerability of species based on topology and realized pathways of effects in the food web of the Northern Gulf of St. Lawrence, Canada, prior to a groundfish stock collapse in the 1990s. We find that heavily exploited species appear to be the most vulnerable trophically, while fisheries transitioned to insensitive or beneficiary species post-collapse.

⁹⁴ 2 Introduction

Global changes and human activities result in increasingly intricate environmental stress exposure regimes that can induce complex and unpredictable effects (Côté et al. 2016; Bowler et al. 2019; Halpern et al. 2019). This cocktail of environmental pressures impedes our ability to evaluate and partition the effects of interacting drivers in cumulative effects assessments (Canter & Ross 2010; Jones 2016; Sinclair et al. 2017). This is in part due to the breadth and interaction potential of environmental pressures operating on natural 100 systems (Côté et al. 2016), compounding the pathways of effects through which natural 101 systems can be impacted. Another factor is the potential for non-additive affects, when the 102 effect of multiple interacting drivers is greater (i.e. synergism) or lower (i.e. antagonism) 103 than the sum of their individual parts, which have been found to be the norm rather than 104 the exception (e.g. Darling & Côté 2008; Crain et al. 2008; Piggott et al. 2015; Jackson et 105 al. 2016). 106

Common drivers of environmental stress include climate change, resource exploitation and 107 pollution (Boonstra et al. 2015; Halpern et al. 2019). Drivers have typically been described 108 according to their effects on habitats (e.g. Ban et al. 2010; Halpern et al. 2019). For instance, fisheries can destroy benthic habitats and extract biomass. Focusing on habitats 110 conveniently circumscribes assessments to a set of tractable units. It also has the drawback 111 of aggregating processes operating at lower levels of ecological organization that we know 112 respond differently to driver exposure (Halpern & Fujita 2013; Giakoumi et al. 2015). For 113 example, hypoxia decreases overall habitat quality but has species-dependent effects, ranging 114 from well-adapted (Pillet et al. 2016) to avoidance behaviour (Chabot & Claireaux 2008), 115 reduced growth (Dupont-Prinet et al. 2013) and mortality (Eby et al. 2005; Belley et 116 al. 2010). As a consequence, current practice to assess the effects of multiple drivers has 117 offered little insight into underlying ecological mechanisms (Griffen et al. 2016; Jackson et 118 al. 2016; De Laender 2018; Schäfer & Piggott 2018). Focusing on ecosystem components 119

such as species and communities has thus been deemed necessary to provide a mechanistic understanding of the effects of multiple drivers [Giakoumi et al. (2015); refs?]

At the species and community scales, drivers may be more appropriately described as eco-122 logical process modifiers, which we define as natural or anthropogenic processes resulting in 123 a disturbance to ecological processes (Figure 1A). Drivers may disturb a variety of ecological 124 processes such as behaviour (e.q. Chabot & Claireaux 2008; Hale et al. 2017), reproduc-125 tion [e.g. ref], physiology (e.g. Dupont-Prinet et al. 2013), mortality (e.g. Belley et al. 126 2010), and species interactions [e.g. ref]. Multiple processes may be affected by a single 127 driver, while multiple drivers may target a single process. Through this lens, disturbances 128 to cod behaviour and mortality may arise from benthic habitat destruction and from direct 129 extraction, respectively. 130

Species interactions are particularly relevant in the context of multiple disturbances, as they 131 may serve as the indirect pathways through which pressures permeate entire ecological com-132 munities (Wootton 2002; Bascompte 2009; Montoya et al. 2009; Thompson et al. 2018). 133 Indirect effects, i.e. when two or more direct effects are linked by a single species involved 134 in both effects, may be as important of, and propagate faster than, direct effects (Woot-135 ton 1993, 2002; Menge 1995; Yodzis 2000). In multi-species systems, where both direct 136 and indirect effects are operating simultaneously, it is expected that the effects of envi-137 ronmental pressures will be amplified or dampened through biotic interactions (Ives 1995; 138 Wootton 2002; Thompson et al. 2018). Provide examples here, cite ogorman2009; 139 ogorman2012; ghedi2015 Interaction strength and type (e.q. omnivory vs apparent com-140 petition) have also been linked to enhanced or decreased community persistance (McCann 141 et al. 1998; Wootton 2002; Allesina & Pascual 2008). How species are embedded in complex 142 communities is therefore likely to affect their sensitivity to and amplification of single and 143 multiple disturbances.

