Morning Pascal. I have a look at the ms now and try to give a bit more guidance. I made a section at the very end in which I move text that we might or might not need.

# Possible titles:

Symmetry of ecosystem tipping points is controlled by trait dissimilarity in a simple ecosystem model

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# Abstract

To be written.

# Introduction

Changing environmental conditions like temperature, nutrient and toxin concentrations or food web structures force ecosystems on different scales to respond(Holling 1973, Tilman and Lehman 2001). Depending on ecosystem connectivity and functionality, arising from interactions between and inside the biotic and abiotic compartment (Jorgensen 2009), such response occurs in various patterns(Walther 2010). One type of response is when a small change in an environmental condition causes a large and rapid change in the state of the ecosystem. Examples of such responses include collapse of fishery stocks(Peterman 1977, Walters and Kitchell 2001, Jones and Walters 2011), invasions of exotic species(Mack et al. 2000, With et al. 2002) and changes in aquatic (Scheffer et al. 1993) and terrestrial(Dublin et al. 1990)vegetation.

Such abrupt and large responses, sometimes termed catastrophic shifts (citation please) are of considerable important for ecosystem conservation and management (citation please). They can also be associated with hysteresis, whereby reversal of the catastrophic shift occurs only after a large reversal in environmental conditions past the point where the original catastrophic shift occurred (citation please). This hysteresis phenomenon has important implications for restoration practices, as well as for prevention of the original shift. Such hysteresis loops are displayed from a wide range of ecosystems in terrestrial , marine and freshwater habitats(Scheffer et al. 2001).

Catastrophic shifts and hysteresis can result from an ecosystem having alternative stable states. An ecosystem has alternate stable states when at one set of environmental conditions it can exist in any of multiple stable states. Which state the ecosystem is in then depends on its history. For example, for a given rate of nutrient input a shallow lake could be in a clear water or in a turbid water state depending on whether rates of nutrient input were historically low or high (citation please). The presence of alternate stable states is primarily determined by the strength of positive feedback loops in an ecosystem(Kéfi et al. 2016). For example, mutual inhibition between two functional groups of organisms can cause each to favour an ecosystem state that is unfavourable to the other, and thus create alternate stable states whereby each of the functional groups can exclude the other, given the opportunity to do so.

One feature of these types of ecosystem responses to environmental change is the symmetry of the magnitude of the catastrophic shift. High symmetry would be when the magnitude of the shift is equal in both directions of environmental change (Figure 1a), while low symmetry would be when the magnitude of the shift is greater in one direction of environmental change than the other direction (Figure 1b). Existing models often display asymmetry in the magnitude of the catastrophic shift (citations, Figure 1c) and some empirical data also appear to display asymmetry. [Likely we need a sentence or two saying why asymmetry is important to consider.]

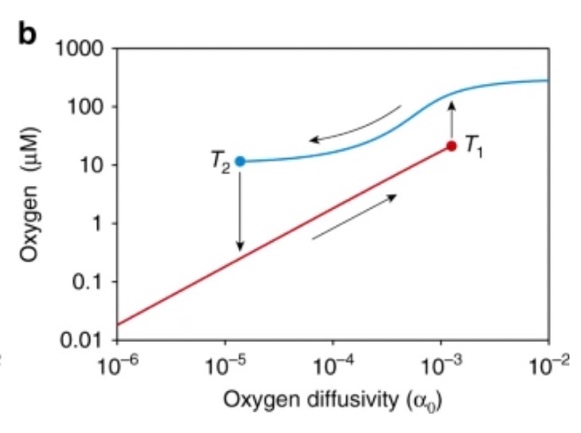
Nevertheless, the symmetry of the response of the ecosystem has received relatively little attention, and we know of no investigation about how symmetry or asymmetry may be produced. We address this gap in knowledge by exploring the response of a simple model ecosystem to an environmental change. We predict that when the model is symmetric in the effect and response traits of the organisms that dominate each of two functional groups, then the ecosystem will display high symmetry in the magnitude of its catastrophic shifts. We also predict that greater difference in trait values will result in greater asymmetry in the magnitude of the catastrophic shifts.

