Effects of multiple stressors on food web structure

David Beauchesne[1,2,], Dominique Gravel[3], Philippe Archambault[2]*

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

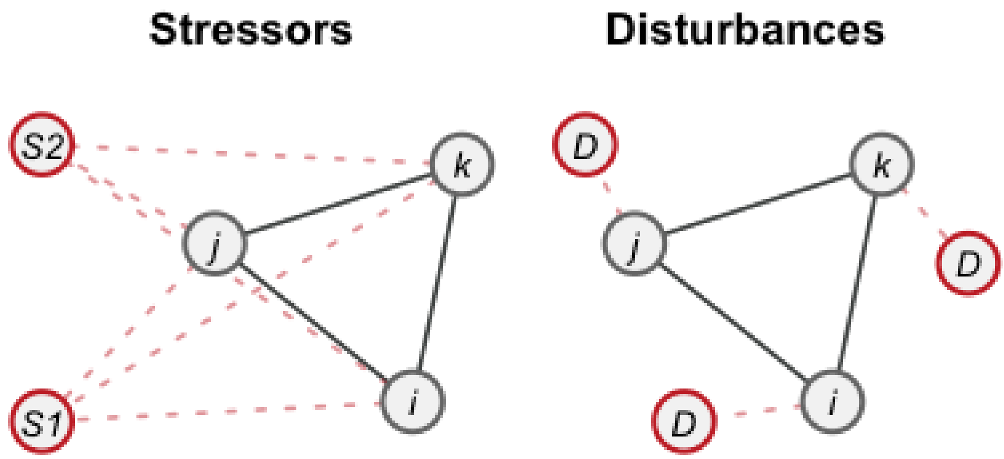

Figure 1: Omnivory 3-species motif affected by two different drivers on the left and by 3 unidentified disturbances on the right. Disturbances could stem from multiple stressors or from a single stressor affecting multiple species.

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.

4 Pathways of multiple effects in motifs

A food web can be decomposed into a sets 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).

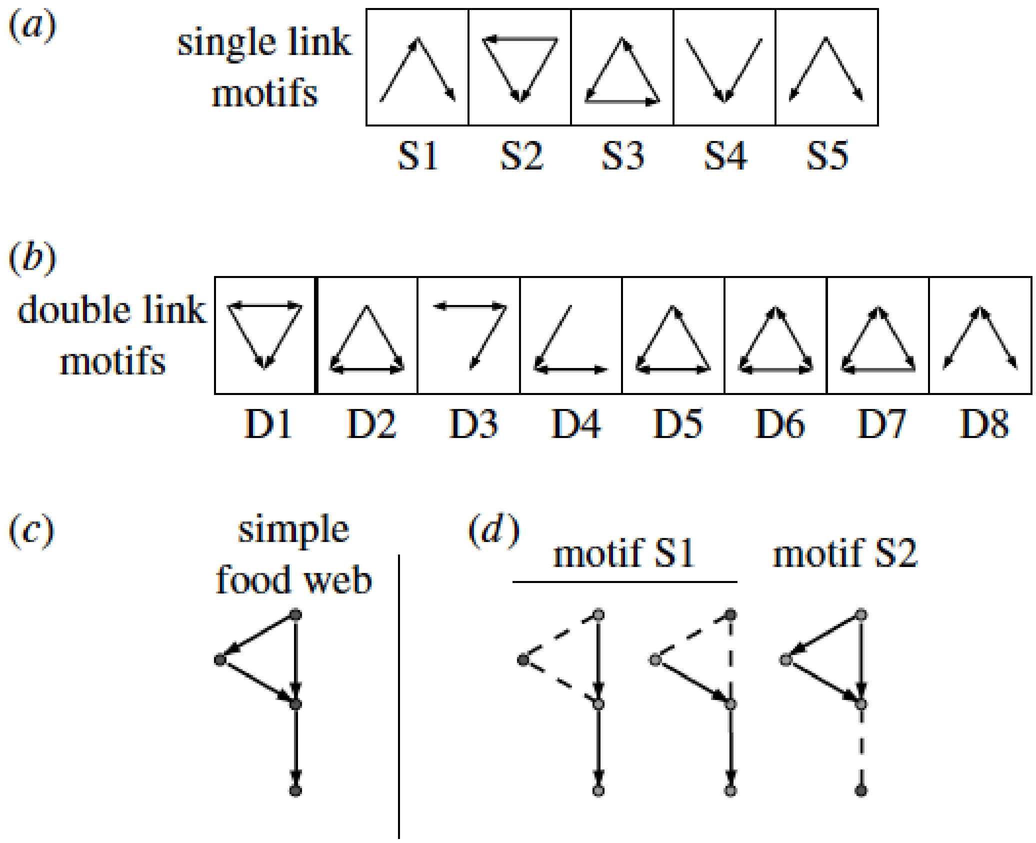

Figure 1. Food-web motifs. When neglecting cannibalism, there are 13 unique food-web motifs composed of three species (Milo *et al.* 2002). To simplify our analysis and presentation, we separate the 13 motifs into two groups: (*a*) motifs S1–S5 that include only single links and (*b*) motifs D1–D8 that 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***.