The complexity of empirical food webs is however prohibitive to investigations of community

dynamics. Studying smaller subgraphs - community motifs or modules - has thus emerged
as an alternative to gather insights into the dynamics and stability of complex ecological
communities (Holt 1997; Holt & Hochberg 2001). Motifs are collections of *n*-species that,
when put together, construct whole food webs (Milo *et al.* 2002; Stouffer *et al.* 2007). They
form the backbone of food webs and provide a mesoscale characterization of community
structure (Bascompte & Melián 2005; Stouffer *et al.* 2007). A species can be described as a
function of all *n*-species motifs it is involved in in an empirical food web (Figure 1B; Stouffer *et al.* 2012).

There are 13 distinct 3-species motifs composed of 30 unique positions (Milo et al. 2002;
Stouffer et al. 2007, 2012). Four 3-species motifs have received particular attention in
theoretical and empirical studies due to their roles [ref] 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. Add some discussion here
on archetypes of each motifs, trophic cascades and compensatory dynamics. To
cite: cote1995; ogorman2010; ogorman2012;

Motif dynamics has been studied extensively to uncover how structural properties of food 161 webs can benefit community persistence and stability (Allesina & Pascual 2008; Kondoh 162 2008; Stouffer & Bascompte 2010, 2011; Monteiro & Faria 2016) and to assess the structural 163 roles of species within food webs (Stouffer et al. 2012; Cirtwill & Stouffer 2015). These 164 provide meaningful insights for conversation efforts. For example, results from Stouffer et 165 al. (2012) suggest that species benefit whole community persistence based on their trophic 166 position and that the diversity of trophic roles found in empirical food webs does not correlate 167 to species richness. Using roles as targets may thus be valuable for community conservation 168 (Stouffer et al. 2012). Additional insights into the structural properties of food webs could 169 be gathered by studying motifs at equilibrium, i.e. when system dynamics is constrained by 170 species coexistance (Figure 1C). This is of particular relevance to managers using ecosystembased approaches to manage and maintain exploited populations, rather than ensure the 173 persistance of species.

Here, we study the equilibrium dynamics of the most prevalent 3-species motifs in food webs

(i.e. food chain, omnivory, exploitative competition, and apparent competition) to investigate and infer the structural role of species and their interactions in mediating the effects of
individual and 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 separately or in combination,
and 3) which species are most vulnerable to disturbances based on their trophic position?

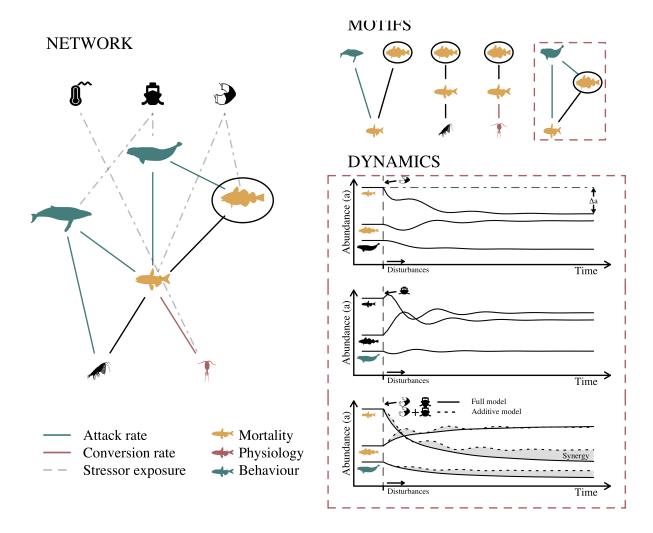


Figure 1: Conceptualization of the effects of multiple sources of environmental stress on the dynamics of a theoretical food web. A) Drivers such as sea surface temperature, marine traffic and fisheries penetrate food webs through various pathways of effects by disturbing ecological processes governing populations and communities. For instance, marine traffic disturbs whale feeding behaviour, which may lead to decreased attack rates on prey species. B) A species position in a food web can be decomposed in a suite of n-species submodules called motifs that are informative of the role played by a species in the entire food web. Different types of interaction types will lead to different types of community dynamics and a species can be described as a function of the number and types of interactions it is involved in. For instance, the interactions of the meso-predator can be decomposed into 1 exploitative competition, 2 food chains and 1 omnivory motifs. C) The dynamics of motifs can uncover if and how disturbances arising from individual and multiple drivers are propagated and amplified through different types of species interactions. Variations in species abundance due to driver induced disturbances provide an evaluation of motif species sensitivity (C1-3). The difference between the summed effects of individual drivers (i.e. additive model; C1-2) and the joint effects of multiple drivers (i.e. full model; C3) provides an evaluation of disturbance amplification.

