Effects of multiple stressors on food web structure

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1 Introduction

Global changes, be they natural or human-induced, are resulting in increasingly intricate environmental stress exposure regimes (Bowler et al., 2019; Halpern et al., 2015). Exposure to multiple interacting stressors can induce complex and unpredictable environmental effects that can propagate through entire ecological communities by way of interactions linking species together (**???**). Net effects of multiple stressors can be additive (*i.e.* joint effect equal to the sum of individual effects), synergistic (joint effect superior to the sum of individual effects), antagonistic (joint effect inferior to the sum of individual effects) or dominant (joint effect equal to an individual effect) (e.g. Crain et al., 2008; Côté et al., 2016; Darling and Côté, 2008). There is a rich literature documenting the effects of disturbances on communities and how network structure contributes to community resistance (**???**). It however remains unclear how network structure influences community resistance to multiple disturbances. Recent efforts have focused on [...]. (Galic et al., 2018; Schäfer and Piggott, 2018; Thompson et al., 2018a) Here, we seek to identify what characteristics of network structure and the role of species in buffering against or multiplying the effects of multiple stressors.

2 Objectives

The overarching goal is to conceptualize how the structure of food webs affects the direct and indirect propagation of multiple sources of stress non-linearly and affects the likelihood of observing antagonistic or synergistic effects of multiple stressors. The objectives are to 1) identify network characteristics that make them more or less sensitive or resistant to multiple stressors and 2) what is the role of species and their interactions contributing to the propensity of networks in buffering against or amplifying the effects of multiple stressors.

3 Non-linear effects

Let's begin by conceptualizing the effects of 2 environmental stressors on a simple 3-species omnivory food web (Figure 1). For our exercise, we are not truly interested in the identify of the sources of stress. We rather focus on the resulting disturbance on species themselves. This means that we will not investigate the effects of multiple stressors applied to a single species in the food web. This precludes us from investigating the sensitivity of species to each individual stressor. Rather, we investigate the effects of disturbances to multiple

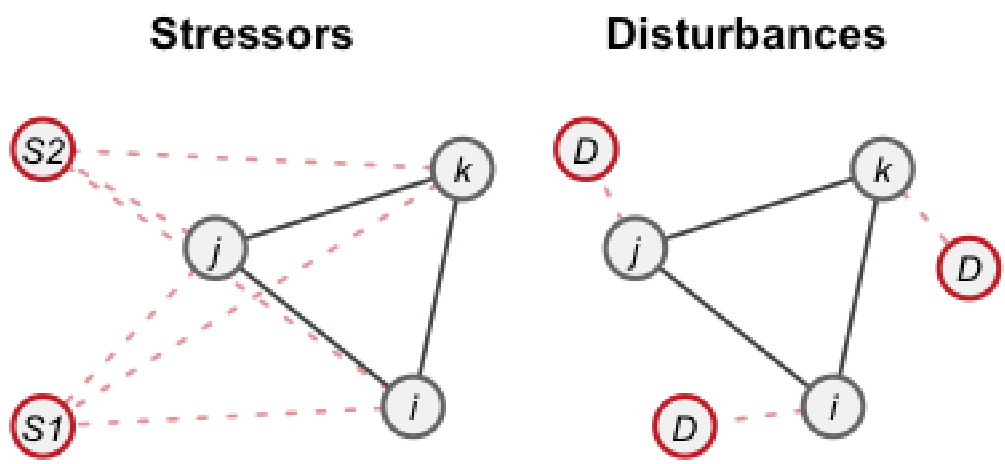

Figure 1: Omnivory 3-species motif affected by two different drivers on the left and by 3 unidentified disturbances on the right. Disturbances could stem from multiple stressors or from a single stressor affecting multiple species.

species simultaneously. But see Thompson et al. (2018b) and Thompson et al. (2018a) for a description of a modelling approaching incorporating multiple sources of stress in a food web.

By investigating the effects of multiple disturbances on multiple species, there are essentially 7 distinct pathways of effects in the 3-species system:

Pathways of effect
D_i
D_j
D_k
$D_{i,j}$
$D_{i,k}$
$D_{j,k}$
$D_{i,j,k}$

D denotes a disturbance to species i, j or k.