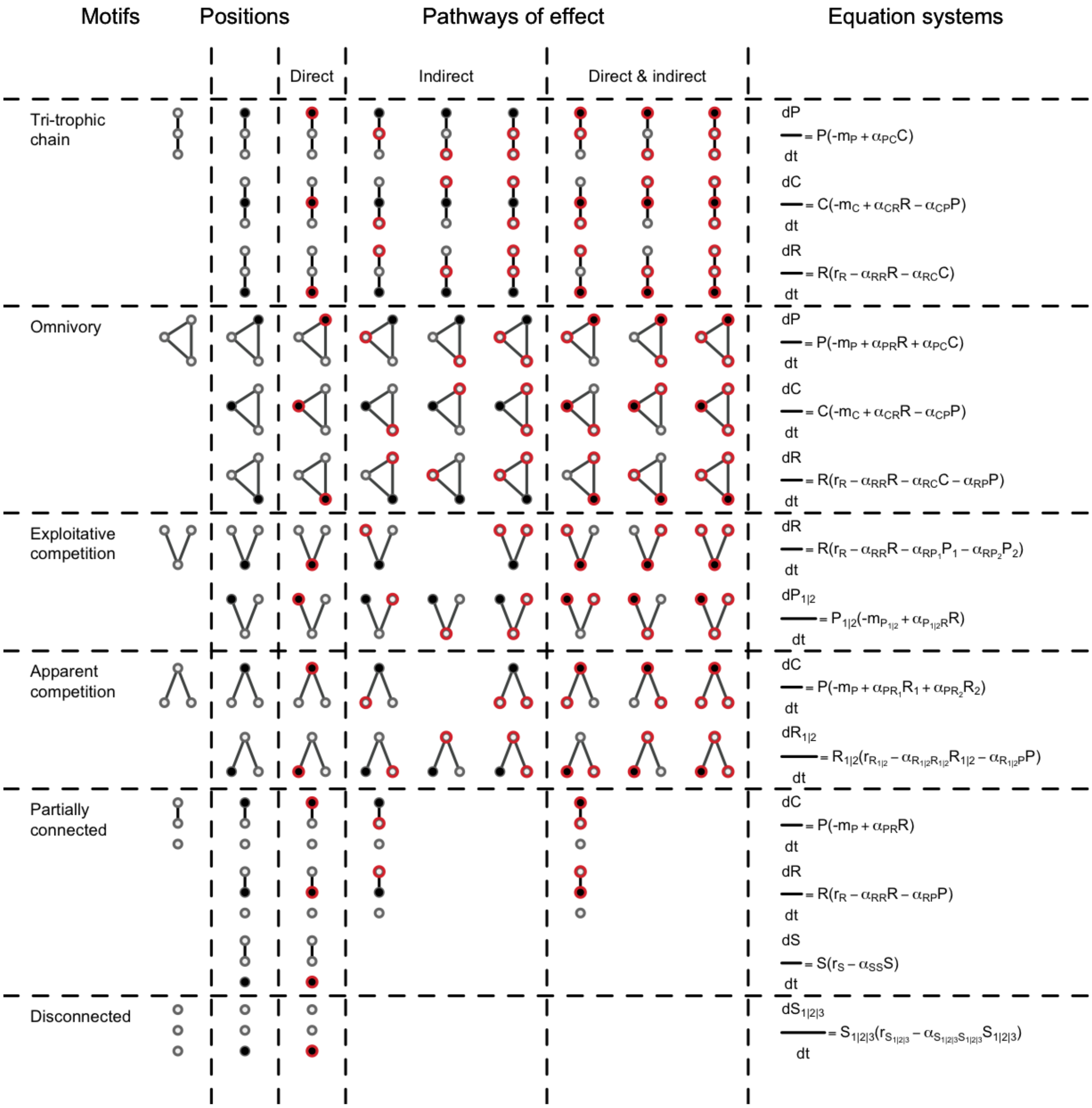

Figure 3: Description of distinct pathways of effect on 14 distinct positions in 6 different network motifs. Black nodes are focal species and red circles represent pathways of effects (or points of entry in food webs?).

5 Equation systems

Using lotka-volterra predator-prey equations with resource logistic growth, we evaluate analytically the effects of multiple disturbances on species contained in the different motifs considered. The parameters considered are the following.

Parameters	Description	Units
x	Species x abundance	n
y	Species y abundance	n
z	Species z abundance	n
r	Growth rates	$1/t$
m	Mortality rates	$1/t$
α_{ii}	Density dependent effect of species i on itself	$1/At$
α_{ij}	Effect species j on species i	$1/At$

The effects α of species on each other can be further defined as being attack and conversion rates. The conversion rates are equal to a scaling parameters (μ, ν, ω) multiplied by the attack rate and the conversion rate cannot exceed the attack rate, so that the scaling parameters is < 1. Hence, the full set of parameters used for the motif models is:

Parameters	Description	Units
x	Species x abundance	n
y	Species y abundance	n
z	Species z abundance	n
r_x	Growth rates	$1/t$
r_y	Growth rates	$1/t$
r_z	Growth rates	$1/t$
m_y	Mortality rates	$1/t$
m_z	Mortality rates	$1/t$
α_x	Density dependent effect of i on itself	$1/At$
α_y	Density dependent effect of y on itself	$1/At$
α_z	Density dependent effect of z on itself	$1/At$
β	Attack rate of y on x	$1/At$
δ	Attack rate of z on y	$1/At$
γ	Attack rate of z on x	$1/At$
μ	Scaling parameter for conversion rate y on x	$1/At$
ν	Scaling parameter for conversion rate z on x	$1/At$
ω	Scaling parameter for conversion rate z on y	$1/At$

The subscript identifying species for growth rates (r), density-dependence effects (α) and mortality rates (m) is not used in motifs where the parameter exists for a single species.

5.1 Tri-trophic chain

5.1.1 Equations

$$\begin{aligned}
\frac{dx}{dt} &= x(r - \alpha x - \beta y) \\
\frac{dy}{dt} &= y(\mu\beta x - \delta z - m_y) \\
\frac{dz}{dt} &= z(\omega\delta y - m_z)
\end{aligned} \tag{1}$$

5.1.2 Equilibria

We identify the equilibria of the equations system using sage and focus only on the equilibria including all species. See `modules.sage` file for code for tri-trophic food chain equilibrium.

$$\begin{aligned}
x &= \frac{\delta r\omega - \beta m_z}{\alpha\delta\omega} \\
y &= \frac{m_z}{\delta\omega} \\
z &= -\frac{\beta^2 m_z\mu - (\beta\delta r\mu - \alpha\delta m_y)\omega}{\alpha\delta^2\omega}
\end{aligned} \tag{2}$$

5.1.3 Jacobian

$$J = \begin{bmatrix} -2\alpha x - \beta y + r & -\beta x & 0 \\ \beta\mu y & \beta\mu x - \delta z - m_y & -\delta y \\ 0 & \delta\omega z & \delta\omega y - m_z \end{bmatrix}$$

5.1.4 Parameter space

5.1.4.1 Default parameters

For now, I manually chose default parameters to initiate the simulations. This should be done more rigorously for an actual scientific paper, but for exploratory purposes it will serve.

$$
\begin{aligned}
r &= 1 \\
\alpha &= 0.001 \\
\beta &= 0.01 \\
\mu &= 0.1 \\
\delta &= 0.01 \\
\omega &= 0.5 \\
m_y &= 0.01 \\
m_z &= 0.1
\end{aligned}
\tag{3}
$$

5.1.4.2 Analytical simulations

We now explore the parameter space by varying parameters on all possible combinations to simulate disturbances. For the simulations, we assume that disturbances are always negative, *e.g.* causing a decrease in predator attack rate or an increase in mortality. Parameter variations are randomly drawn from a uniform distribution within a 40% parameter range from the default value.

I believe that this should eventually be modified to explore the parameter space so that we explore the full range of parameters that ensures species co-existance and evaluate which parameters are more robust to modifications. For now, though, I set this to 40% because it allows me to better explore the disturbances that are dominant. For example, certain parameters have no effect on the abundance of certain species.