3 Sumulating disturbances

$_{\scriptscriptstyle 2}$ 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

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

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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

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

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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

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

For each motif, a 1% change in initial equilibria equations parameter values was applied

were included in the consumer models to constrain their growth.

$_{\scriptscriptstyle{04}}$ 3.2 Disturbances

to simulate negative disturbances through all possible unique pathways of univariate and 206 multivariate effects. Parameters selected to simulate disturbances were those related to 207 population growth (r and m) and interaction rates $(e \text{ and } \alpha_{ij})$, as their effects on population 208 dynamics can readily be attributed to environmental pressure effects. For example, cod 209 mortality will increase through fishing activities, whale attack rates on krill will be altered 210 by behavioural changes induced by marine traffic, and conversion rates of copepods by capelin 211 will be reduced through physiological effects of temperature anomalies on copepods. 212 Initial parameter values for intrinsic growth (r) and resource density-dependence (α_{ii}) were 213 fixed to 1 and 0.001, respectively, to bound all resource solutions. Competitive parameters 214 for the exploitative competition motif were also fixed at 0.001 since those parameters were 215 not to be investigated in our analyses. Conversion rates (e) were fixed to 0.5. Finally, a 216 total of 100 sets of mortality (m) and attack rates (α_{ij}) were evaluated using a simulated 217 annealing algorithm optimizing for consumer abundance.

²¹⁹ 4 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:

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

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 as particularly sensitive pathways of effect $(|S_{i,j}| > 1)$ or motif positions $(|S_i| > 1)$, while biotic sinks are insensitive pathways of effects $(|S_{i,j}| = 0)$ or motif positions $(|S_i| = 0)$.

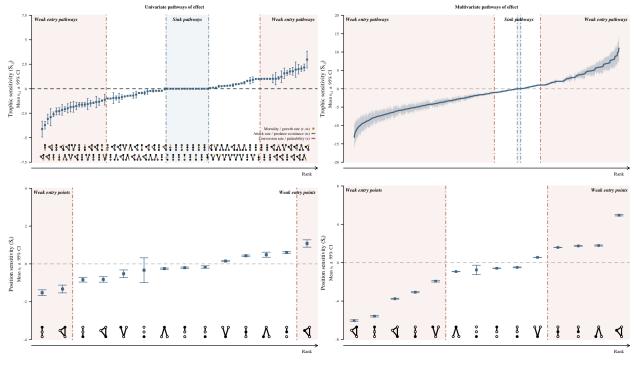


Figure 2

5 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

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

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 amplifiers as multivariate pathways of effect or motif positions that are more affected than expected from an additive model $(A_{i,j} > 0.0005, A_i > 0.0005)$. Biotic buffers are multivariate pathways of effect or motif positions that are less afefcted than expected from an additive model $(A_{i,j} < 0.0005, A_i < 0.0005)$.

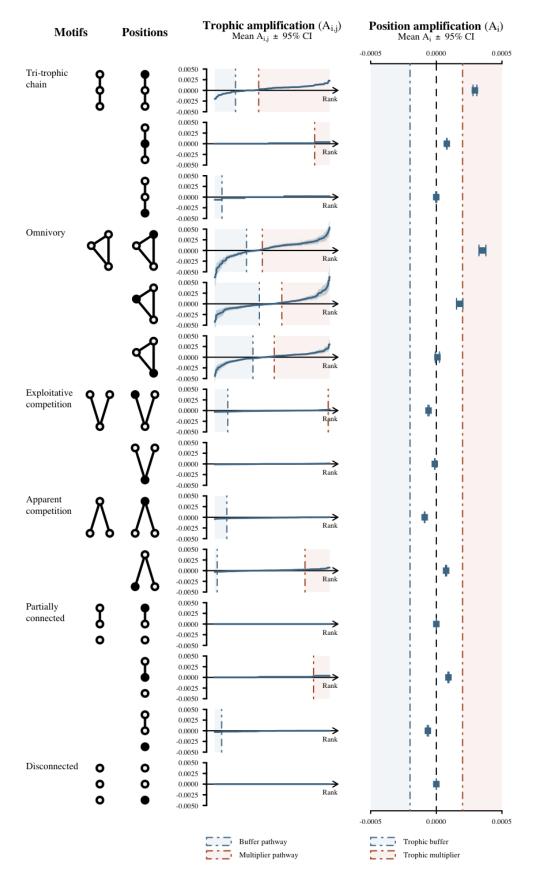


Figure 3

²⁴⁹ 6 Species vulnerability

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, jare 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