Moreover, it is unclear if hysteresis in the microbial compositions observed in stratified waters arises from the imbalance between the regimes or is also possible in balanced ecosystems. This gap is addressed by exploring the dynamics to environmental change of a balanced, symmetric ecosystem model derived from previous research(Bush et al. 2017). Further advantage of a balanced system is the facilitation to locate the unstable equilibrium. From stability theory(Holling 1973, Scheffer et al. 2001) it is given that an unstable equilibrium must lie within the bistable area and that the system becomes stable between the stable states given no previous history, no favourability by stress and no perturbation(Scheffer et al. 2001). Complete balance in a system implements determination of the location of the unstable equilibrium, as the level of environmental stress favouring no state must lie precisely half-distance between the tipping points. This work suggests using a balanced, symmetric ecosystem model to prove the existence of this unstable equilibrium after the system’s parameterization has been developed to exhibit a symmetric hysteresis response to gradually changing environmental stressors.

A picture containing diagram

Description automatically generatedDiagram

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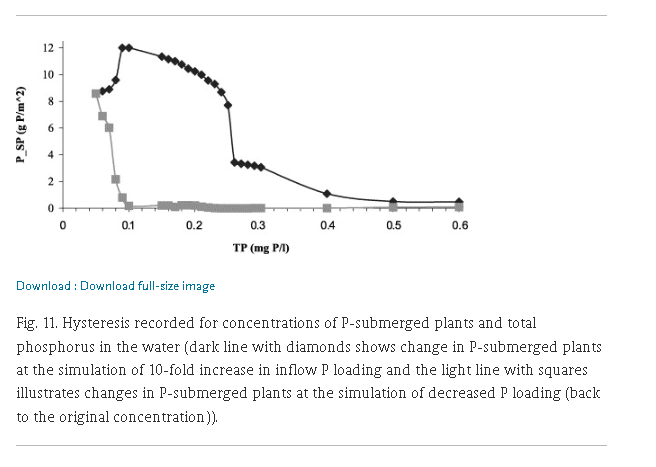


Figure 1. (a) Catastrophic shifts that have equal magnitude in both directions of environmental change. (b) Catastrophic shifts whose magnitude depends on the direction of environmental change. (c) A model ecosystem showing such dependence (reproduced from Bush et al 2017 with permission). (d) An aquatic ecosystem showing such dependence (reproduced from Zhang 2003 with permission). Zhang: interesting figures are also simulations!

# Methods

## The ecosystem model

Our approach was to modify an existing ecosystem model to make it symmetric in effect and response traits of the organisms dominating each of two alternate states. The existing model was that of Bush et al. (2017) of oxic-anoxic regime shifts caused by mutual inhibition between cyanobacteria and sulfur bacteria. To develop a symmetric model, we had to reduce the biological realism, for example, by removing one of the three functional groups of organisms so that only two remained. This consequences of this reduction in biological realism are explored in the Discussion section.

The modified model is shown in Figure 2. The two functional groups are cyanobacteria and sulfur bacteria. Both consume phosphorous and thereby grow, and both are inhibited by a single substrate that is produced by the other. The two substrates can diffuse in and out of the system, and both react with each other and then are lost from the system. Thus, the system is symmetrical in the pattern of interactions. Furthermore, we made the system symmetrical in the values of the various growth, inhibition, consumption, production, and diffusion parameters (Table 1).

Graphical user interface, text, application, email

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Table 1: red ones were treated as hyperparameters, black ones given by Bush papers cyanobacteria

Diagram

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Figure 2: Schematic diagram of model system interactions

Diagram

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Figure 7: Schematic model diagram of balanced, symmetrical model system

### ODEs describing system dynamics

To account for the schematic removal of one functional group and a nutrient (Figure 3) mathematically the set of ordinary differential equations defined in Bush et al. (2017) needs to be updated. The key changes that are made is defining the change of oxidized sulfur and phototrophic sulfur bacteria to be equal to zero and to define the same growth function (Equation (1.1)) for sulfate-reducing bacteria and cyanobacteria.