Analytical abundance results for each species are then compared to those using the default parameters to evaluate the percent change in abundance. To compare whether disturbances are additive or non-additive, we then compare the additive model, *i.e.* the sum of the individual parameter changes, with the joint models, *i.e.* parameters changed simultaneously. Comparisons are performed by substracting the percent abundance change of the joint model with that of the additive model. A null difference signifies either an absence of effect, an additive effect or a dominant effect. A negative difference means a greater difference from the additive model than the joint model, hence an antagonistic effect for the joint model, while a positive difference is the inverse, *i.e.* a synergistic effect for the joint model. Results are presented as a series of boxplot as an initial exploratory analysis.

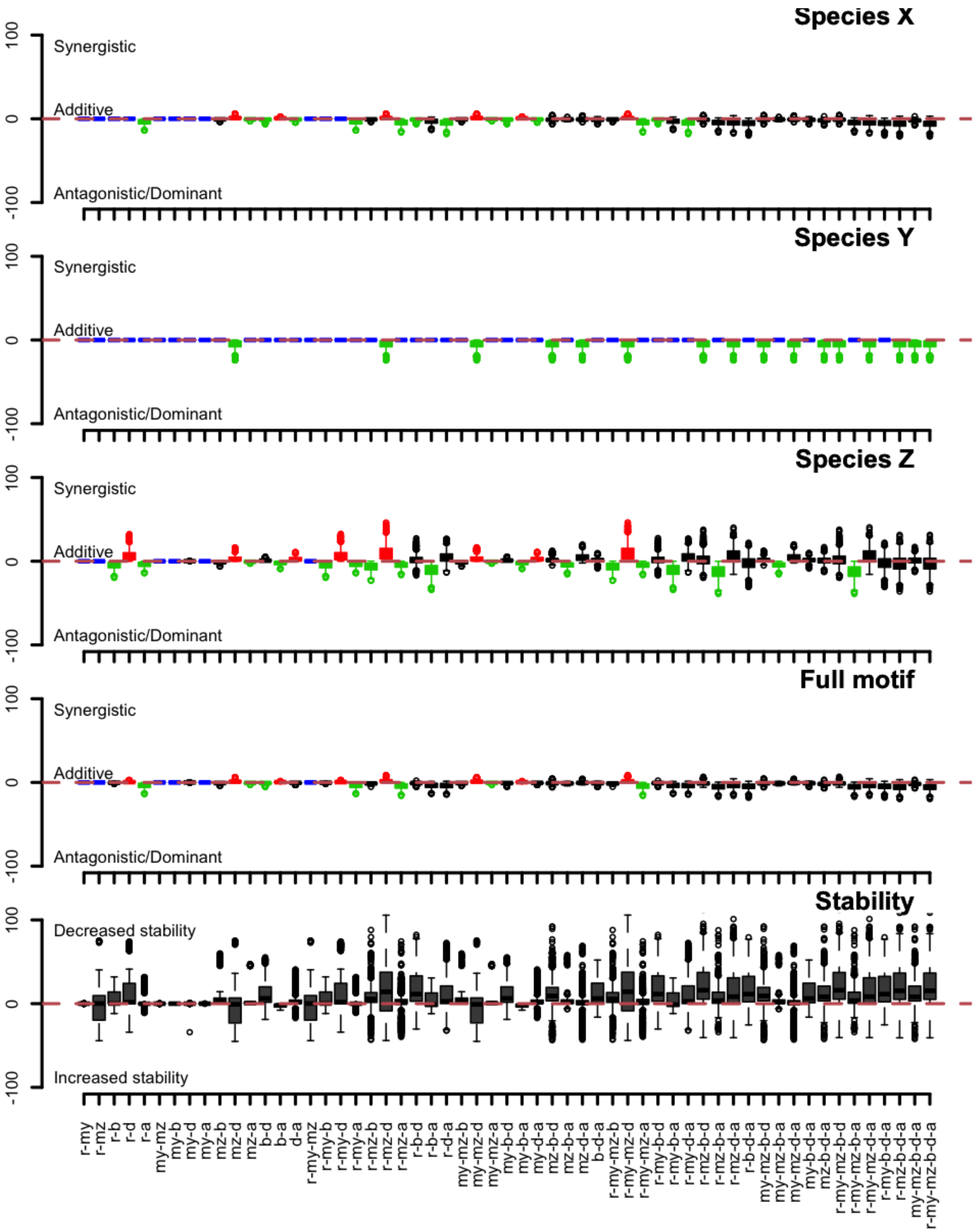

Figure 4: Analytical simulation of disturbances to combinations of parameters for the tri-trophic food chain.

5.2 Omnivory

5.2.1 Equations

$$\begin{aligned}
\frac{dx}{dt} &= x(r - \alpha x - \beta y - \gamma z) \\
\frac{dy}{dt} &= y(\mu\beta x - \delta z - m_y) \\
\frac{dz}{dt} &= z(\nu\gamma x + \omega\delta y - m_z)
\end{aligned} \tag{4}$$

5.2.2 Equilibria

$$\begin{aligned}
x &= \frac{\beta m_z - (\gamma m_y + \delta r)\omega}{\beta\gamma\nu - (\beta\gamma\mu + \alpha\delta)\omega} \\
y &= -\frac{\beta\gamma m_z\mu + \alpha\delta m_z - (\gamma^2 m_y + \delta\gamma r)\nu}{\beta\delta\gamma\nu - (\beta\delta\gamma\mu + \alpha\delta^2)\omega} \\
z &= \frac{\beta^2 m_z\mu - \beta\gamma m_y\nu - (\beta\delta r\mu - \alpha\delta m_y)\omega}{\beta\delta\gamma\nu - (\beta\delta\gamma\mu + \alpha\delta^2)\omega}
\end{aligned} \tag{5}$$

5.2.3 Jacobian

$$J = \begin{bmatrix} -2\,\alpha x - \beta y - \gamma z + r & -\beta x & -\gamma x \\ \beta\mu y & \beta\mu x - \delta z - m_y & -\delta y \\ \gamma\nu z & \delta\omega z & \gamma\nu x + \delta\omega y - m_z \end{bmatrix}$$

5.2.4 Parameter space

5.2.4.1 Default parameters

$$
\begin{aligned}
r &= 1\\
\alpha &= 0.001\\
\beta &= 0.0008\\
\mu &= 0.375\\
\gamma &= .0008\\
\nu &= 0.125\\
\delta &= 0.0002\\
\omega &= 0.5\\
m_y &= 0.1\\
m_z &= 0.1
\end{aligned}
\tag{6}
$$