6.1 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

 $_{263}$ food web we use comes from Northern Gulf of St. Lawrence for the mid-1980s, prior to a $_{264}$ groundfish stock collapse (Morissette $et\ al.\ 2003$).

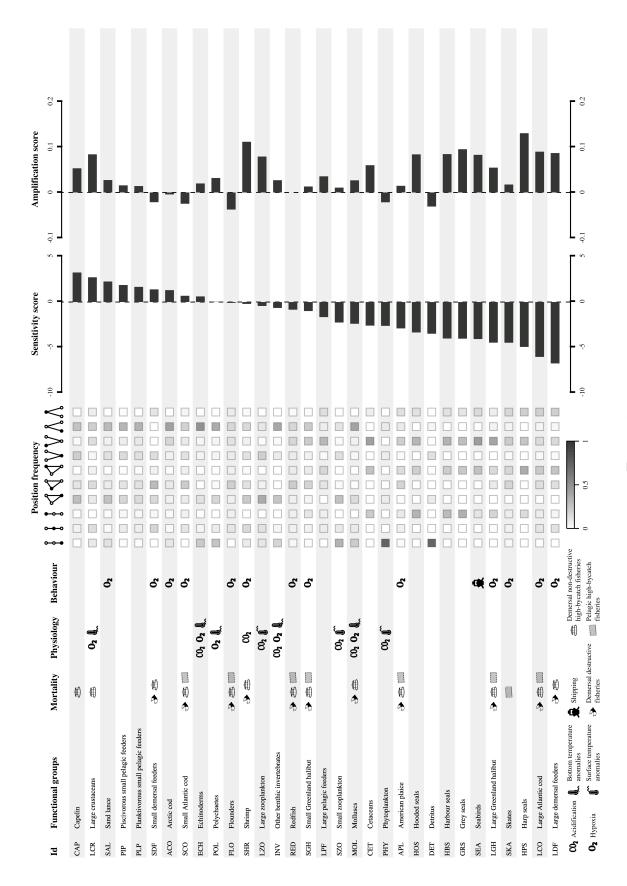


Figure 4

55 7 Supplementary Material

7.1 Models

Motifs	Equation systems	Initial parameters values
Tri-trophic food chain	$ \frac{\frac{dX_i}{dt}}{\frac{dX_j}{dt}} = X_i(r_i - \alpha_{ii}X_i - \alpha_{ij}X_j) $ $ \frac{\frac{dX_j}{dt}}{\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	$\frac{\frac{dX_i}{dt}}{\frac{dX_j}{dt}} = X_i(r_i - \alpha_{ii} - \alpha_{ij}X_j - \alpha_{ik}X_k)$ $\frac{\frac{dX_j}{dt}}{\frac{dX_k}{dt}} = X_j(e_{ij}\alpha_{ij}X_i - \alpha_{jj}\alpha_{jk}X_k - \alpha_{jj}X_j - m_j)$ $\frac{dX_k}{dt} = X_k(e_{ik}\alpha_{ik}X_i - \alpha_{kk}\alpha_{kj}X_j - \alpha_{kk}X_k - m_k)$	$r_{i} = 1$ $\alpha_{ii}, \alpha_{jj}, \alpha_{kk}, \alpha_{jk}, \alpha_{kj} = 0.001$ $\alpha_{ij}, \alpha_{ik}, \in [0.0001, 0.01]$ $e_{ij}, e_{ik} = 0.5$ $m_{j}, m_{k} \in [0.01, 0.5]$
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{\frac{dX_i}{dt}}{\frac{dX_j}{dt}} = X_i(r_i - \alpha_{ii}X_i - \alpha_{ik}X_k) $ $ \frac{\frac{dX_j}{dt}}{\frac{dX_k}{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

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