#### Change of microbial population densities

To construct symmetry, population densities of both groups are equally affected by the maximum growth rates upon phosphorus, the inhibition by the contrary substrates and the mortality rates are equal for both bacteria groups. Derived from the work of bush et al 2017 the change of cyanobacteria (NCB) and sulfate-reducing bacteria (NSB) are described as:

(1)

|  |  |
| --- | --- |
|  |  |

where the function describes the growth of a bacteria group on P (i.e. phosphorus) and the inhibition on S, the substrate produced by the contrary group. The equation is negatively influenced by the mortality rate , due to grazing by predators or viral lysis. The subset B stands for “bacteria”, indicating the generalization of the equation for both groups The growth function is described by the Monod equation for growth, when the growth rate is determined by one nutrient:

(1.1)

where is the maximum specific growth rate and the half-saturation constant for both groups on substrate S (i.e. oxygen/ reduced sulfur) in μM. The inhibition of microbial growth is described by the Haldane equation:

(1.2))

where is an interpretation of the half-saturation constant (IC50), i.e. the concentration of inhibitory substance at which the growth rate of both groups is reduced to 50% compared to

#### Change of chemical substrates

Reduced sulfur results as a substrate from the growth of sulfate-reducing bacteria on phosphorus. Depending on the concentration gradient and a substrate-specific diffusivity , there is either diffusive flux into or out of the system. Oxidation through the geochemical abiotic oxidation cycle removes reduced sulfur from the system. Accordingly, changes in the concentration of reduced sulfur are derived from the description in Bush et al. 2017 as:

(2)

where is the production constant of the substrate (i.e. reduced sulfur) in μM cell-1 by group B (i.e. sulfate reducing bacteria), *c* is the oxidation rate by the abiotic cycle and is the background concentration of reduced sulfur, determining the concentration gradient of the flux together with the concentration of inside the system.

Similarly, oxygen is produced by cyanobacteria and diffuses into or out of the system depending on the concentration gradient and is removed from the system by the abiotic oxidation cycle. Derived from Bush et al 2017, changes in concentration of oxygen are be described as:

(3)

where, again, is the production of the substrate (i.e. oxygen) in μM cell-1 by group B (i.e. cyanobacteria) and the background concentration of oxygen, determining the concentration gradient.

The change of concentration of the nutrient consumed by both microbial groups, phosphorus, is determined by its consumption and diffusive flux across the system boundary. Direction and strength of this flux is determined by the concentration gradient and the nutrient specific diffusivity . Derived from ush et al. 2017 the change is described as:

(4)

where is the yield in cells μM-1 of group B on phosphorus.

## Experimental Design

Experiments of Bush et al (2017) revolved around changing only oxygen diffusivity to induce regime shifts. This work, however, modified both diffusivities of sulfur and oxygen to maintain the balanced conditions. Thus, when oxygen diffusivity was increased the one of sulfur was decreased with the same rate and vice-versa. To find stable states, the condition where tipping points become fixed, two stepwise simulations in each direction of diffusivity change were made. For 300 uniformly distributed values in a range from 0 to -2 (log10h-1) dynamics were simulated for 106 hours, being sufficient for them to become stable. Simulations in both directions were initialized with functional groups being equally abundant with 105 cells L-1. To avoid critically low abundances of either group causing computational interference, 1 cell L-1 was added every 1000 hours to all biological state variables. Simulations of the parameterized system are performed with the radau method being implemented into a spatio-temporal modelling framework(Hairer and Wanner 1999). Thus, the final condition of every combination of diffusivity values becomes the initial condition for simulating the next values. Once the simulation parameters for a stable system were obtained, an unstable equilibrium may be simulated. Given theoretical conditions(Scheffer et al. 2001) (maybe better citation) such equilibrium may occur when initial conditions favour no state and no perturbation arises throughout the simulation. Thus, the diffusivities were simulated in the same framework but kept constant, enabling the balanced model to thrive in completely neutral environment. To proof instability of such equilibrium the simulation was run without adding the cells and with, to mimic small perturbations.