5.2.4.2 Analytical simulations

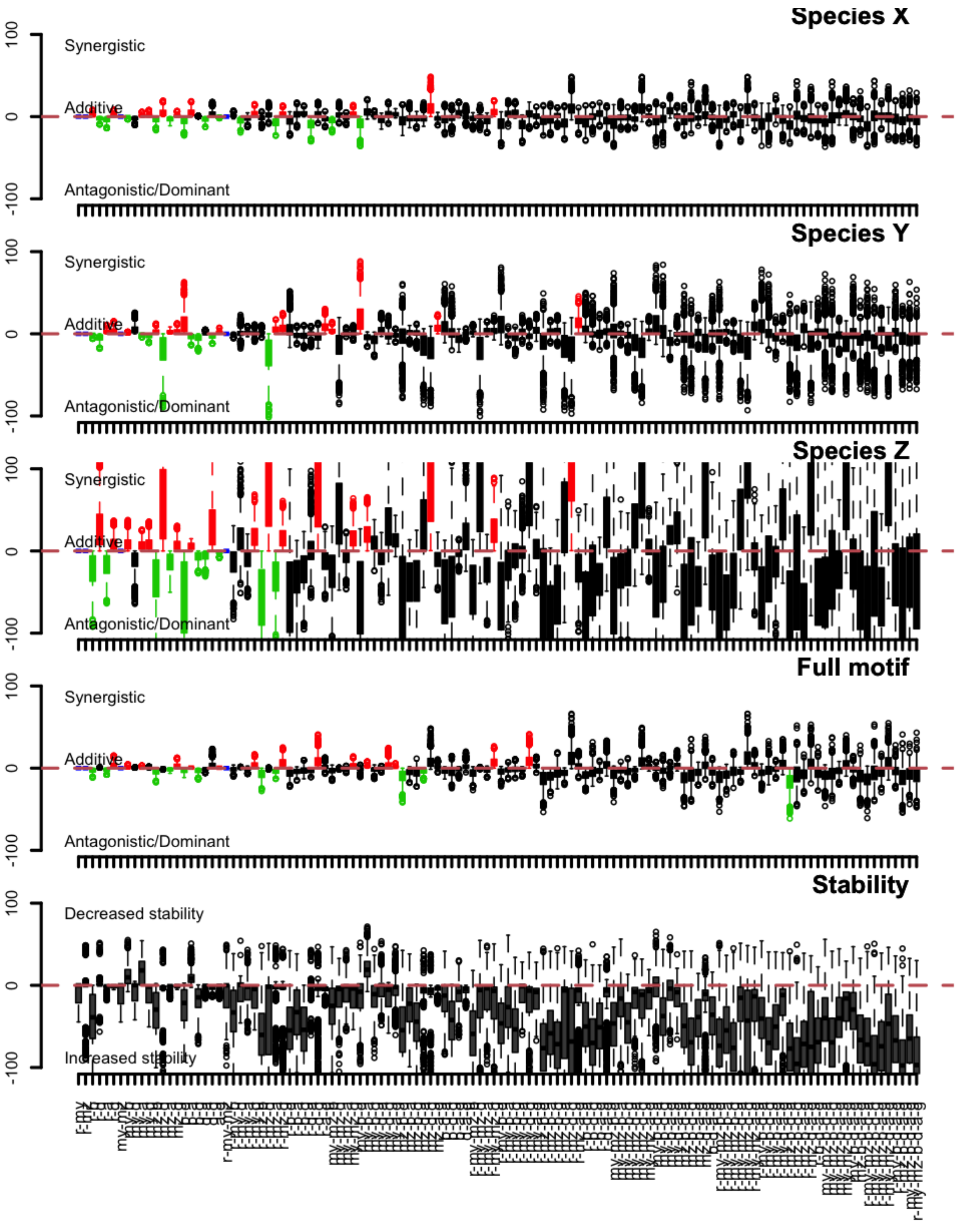

Figure 5: Analytical simulation of disturbances to combinations of parameters for the tri-trophic food chain.

5.3 Exploitative competition

5.3.1 Equations

$$
\begin{aligned}
\frac{dx}{dt} &= x(r - \alpha x - \beta y - \gamma z) \\
\frac{dy}{dt} &= y(\mu\beta x - m_y) \\
\frac{dz}{dt} &= z(\nu\gamma x - m_z)
\end{aligned}
\tag{7}
$$

5.3.2 Equilibria

NO EQUILIBRIUM EXISTS FOR ALL 3 SPECIES

I tried with a density-dependent effect and competition parameters for the predators. This will have to be verified. I have not formatted the math for this yet.

5.4 Exploitative competition - competitive parameters and density-dependence

5.4.1 Equations

$$
\begin{aligned}
\frac{dx}{dt} &= -(\alpha_{xx}x + by + gz - r)x \\
\frac{dy}{dt} &= (bux - ajjajkz - ajjy - my)y \\
\frac{dz}{dt} &= (gvx - akjakky - akkz - mz)z
\end{aligned}
\tag{8}
$$

5.4.2 Equilibria

$$
\begin{aligned}
x &= \frac{(\alpha_{yy}\alpha_{yz}\alpha_{zy} - \alpha_{yy})\alpha_{zz}r + (\alpha_{zy}\alpha_{zz}\gamma - \alpha_{zz}\beta)m_y + (\alpha_{yy}\alpha_{yz}\beta - \alpha_{yy}\gamma)m_z}{(\alpha_{xx}\alpha_{yy}\alpha_{yz}\alpha_{zy} - \alpha_{xx}\alpha_{yy})\alpha_{zz} + (\alpha_{zy}\alpha_{zz}\beta\gamma - \alpha_{zz}\beta^2)\mu + (\alpha_{yy}\alpha_{yz}\beta\gamma - \alpha_{yy}\gamma^2)\nu} \\
y &= -\frac{\alpha_{xx}\alpha_{yy}\alpha_{yz}m_z - \alpha_{xx}\alpha_{zz}m_y + (\beta\gamma m_z + \alpha_{zz}\beta r)\mu - (\alpha_{yy}\alpha_{yz}\gamma r + \gamma^2 m_y)\nu}{(\alpha_{xx}\alpha_{yy}\alpha_{yz}\alpha_{zy} - \alpha_{xx}\alpha_{yy})\alpha_{zz} + (\alpha_{zy}\alpha_{zz}\beta\gamma - \alpha_{zz}\beta^2)\mu + (\alpha_{yy}\alpha_{yz}\beta\gamma - \alpha_{yy}\gamma^2)\nu} \\
z &= -\frac{\alpha_{xx}\alpha_{zy}\alpha_{zz}m_y - \alpha_{xx}\alpha_{yy}m_z - (\alpha_{zy}\alpha_{zz}\beta r + \beta^2 m_z)\mu + (\beta\gamma m_y + \alpha_{yy}\gamma r)\nu}{(\alpha_{xx}\alpha_{yy}\alpha_{yz}\alpha_{zy} - \alpha_{xx}\alpha_{yy})\alpha_{zz} + (\alpha_{zy}\alpha_{zz}\beta\gamma - \alpha_{zz}\beta^2)\mu + (\alpha_{yy}\alpha_{yz}\beta\gamma - \alpha_{yy}\gamma^2)\nu}
\end{aligned}
$$