Studying the effects of multiple disturbances means that we will be focusing on disturbances affecting multiple species, referred to as pathways of multiple effects ($D_{i,j}$, $D_{i,k}$, $D_{j,k}$, and $D_{i,j,k}$).

In a food web context, we will define linear and non-linear effect as a function of whether these pathways of multiple effects result in additive ($D_{i,j} = D_i + D_j$), synergistic ($D_{i,j} >> D_i + D_j$), antagonistic ($D_{i,j} << D_i + D_j$) or dominant ($D_{i,j} = D_i \veebar D_j$) effects.

Joint	Individual	Additive	Synergistic	Antagonistic	Dominant
$D_{i,j}$	$D_i + D_j$	=	»	«	$D_i \veebar D_j \veebar i$
$D_{i,k}$	$D_i + D_k$	=	»	«	$D_i \veebar D_k$
$D_{j,k}$	$D_j + D_k$	=	»	«	$D_j \veebar D_k$
$D_{i,j,k}$	$D_i + D_j + D_k$	=	»	«	$D_i \veebar D_j \veebar D_k$

4 Species roles

Species can occupy different roles in these pathways of multiple effects. Investigating species profile (e.g.* Stouffer et al., 2012) could thus inform us on the role played by individual species in buffering against or amplifying the effects of multiple disturbances. We refer to focal species as the species under investigation and peripheral species as the other species in the food web. We define 5 key roles in species propagating or buffering against multiple disturbances:

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

5 Pathways of multiple effects in motifs

A food web can be decomposed into a set of smaller n-species subgraphs called motifs (Milo et al., 2004; Stouffer et al., 2007). For example, there are 13 distinct 3-species motifs composed of 30 unique positions (Figure 2; Stouffer et al., 2007, 2012). These motifs form the backbone of food web and their over- or under-representation in food webs can provide valuable insights into community dynamics. Motifs have been used to investigate the persistence of food web to species extinctions (Stouffer and Bascompte, 2010) and the benefit associated to each species in food web persistence (Stouffer et al., 2012).

Here, we use 3-species motifs to investigate whether multiple disturbances applied to different motifs are more or less likely to result in non-linear effects. We focus on the four most frequent motifs found in food webs, *i.e.* tri-trophic chains, omnivory, exploitative competition and apparent competition (Figure 3; Camacho et al., 2007; Stouffer and Bascompte, 2010). Two additional motifs, *i.e.* partially connected and disconnected were also considered in order to evaluate whether interactions in food webs are truly more likely to be characterized by non-linear effects (Figure 3).

This results in 6 distinct motifs, 14 different positions and 74 distinct pathways of effect (Figure 3). There are 34 single pathways of effects, of which 14 are direct and 20 are strictly indirect. There are also 10 strictly indirect (*i.e.* only peripheral species disturbed) double pathways of effect, and 21 double and 10 triple pathways of effects with both direct and indirect effects (*i.e.* involving focal and peripheral species; Figure 3).