## Measures of symmetry

To show the symmetry that dynamics display, visualization of the trajectories may be sufficient for a qualitative analysis. However, this work found a way to quantify amounts of symmetric response by combining properties of the symmetric model with features typical for hysteresis displaying systems. A key role in the measurement of symmetric response plays the comparison between trajectories of opposed alternative stable states. Regime shifts to alternative stable states occur with varying magnitudes, correlating with the effort to recover the pre-collapse state. Thus, the hysteresis behaviour of a system may be characterized by shift magnitudes of recovery and collapse of the respective environmental states. As antagonistic variables in the symmetric system are driven by identical ODEs, the recovery and collapse shift magnitudes of opposed environmental state are expected to be identical. Thus, the amount of symmetric response by a system can be quantified by similarity of the respective shift magnitudes. Another, yet related approach is to calculate the area between the recovery and the collapse trajectory bound by the tipping points. Again, from a complete symmetric response such areas between antagonistic variables are expected to be identical. This measure completes the latter

Combining these two quantification of symmetric response, allows to compare amounts of symmetry of the simulations of Bush et al (2017) and this works model from to related, yet different perspectives

Comparing dynamics resulting from the symmetric model to the ones of the model by Bush et al (2017) requires

# Results

**Response of the balanced model**

* Symmetry regarding tipping points, hysteresis area and dynamic trajectories
* Compare to symmetry in one simulation of bush

**Unstable Eq**

* How it differs from stable eq, which perturbations are tolerated
* Whether it is possible to reach with history

# Discussion

## Consequences of reduced biological realism

# References

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# Text that we removed but may still want to use some of

Introduction

To further comprehend the effect of changing environmental conditions like temperature, nutrient and toxin concentrations or food web structures on ecosystems, the variety of approaches to interpret ecosystem response is rising. “cite some approaches” (or the next red sentence)

Alternative stable states occur where an ecosystem is locally stable at different equilibria. This means that distinct selected configurations of biotic and abiotic factors persists small perturbations by returning to the same stable configuration, but may shift to a different configuration after a large perturbation12.

However, environmental change often occurs gradually, also linearly in time, rather than catastrophic13,14. The state of the ecosystems may respond in a continuous way15, either steady as in benthic macroinvertebrate compositions16 or inert when a critical threshold is passed displayed by mangrove species to nutrient enrichment17. Such abrupt responses and threshold conditions are often attributed with alternative stable states12. A continuous response simultaneously suggests one stable equilibrium per level of environmental condition implying that a certain configuration of biotic and abiotic factors is followed by an inherent ecosystem response15.

A crucially distinct pattern is shown where response is discontinuous, thus the critical thresholds of stress, called tipping points, depend on the direction of environmental change. Therefore, ecosystems displaying discontinuous response that went through a state shift requires lower levels of environmental stress to recover to the old state, compared to the level that led to shift to the new state15. The difficulty to recover the earlier collapsed state is called the resilience of the new state1 and may be primarily determined by the strength of positive feedback between biotic and abiotic compartment18. In the bistable area, the range of environmental stress where either of the states may occur, the exhibited state depends on the history of the ecosystem . This phenomenon is termed hysteresis12,15 and is also characterized by unstable equilibria being located inside the bistable area. Hence, several equilibria are possible at intermediate levels of environmental stress and there is no unique configuration to stable equilibrium relationship. Depending on initial conditions and the history of the ecosystem unstable equilibria tilt to either of the stable equilibria. Such hysteresis loops are displayed from a wide range of ecosystems in terrestrial , marine and freshwater habitats15.

Bush et al. (2017) explored a microbial ecosystem driving biogeochemical cycles of aquatic environments. Intermediate layers of stratified lakes containing microbes may respond with oxic-anoxic regime shifts to a vertical oxygen gradient19–21. They implemented such dynamics in a mathematical model21 with few, simple interacting processes. With changing oxygen influx the modelled system responds with oxic-anoxic regime shifts, the dynamics of the regime shifts differ with the direction of change, however. A possible explanation for the variation in the two shifts is that the regimes differ in microbial community composition21. Comparing regime-dominating compositions, reveals an asymmetric structure of the model regarding the number of functional groups and biogeochemical dynamics21. Here, we reduced the model to balance the interactions between the regimes to investigate in the role of symmetry in ecosystems exhibiting catastrophic shifts.