5.4.3 Jacobian

$$J = \begin{bmatrix} -2\,\alpha_{xx}x - \beta y - \gamma z + r & -\beta x & -\gamma x \\ \beta \mu y & \beta \mu x - \alpha_{yy}\alpha_{yz}z - 2\,\alpha_{yy}y - m_y & -\alpha_{yy}\alpha_{yz}y \\ \gamma \nu z & -\alpha_{zy}\alpha_{zz}z & \gamma \nu x - \alpha_{zy}\alpha_{zz}y - 2\,\alpha_{zz}z - m_z \end{bmatrix}$$

5.4.4 Parameter space

5.4.4.1 Default parameters

$$\begin{aligned} r &= 1, \\ aii &= 0.001, \\ b &= 0.01, \\ u &= 0.1, \\ g &= 0.01, \\ v &= 0.1, \\ my &= 0.1, \\ mz &= 0.1, \\ ajj &= 0.01, \\ ajk &= 0.01, \\ akk &= 0.01, \\ akj &= 0.01 \end{aligned} \tag{9}$$

5.4.4.2 Analytical simulations

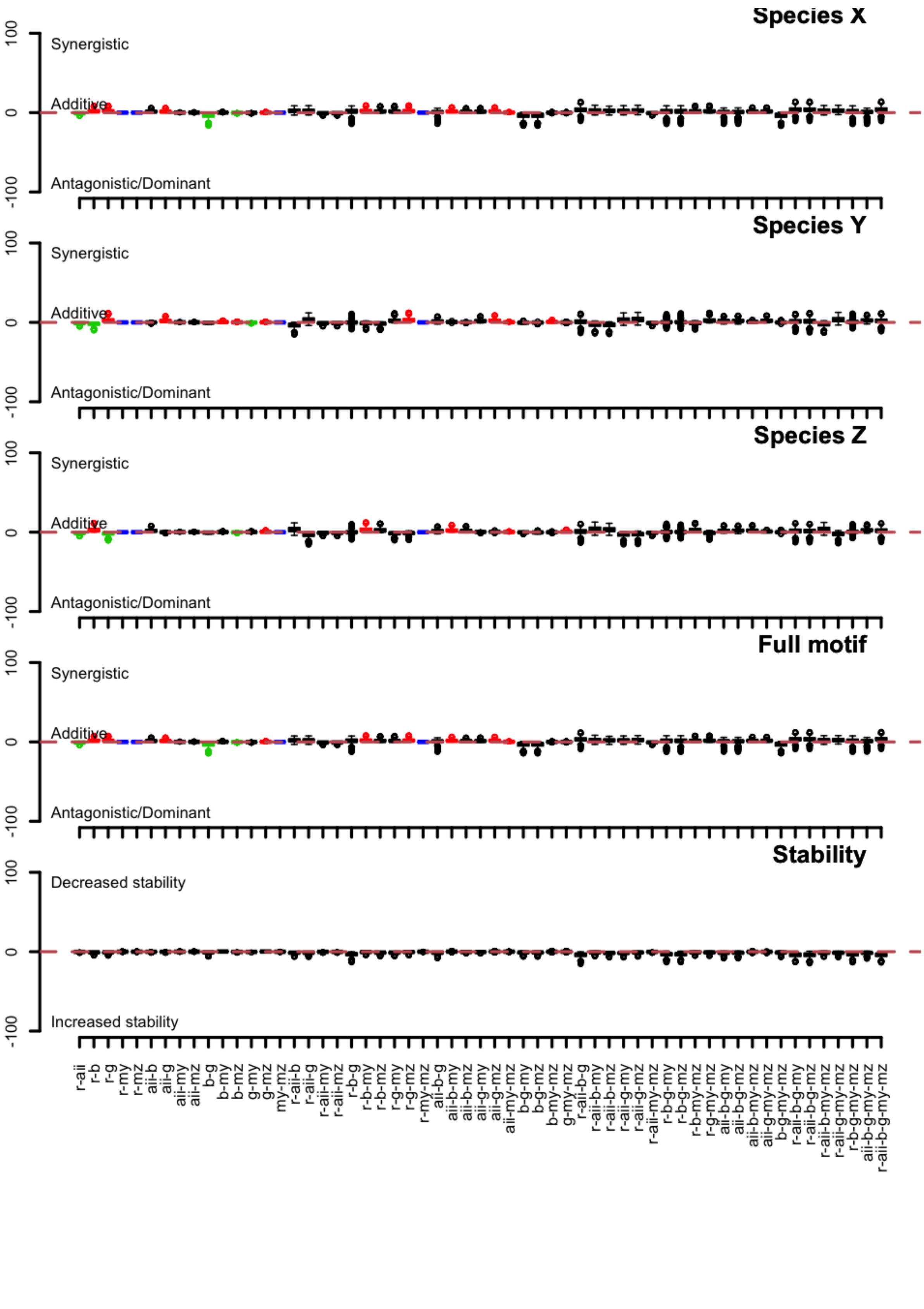

Figure 6: Analytical simulation of disturbances to combinations of parameters for the tri-trophic food chain.

5.5 Apparent competition

5.5.1 Equations

$$\begin{aligned} \frac{dx}{dt} &= x(r_x - \alpha_x x - \gamma z) \\ \frac{dy}{dt} &= y(r_y - \alpha_y y - \delta z) \\ \frac{dz}{dt} &= z(\nu\gamma x + \omega\delta y - m_z) \end{aligned} \tag{10}$$

5.5.2 Equilibria

$$\begin{aligned} x &= \frac{\alpha_y \gamma m z + (\delta^2 r_x - \delta\gamma r_y)\omega}{\alpha_y \gamma^2 \nu + \alpha_x \delta^2 \omega} \\ y &= \frac{\alpha_x \delta m z - (\delta\gamma r_x - \gamma^2 r_y)\nu}{\alpha_y \gamma^2 \nu + \alpha_x \delta^2 \omega} \\ z &= \frac{\alpha_y \gamma r_x \nu + \alpha_x \delta r_y \omega - \alpha_x \alpha_y m z}{\alpha_y \gamma^2 \nu + \alpha_x \delta^2 \omega} \end{aligned} \tag{11}$$

5.5.3 Jacobian

$$J = \begin{bmatrix} -2\,a_x x - \gamma z + r_x & 0 & -\gamma x \\ 0 & -2\,a_y y - \delta z + r_y & -\delta y \\ \gamma\nu z & \delta\omega z & \gamma\nu x + \delta\omega y - m_z \end{bmatrix}$$

5.5.4 Parameter space

5.5.4.1 Default parameters

$$
\begin{aligned}
r_x &= 1\\
r_y &= 1\\
\alpha_x &= 0.001\\
\alpha_y &= 0.001\\
\gamma &= 0.01\\
\nu &= 0.1\\
\delta &= 0.01\\
\omega &= 0.1\\
m_z &= 0.1
\end{aligned}
\tag{12}
$$