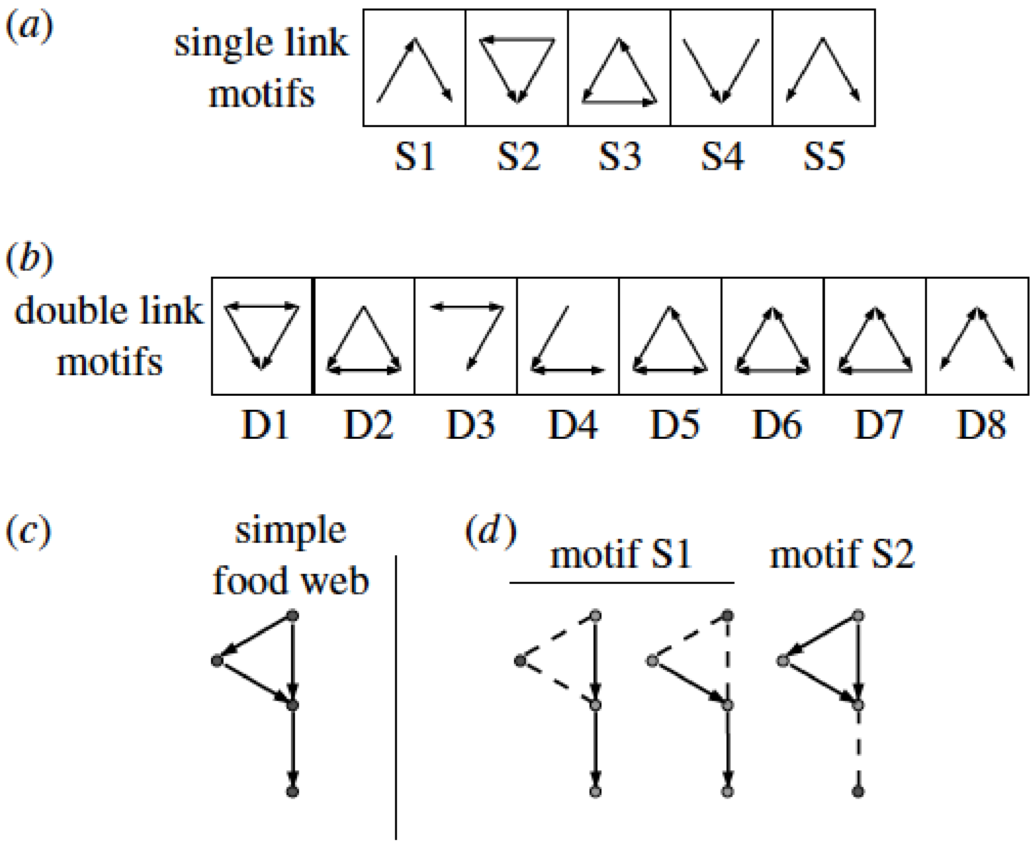

Figure 1. Food-web motifs. When neglecting cannibalism, there are 13 unique food-web motifs composed of three species (Milo *et al.* 2002). To simplify our analysis and presentation, we separate the 13 motifs into two groups: (*a*) motifs S1–S5 that include only single links and (*b*) motifs D1–D8 that include double links (mutual predation). (*c*) A simple food web. (*d*) If we search the food web in (*c*) for food-web motifs, we find two instances of motif S1 and one instance of motif S2. Note that enumeration of food-web motifs counts separately all connected species triplets.

Figure 2: 3-soecies food web motifs, from Stouffer et al. (2007). ***Cannot be used as is. Simply used as a reference.***

