

On the sensitivity of food webs to multiple disturbances

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1 Introduction

Global changes 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 biotic interactions (???, ???).

Pathways of effect

Literature on the effects of disturbances on the structure of empirical and simulated networks

Recent attempts have focused on

In this paper, we investigated

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

Our goal was to investigate the impact of disturbances targetting multiple pathways of effect (*e.g.* mortality and physiology) on the

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 Methodology

3.1 Models

The dynamics of the four most abundant 3-species motifs (*i.e.* tri-trophic food chain, omnivory, exploitative and apparent competition) in empirical food webs (Stouffer and Bascompte, 2010) were modeled using Lotka-Volterra equation systems solved at equilibrium. We also included two additional motifs [...]

Resources were modeled using logistic growth equations of the form $\frac{dX_i}{dt} = X_i(r_i - \alpha_{ii}X_i - \sum \alpha_{ij}X_j)$, where X are species, i is the resource, j are the consumers, r_i is the intrinsic resource growth rate, α_{ii} is the density-dependent effect of the resource on itself and α_{ij} is the rate at which consumer j affects resource i , *i.e.* the attack rate.

Consumers and predators were modeled with a Type I functional response of the form $\frac{dX_j}{dt} = X_j(-m_j + \sum e_{ij}\alpha_{ij}X_i - \alpha_{jk}X_k)$, where m is the mortality rate and e is the rate at which resource biomass is transformed into consumer biomass, *i.e.* the conversion rate. e is a scaling parameter of the attack rate which cannot exceed 1, since 1 unit of resource biomass cannot be transformed into more than 1 unit of consumer biomass.

As no equilibrium exists for the exploitative competition motif with Lotka-Volterra models of these forms, competitive parameters of the form $\alpha_{jj}\alpha_{jk}X_jX_k - \alpha_{jj}X_j^2$ were included in the consumer models to constrain their growth and obtain solutions at equilibrium. Sage (???) was used to solve all equation systems at equilibrium. All other analyses were performed using R (???). All code and data used to perform the simulations and analyses are available at [...].

Initial parameter values were set by using a simulated annealing algorithm optimizing for consumer and predator abundance.

Model parameter values for intrinsic growth and resource density-dependence parameters were fixed to 1 and 0.001, respectively, to bound all solutions. Competitive parameters for the exploitative competition motif were also fixed at 0.001 since those parameters were not to be investigated in our analyses. Conversion rates were fixed to 0.5. Finally, a total of 100 sets of mortality and attack rates were evaluated using a simulated annealing algorithm optimizing for consumer abundance.