5.5.4.2 Analytical simulations

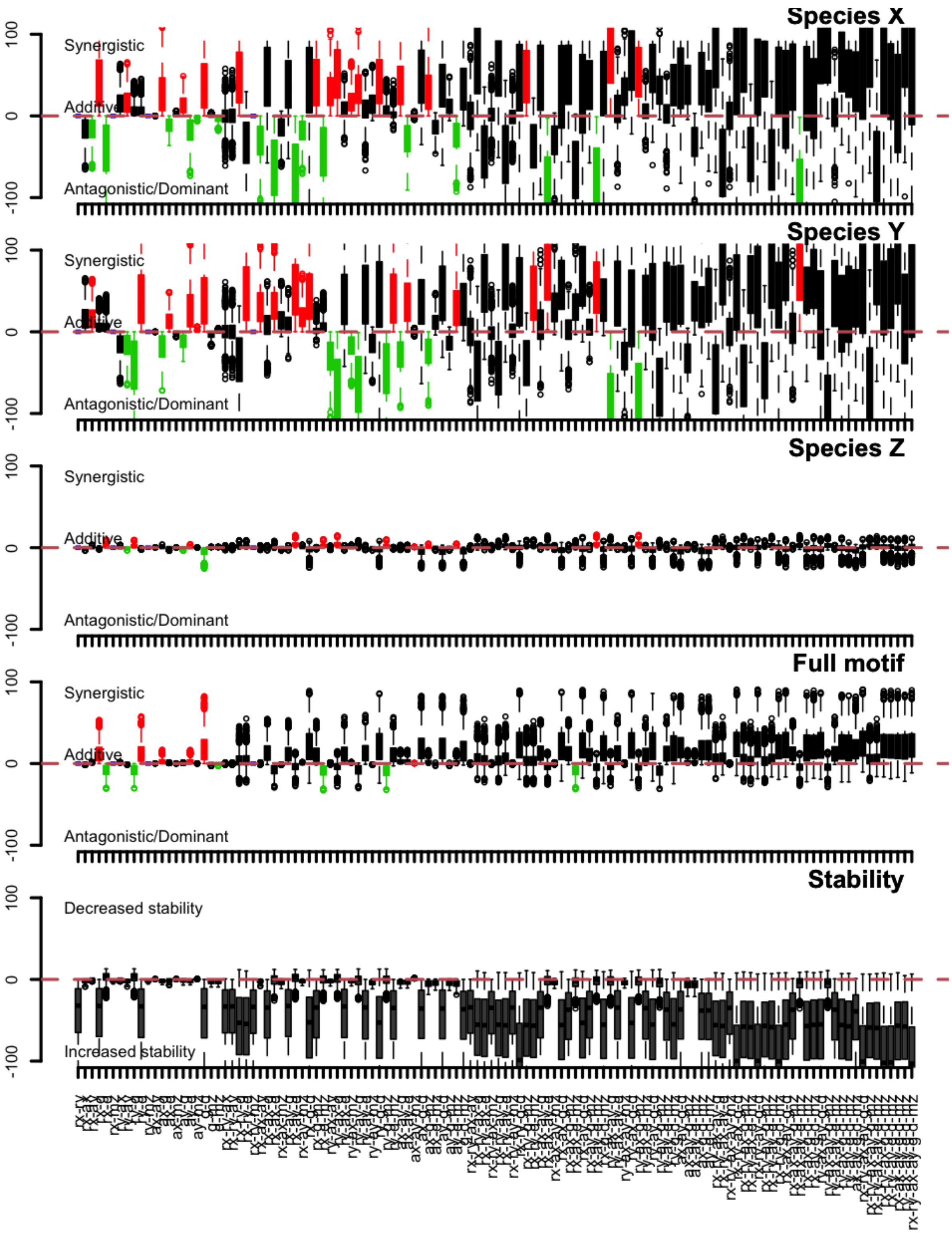

Figure 7: Analytical simulation of disturbances to combinations of parameters for the .

5.6 Partially disconnected

5.6.1 Equations

$$\begin{aligned}
\frac{dx}{dt} &= x(r_x - \alpha_x x - \beta y) \\
\frac{dy}{dt} &= y(\mu\beta x - m_y) \\
\frac{dz}{dt} &= z(r_z - \alpha_z z)
\end{aligned} \tag{13}$$

5.6.2 Equilibria

$$\begin{aligned}
x &= \frac{m_y}{\beta\mu} \\
y &= \frac{\beta r_x \mu - \alpha_x m_y}{\beta^2 \mu} \\
z &= \frac{r_z}{a_z}
\end{aligned}$$

5.6.3 Jacobian

$$J = \begin{bmatrix} -2\,a_x x - \beta y + r_x & -\beta x & 0 \\ \beta\mu y & \beta\mu x - m_y & 0 \\ 0 & 0 & -2\,a_z z + r_z \end{bmatrix}$$

5.6.4 Parameter space

5.6.4.1 Default parameters

$$\begin{aligned}
r_x &= 1 \\
a_x &= 0.001 \\
r_z &= 1 \\
a_z &= 0.001 \\
\beta &= 0.01 \\
\mu &= 0.1 \\
m_y &= 0.1
\end{aligned} \tag{14}$$