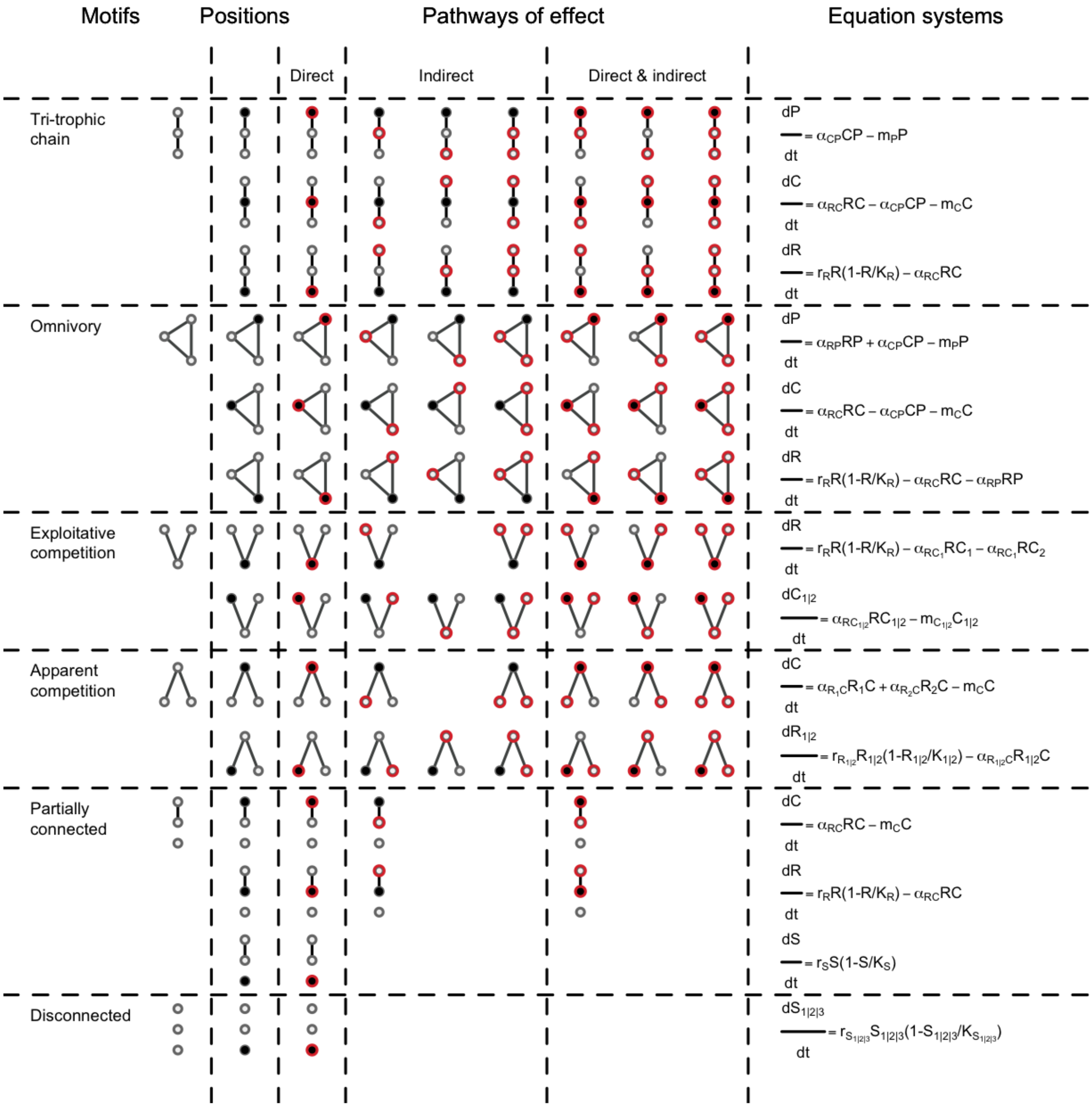

Figure 3: Description of distinct pathways of effect on 14 distinct positions in 6 different network motifs. Black nodes are focal species and red circles represent pathways of effects (or points of entry in food webs?).

6 Equation systems and Jacobian matrix formulas

6.1 Tri-trophic chain

6.1.1 Archetypes

Beluga <- Cod <- Snow crab / shrimp

Blue whale <- Krill <- Primary producer

6.1.2 Equation system

Resource: $\frac{dR}{dt} = r_R R(1 - \frac{R}{K_R}) - \alpha_{RC} RC$

Competitor: $\frac{dC}{dt} = \alpha_{RC} RC - \alpha_{CP} CP - m_C C$

Predator: $\frac{dP}{dt} = \alpha_{CP} CP - m_P P$

6.1.3 Jacobian matrix

$$J = \begin{bmatrix} \frac{d(\frac{dR}{dt})}{dR} & \frac{d(\frac{dR}{dt})}{dC} & \frac{d(\frac{dR}{dt})}{dP} \\ \frac{d(\frac{dC}{dt})}{dR} & \frac{d(\frac{dC}{dt})}{dC} & \frac{d(\frac{dC}{dt})}{dP} \\ \frac{d(\frac{dP}{dt})}{dR} & \frac{d(\frac{dP}{dt})}{dC} & \frac{d(\frac{dP}{dt})}{dP} \end{bmatrix}$$

$$J = \begin{bmatrix} r_R(1 - \frac{2R}{K_R}) - \alpha_{RC} C & -\alpha_{RC} R & 0 \\ \alpha_{RC} C & \alpha_{RC} R - \alpha_{CP} P - m_C & -\alpha_{CP} C \\ 0 & \alpha_{CP} P & \alpha_{CP} C - m_P \end{bmatrix}$$