3.2 Initial parameter values

3.3 Disturbances

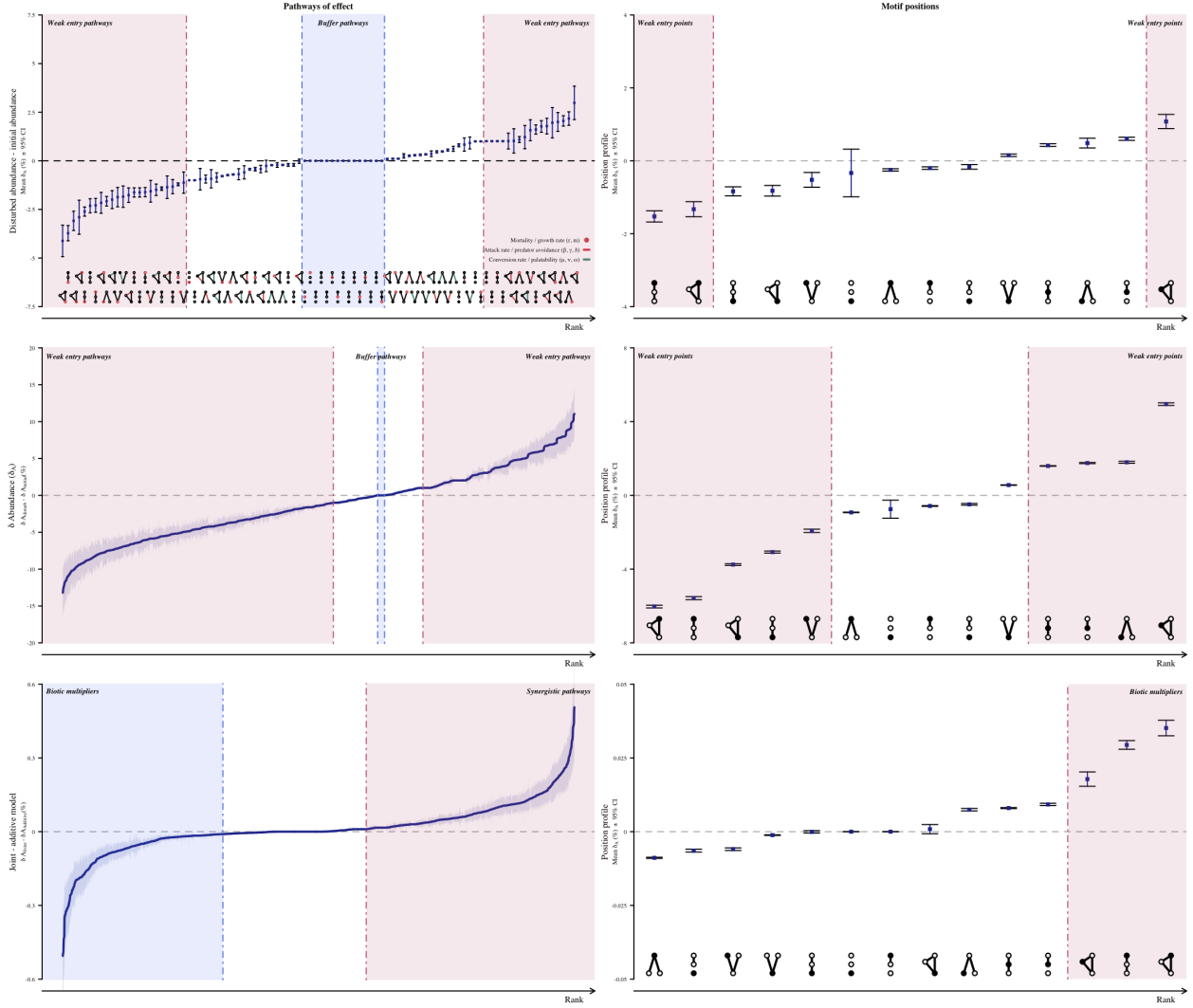


Figure 1: Disturbances

4 Results

4.1 Univariate disturbances

4.2 Multivariate disturbances

4.3 Additivity

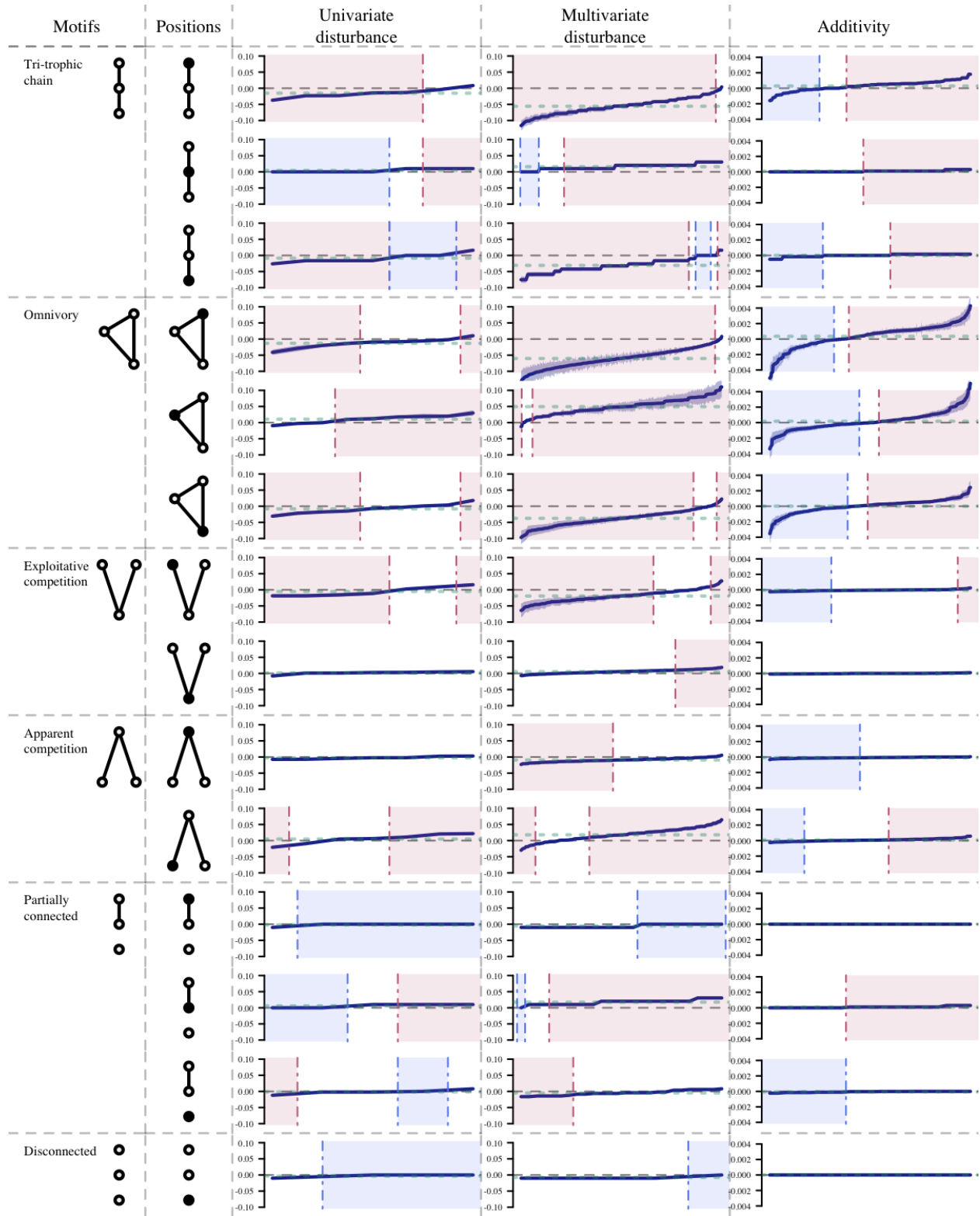


Figure 2: Positions

5 Supplementary Material

5.1 Models

| Motifs | Equation systems | Parameters |
|--------------------------|---|--|
| Tri-trophic food chain | $\begin{aligned}\frac{dX_i}{dt} &= X_i(r_i - \alpha_{ii}X_i - \alpha_{ij}X_j) \\ \frac{dX_j}{dt} &= X_j(e_{ij}\alpha_{ij}X_i - \alpha_{jk}X_k - m_j) \\ \frac{dX_k}{dt} &= X_k(e_{jk}\alpha_{jk}X_j - m_k)\end{aligned}$ | $\begin{aligned}r_i &= 1 \\ \alpha_{ii} &= 0.001 \\ \alpha_{ij}, \alpha_{jk} &\in [0.0001, 0.01] \\ e_{ij}, e_{jk} &= 0.5 \\ m_j, m_k &\in [0.01, 0.5]\end{aligned}$ |
| Omnivory | $\begin{aligned}\frac{dX_i}{dt} &= X_i(r_i - \alpha_{ii} - \alpha_{ij}X_j - \alpha_{ik}X_k) \\ \frac{dX_j}{dt} &= X_j(e_{ij}\alpha_{ij}X_i - \alpha_{jk}X_k - m_j) \\ \frac{dX_k}{dt} &= X_k(e_{ik}\alpha_{ik}X_i + e_{jk}\alpha_{jk}X_j - m_k)\end{aligned}$ | $\begin{aligned}r_i &= 1 \\ \alpha_{ii} &= 0.001 \\ \alpha_{ij}, \alpha_{ik}, \alpha_{jk} &\in [0.0001, 0.01] \\ e_{ij}, e_{ik}, e_{jk} &= 0.5 \\ m_j, m_k &\in [0.01, 0.5]\end{aligned}$ |
| Exploitative competition | $\begin{aligned}\frac{dX_i}{dt} &= X_i(r_i - \alpha_{ii} - \alpha_{ij}X_j - \alpha_{ik}X_k) \\ \frac{dX_j}{dt} &= X_j(e_{ij}\alpha_{ij}X_i - \alpha_{jj}\alpha_{jk}X_k - \alpha_{jj}X_j - m_j) \\ \frac{dX_k}{dt} &= X_k(e_{ik}\alpha_{ik}X_i - \alpha_{kk}\alpha_{kj}X_j - \alpha_{kk}X_k - m_k)\end{aligned}$ | $\begin{aligned}r_i &= 1 \\ \alpha_{ii}, \alpha_{jj}, \alpha_{kk}, \alpha_{jk}, \alpha_{kj} &= 0.001 \\ \alpha_{ij}, \alpha_{ik} &\in [0.0001, 0.01] \\ e_{ij}, e_{ik} &= 0.5 \\ m_j, m_k &\in [0.01, 0.5]\end{aligned}$ |
| Apparent competition | $\begin{aligned}\frac{dX_i}{dt} &= X_i(r_i - \alpha_{ii}X_i - \alpha_{ik}X_k) \\ \frac{dX_j}{dt} &= X_j(r_j - \alpha_{jj}X_j - \alpha_{jk}X_k) \\ \frac{dX_k}{dt} &= X_k(e_{ik}\alpha_{ik}X_i + e_{jk}\alpha_{jk}X_j - m_k)\end{aligned}$ | $\begin{aligned}r_i, r_j &= 1 \\ \alpha_{ii}, \alpha_{jj} &= 0.001 \\ \alpha_{ik}, \alpha_{jk} &\in [0.0001, 0.01] \\ e_{ik}, e_{jk} &= 0.5 \\ m_k &\in [0.01, 0.5]\end{aligned}$ |
| Partially disconnected | $\begin{aligned}\frac{dX_i}{dt} &= X_i(r_i - \alpha_{ii}X_i - \alpha_{ik}X_k) \\ \frac{dX_j}{dt} &= X_j(r_j - \alpha_{jj}X_j) \\ \frac{dX_k}{dt} &= X_k(e_{ik}\alpha_{ik}X_i - m_k)\end{aligned}$ | $\begin{aligned}r_i, r_j &= 1 \\ \alpha_{ii}, \alpha_{jj} &= 0.001 \\ \alpha_{ik} &\in [0.0001, 0.01] \\ e_{ik} &= 0.5 \\ m_k &\in [0.01, 0.5]\end{aligned}$ |
| Disconnected | $\begin{aligned}\frac{dX_i}{dt} &= X_i(r_i - \alpha_{ii}X_i) \\ \frac{dX_j}{dt} &= X_j(r_j - \alpha_{jj}X_j) \\ \frac{dX_k}{dt} &= X_k(r_k - \alpha_{kk}X_k)\end{aligned}$ | $\begin{aligned}r_i, r_j, r_k &= 1 \\ \alpha_{ii}, \alpha_{jj}, \alpha_{kk} &= 0.001\end{aligned}$ |

Table 1: Systems of Lotka-Volterra equations used to model the effect of multiple disturbances

6 Introduction

Global changes, , 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.

7 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.

8 Non-linear effects

Let's begin by conceptualizing the effects of 2 environmental stressors on a simple 3-species omnivory food web (Figure 8). 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 species simultaneously. But see Thompson et al. (2018b) and Thompson et al. (2018a) for a description of a modelling approach incorporating multiple sources of stress in a food web.

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.

9 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 9; 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).

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

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 9; 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 9).

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?).

10 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 x 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 x on z | $1/At$ |
| 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 x 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.

11 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

12 Interesting points

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

13 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)

14 References

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