5.6.4.2 Analytical simulations

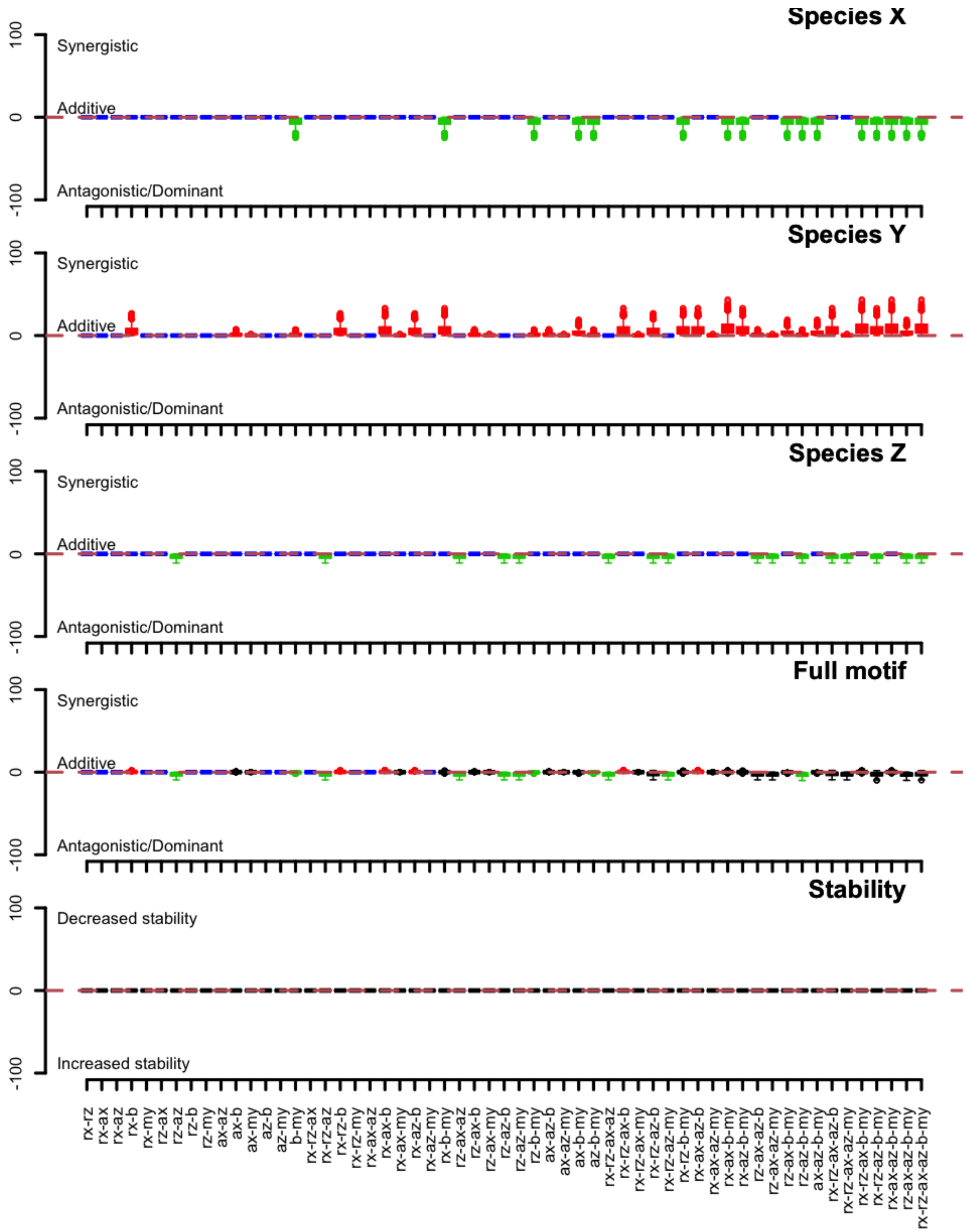

Figure 8: Analytical simulation of disturbances to combinations of parameters for the .

5.7 Disconnected

5.7.1 Equations

$$
\begin{aligned}
\frac{dx}{dt} &= x(r_x - \alpha_x x) \\
\frac{dy}{dt} &= y(r_y - \alpha_y y) \\
\frac{dz}{dt} &= z(r_z - \alpha_z z)
\end{aligned}
\tag{15}
$$

5.7.2 Equilibria

$$
\begin{aligned}
x &= \frac{r_x}{a_x} \\
y &= \frac{r_y}{a_y} \\
z &= \frac{r_z}{a_z}
\end{aligned}
$$

5.7.3 Jacobian

$$
J = \begin{bmatrix} -2\,\alpha_x x + r_x & 0 & 0 \\ 0 & -2\,\alpha_y y + r_y & 0 \\ 0 & 0 & -2\,\alpha_z z + r_z \end{bmatrix}
$$

5.7.4 Parameter space

5.7.4.1 Default parameters

$$
\begin{aligned}
r_x &= 1 \\
a_x &= 0.001 \\
r_y &= 1 \\
a_y &= 0.001 \\
r_z &= 1 \\
a_z &= 0.001
\end{aligned}
\tag{16}
$$

5.7.4.2 Analytical simulations

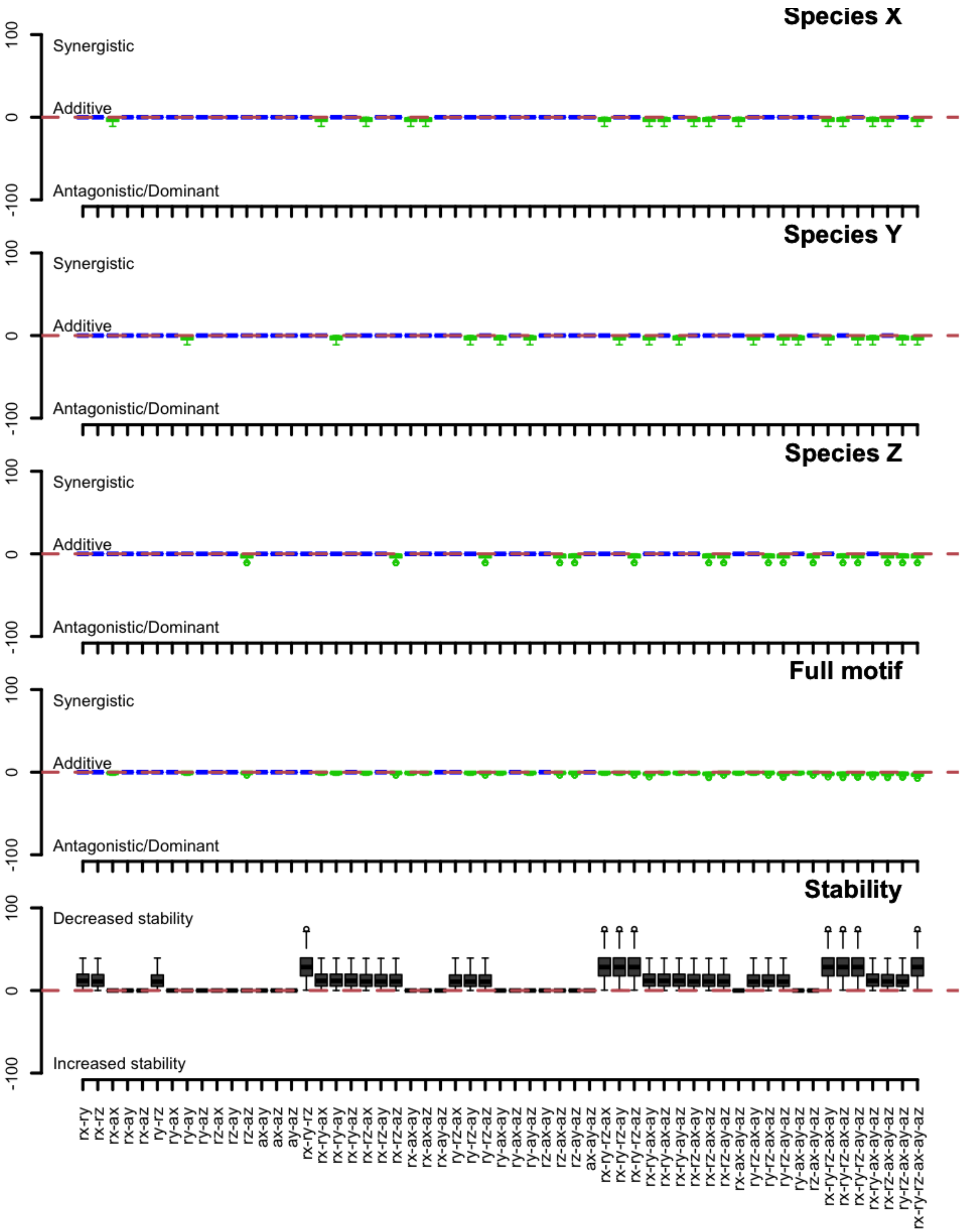

Figure 9: Analytical simulation of disturbances to combinations of parameters for the .