6.2 Omnivory

6.2.1 Archetypes

6.2.2 Equation system

Resource: $\frac{dR}{dt} = r_R R(1 - R/K_R) - \alpha_{RC} RC - \alpha_{RP} RP$

Competitor: $\frac{dC}{dt} = \alpha_{RC} RC - \alpha_{CP} CP - m_C C$

Predator: $\frac{dP}{dt} = \alpha_{RP} RP + \alpha_{CP} CP - m_P P$

6.2.3 Jacobian matrix

$$J = \begin{bmatrix} \frac{d(\frac{dR}{dt})}{dR} & \frac{d(\frac{dR}{dt})}{dC} & \frac{d(\frac{dR}{dt})}{dP} \\ \frac{d(\frac{dC}{dt})}{dR} & \frac{d(\frac{dC}{dt})}{dC} & \frac{d(\frac{dC}{dt})}{dP} \\ \frac{d(\frac{dP}{dt})}{dR} & \frac{d(\frac{dP}{dt})}{dC} & \frac{d(\frac{dP}{dt})}{dP} \end{bmatrix}$$

$$J = \begin{bmatrix} r_R(1 - \frac{2R}{K_R}) - \alpha_{RC} C - \alpha_{RP} P & -\alpha_{RC} R & -\alpha_{RP} R \\ \alpha_{RC} C & \alpha_{RC} R - \alpha_{CP} P - m_C & -\alpha_{CP} C \\ \alpha_{RP} P & \alpha_{CP} C & \alpha_{RP} R + \alpha_{CP} C - m_P \end{bmatrix}$$

6.3 Exploitative competition

6.3.1 Archetypes

6.3.2 Equation system

Resource: $\frac{dR}{dt} = r_R R(1 - R/K_R) - \alpha_{RP_1} RP_1 - \alpha_{RP_1} RP_2$

Predator 1: $\frac{dP_1}{dt} = \alpha_{RP_1} RP_1 - m_{P_1} P_1$

Predator 2: $\frac{dP_2}{dt} = \alpha_{RP_2} RP_2 - m_{P_2} P_2$

6.3.3 Jacobian matrix

$$J = \begin{bmatrix} \frac{d(\frac{dR}{dt})}{dR} & \frac{d(\frac{dR}{dt})}{dP_1} & \frac{d(\frac{dR}{dt})}{dP_2} \\ \frac{d(\frac{dP_1}{dt})}{dR} & \frac{d(\frac{dP_1}{dt})}{dP_1} & \frac{d(\frac{dP_1}{dt})}{dP_2} \\ \frac{d(\frac{dP_2}{dt})}{dR} & \frac{d(\frac{dP_2}{dt})}{dP_1} & \frac{d(\frac{dP_2}{dt})}{dP_2} \end{bmatrix}$$

$$J = \begin{bmatrix} r_R(1 - \frac{2R}{K_R}) - \alpha_{RP_1} P_1 - \alpha_{RP_2} P_2 & -\alpha_{RP_1} R & -\alpha_{RP_2} R \\ \alpha_{RP_1} P_1 & \alpha_{RP_1} R - m_{P_1} & 0 \\ \alpha_{RP_1} P_2 & 0 & \alpha_{RP_2} R - m_{P_2} \end{bmatrix}$$

6.4 Apparent competition

6.4.1 Archetypes

6.4.2 Equation system

Resource 1: $\frac{dR_1}{dt} = r_{R_1}R_1(1 - R_1/K_1) - \alpha_{R_1C}R_1C$

Resource 2: $\frac{dR_2}{dt} = r_{R_2}R_2(1 - R_2/K_2) - \alpha_{R_2C}R_2C$

Predator: $\frac{dP}{dt} = \alpha_{R_1C}R_1C + \alpha_{R_2C}R_2C - m_CC$

6.4.3 Jacobian matrix

$$J = \begin{bmatrix} \frac{d(\frac{dR_1}{dt})}{dR_1} & \frac{d(\frac{dR_1}{dt})}{dR_2} & \frac{d(\frac{dR_1}{dt})}{dP} \\ \frac{d(\frac{dR_2}{dt})}{dR_1} & \frac{d(\frac{dR_2}{dt})}{dR_2} & \frac{d(\frac{dR_2}{dt})}{dP} \\ \frac{d(\frac{dP}{dt})}{dR_1} & \frac{d(\frac{dP}{dt})}{dR_2} & \frac{d(\frac{dP}{dt})}{dP} \end{bmatrix}$$

$$J = \begin{bmatrix} r_{R_1}(1 - \frac{2R_1}{K_{R_1}}) - \alpha_{R_1P}P & 0 & -\alpha_{R_1P}R_1 \\ 0 & r_{R_2}(1 - \frac{2R_2}{K_{R_2}}) - \alpha_{R_2P}P & -\alpha_{R_2P}R_2 \\ \alpha_{R_1P}P & \alpha_{R_2P}P & \alpha_{R_1P}R_1 + \alpha_{R_2P}R_2 - m_P \end{bmatrix}$$

6.5 Partially connected

6.5.1 Archetype

6.5.1.1 Equation system

Resource: $\frac{dR}{dt} = r_R R(1 - R/K_R) - \alpha_{RC} RC$

Predator: $\frac{dP}{dt} = \alpha_{RP} RP - m_P P$

Species: $\frac{dS}{dt} = r_S S(1 - S/K_S)$

6.5.2 Jacobian matrix

$$J = \begin{bmatrix} \frac{d(\frac{dR}{dt})}{dR} & \frac{d(\frac{dR}{dt})}{dP} & \frac{d(\frac{dR}{dt})}{dS} \\ \frac{d(\frac{dP}{dt})}{dR} & \frac{d(\frac{dP}{dt})}{dP} & \frac{d(\frac{dP}{dt})}{dS} \\ \frac{d(\frac{dS}{dt})}{dR} & \frac{d(\frac{dS}{dt})}{dP} & \frac{d(\frac{dS}{dt})}{dS} \end{bmatrix}$$

$$J = \begin{bmatrix} r_R(1 - \frac{2R}{K_R}) - \alpha_{RP} P & -\alpha_{RP} R & 0 \\ \alpha_{RP} P & \alpha_{RP} R - m_P & 0 \\ 0 & 0 & r_S(1 - \frac{2S}{K_S}) \end{bmatrix}$$

6.6 Disconnected

Species 1: $\frac{dS_1}{dt} = r_{S_1}S_1(1 - S_1/K_{S_1})$

Species 2: $\frac{dS_2}{dt} = r_{S_2}S_2(1 - S_2/K_{S_2})$

Species 3: $\frac{dS_3}{dt} = r_{S_3}S_3(1 - S_3/K_{S_3})$

$$J = \begin{bmatrix} \frac{d(\frac{dS_1}{dt})}{dS_1} & \frac{d(\frac{dS_1}{dt})}{dS_2} & \frac{d(\frac{dS_1}{dt})}{dS_3} \\ \frac{d(\frac{dS_2}{dt})}{dS_1} & \frac{d(\frac{dS_2}{dt})}{dS_2} & \frac{d(\frac{dS_2}{dt})}{dS_3} \\ \frac{d(\frac{dS_3}{dt})}{dS_1} & \frac{d(\frac{dS_3}{dt})}{dS_2} & \frac{d(\frac{dS_3}{dt})}{dS_3} \end{bmatrix}$$

$$J = \begin{bmatrix} r_{S_1}(1 - \frac{2S_1}{K_{S_1}}) & 0 & 0 \\ 0 & r_{S_2}(1 - \frac{2S_2}{K_{S_2}}) & 0 \\ 0 & 0 & r_{S_3}(1 - \frac{2S_3}{K_{S_3}}) \end{bmatrix}$$

7 Next points

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

8 Interesting points

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

9 Literature to cite - or at least look at!

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

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