6 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

7 Interesting points

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

8 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)

9 References

Adams, S. M. (2005). Assessing cause and effect of multiple stressors on marine systems. *Marine Pollution Bulletin* 51, 649–657.

Bowler, D., Bjorkmann, A., Dornelas, M., Myers-Smith, I., Navarro, L., Niamir, A., et al. (2019). The geography of the Anthropocene differs between the land and the sea. *bioRxiv*. doi:10.1101/432880.

Brown, C. J., Saunders, M. I., Possingham, H. P., and Richardson, A. J. (2013). Managing for interactions between local and global stressors of ecosystems. *PloS one* 8, e65765.

Brown, C. J., Saunders, M. I., Possingham, H. P., and Richardson, A. J. (2014). Interactions between global and local stressors of ecosystems determine management effectiveness in cumulative impact mapping. *Diversity and Distributions* 20, 538–546. doi:10.1111/ddi.12159.

Camacho, J., Stouffer, D. B., and Amaral, L. A. N. (2007). Quantitative analysis of the local structure of food webs. *Journal of Theoretical Biology* 246, 260–268. doi:10.1016/j.jtbi.2006.12.036.

Christensen, M. R., Graham, M. D., Vinebrooke, R. D., Findlay, D. L., Paterson, M. J., and Turner, M. A. (2006). Multiple anthropogenic stressors cause ecological surprises in boreal lakes. *Global Change Biology* 12, 2316–2322.

Côté, I. M., Darling, E. S., and Brown, C. J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences* 283, 20152592. doi:10.1098/rspb.2015.2592.

Crain, C. M., Kroeker, K., and Halpern, B. S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters* 11, 1304–1315. doi:10.1111/j.1461-0248.2008.01253.x.

Darling, E. S., and Côté, I. M. (2008). Quantifying the evidence for ecological synergies. *Ecology Letters* 11, 1278–1286. doi:10.1111/j.1461-0248.2008.01243.x.

Darling, E. S., McClanahan, T. R., and Côté, I. M. (2013). Life histories predict coral community disassembly under multiple stressors. *Global Change Biology* 19, 1930–1940. doi:10.1111/gcb.12191.

Folt, C. L., Chen, C. Y., Moore, M. V., and Burnaford, J. (1999). Synergism and antagonism among multiple stressors. *Limnology and oceanography* 44, 864–877.

Galic, N., Sullivan, L. L., Grimm, V., and Forbes, V. E. (2018). When things don't add up: Quantifying impacts of multiple stressors from individual metabolism to ecosystem processing. *Ecology Letters* 21, 568–577. doi:10.1111/ele.12923.

Halpern, B. S., Frazier, M., Potapenko, J., Casey, K. S., Koenig, K., Longo, C., et al. (2015). Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature Communications* 6. doi:10.1038/ncomms8615.

Jackson, M. C., Loewen, C. J. G., Vinebrooke, R. D., and Chimimba, C. T. (2016). Net effects of multiple stressors in freshwater ecosystems: A meta-analysis. *Global Change Biology* 22, 180–189. doi:10.1111/gcb.13028.

Kath, J., Thomson, J. R., Thompson, R. M., Kefford, B. J., Dyer, F. J., and Mac Nally, R. (2018). Interactions among stressors may be weak: Implications for management of freshwater macroinvertebrate communities. *Diversity and Distributions* 24, 939–950.

Lange, K., Bruder, A., Matthaei, C. D., Brodersen, J., and Paterson, R. A. (2018). Multiple-stressor effects on freshwater fish: Importance of taxonomy and life stage. *Fish and Fisheries* 19, 974–983.

Milo, R., Itzkovitz, S., Kashtan, N., Levitt, R., Shen-Orr, S., Ayzenshtat, I., et al. (2004). Superfamilies of Evolved and Designed Networks. *Science* 303, 1538–1542. doi:10.1126/science.1089167.

Piggott, J. J., Townsend, C. R., and Matthaei, C. D. (2015). Reconceptualizing synergism and antagonism among multiple stressors. *Ecology and Evolution* 5, 1538–1547. doi:10.1002/ece3.1465.

Schäfer, R. B., and Piggott, J. J. (2018). Advancing understanding and prediction in multiple stressor research through a mechanistic basis for null models. *Global Change Biology* 24, 1817–1826. doi:10.1111/gcb.14073.

Segner, H., Schmitt-Jansen, M., and Sabater, S. (2014). *Assessing the impact of multiple stressors on aquatic biota: The receptor's side matters.* ACS Publications.

Stouffer, D. B., and Bascompte, J. (2010). Understanding food-web persistence from local to global scales. *Ecology Letters* 13, 154–161. doi:10.1111/j.1461-0248.2009.01407.x.

Stouffer, D. B., Camacho, J., Jiang, W., and Nunes Amaral, L. A. (2007). Evidence for the existence of a robust pattern of prey selection in food webs. *Proceedings of the Royal Society B: Biological Sciences* 274, 1931–1940. doi:10.1098/rspb.2007.0571.

Stouffer, D. B., Sales-Pardo, M., Sirer, M. I., and Bascompte, J. (2012). Evolutionary Conservation of Species' Roles in Food Webs. *Science* 335, 1489–1492. doi:10.1126/science.1216556.

Thompson, P. L., MacLennan, M. M., and Vinebrooke, R. D. (2018a). An improved null model for assessing the net effects of multiple stressors on communities. *Global change biology* 24, 517–525.

Thompson, P. L., MacLennan, M. M., and Vinebrooke, R. D. (2018b). Species interactions cause non-additive effects of multiple environmental stressors on communities. *Ecosphere* 9, e02518.

Vinebrooke, R. D., Cottingham, K. L., Scheffer, J. N., Marten, Dodson, S. I., Maberly, S. C., and Sommer, U. (2004). Impacts of multiple stressors on biodiversity and ecosystem functioning: The role of species co-tolerance. *Oikos* 104, 451–457. doi:10.1111/j.0030-1299.2004.13255.x.