Whether the asymmetric response of the ecosystem follows the asymmetric construction of the ecosystem is left uncertain by microbial research on regime shifts. Moreover, it is unclear if hysteresis in the microbial compositions observed in stratified waters arises from the imbalance between the regimes or is also possible in balanced ecosystems. This gap is addressed by exploring the dynamics to environmental change of a balanced, symmetric ecosystem model derived from previous research21. Further advantage of a balanced system is the facilitation to locate the unstable equilibrium. From stability theory1,15 it is given that an unstable equilibrium must lie within the bistable area and that the system becomes stable between the stable states given no previous history, no favourability by stress and no perturbation15. Complete balance in a system implements determination of the location of the unstable equilibrium, as the level of environmental stress favouring no state must lie precisely half-distance between the tipping points. This work suggests using a balanced, symmetric ecosystem model to prove the existence of this unstable equilibrium after the system’s parameterization has been developed to exhibit a symmetric hysteresis response to gradually changing environmental stressors.

~~What is expected: simple model of scheffer 2001 also displays meaning that this should be possible~~

Sketches of figures that could fit:

Figure 1: stable eq in black, unstable eq. in red. asymmetry visible as two extremes visualized as unequal hills (Scheffer 2001)

Figure 2: asymmetric vs. symmetric hill diagramm, location of unstable eq red, stable eq. black (Beisner 2003)

Figure 3: unstable eq. in black, asymmetry in b) (Bush 2017)

Figure 4: asymmetric response in Bush 2017

Figure 5: asymmetric field example Lake Morgan, Zhang 2003

Figure 6: asymmetry example, electron transport in photosynthesis

Methods

Here, a model of an aquatic ecosystem responding with oxic-anoxic regime shifts to changes in oxygen and sulfur diffusivity was studied. During summer many waters in temperate climates experience vertical stratification, inducing a change in microbial community structures21. The heated surface layer is rich in oxygen and dominated by phototrophic bacteria (e.g. cyanobacteria), while deeper layers are depleted of oxygen, providing an anoxic, sulfur-rich environment for heterotrophic organisms eg. In between, where substrates diffuse towards lower concentrations and sulfur meets oxygen, providing a niche for heterotrophic and non-heterotrophic microorganisms22. A model developed by Bush et al. (2017) suggests that this such niche may exhibit oxic-anoxic regime shifts. Phototrophic and heterotrophic bacteria mutually inhibit each other by secreting substrates that are toxic for the competing group, being the critical feedback dynamic leading to alternative stable states. Included are three functional groups (i.e. cyanobacteria, phototrophic sulfur bacteria and sulfur-reducing bacteria), three chemical substrates (i.e. oxygen, oxidized and reduced sulfur) one critical nutrient (i.e. phoshorus) and an abiotic oxidation cycle oxidizing reduced sulfur, connected through four types of interactions (i.e. consumption, production, inhibition and diffusion). Vertical gradients of oxygen in stratified lakes were simulated by changing oxygen diffusivity in the model system, leading to regime shifts towards higher favoured states. This response suggests that the microbial community compositions in intermediate layers of stratified lakes are sensitive to the character of thermo- and resulting chemocline21. Dynamics of the regime shifts of this model however, differed with the direction of oxygen diffusivity change. For instance, the anoxic state recovers in “two steps” (Fig 3), whereas the oxic state recovers in gradual, linear manner. Furthermore, the collapse of Cyanobacteria takes longer compared to the one of the competing groups (Fig 4). Such asymmetric response may be caused by the unbalanced framework of the model ecosystem : The number of abundant functional groups varies among the two regimes, as the oxic environment are dominated by only cyanonbacteria but anoxia can be inhabited by two kinds of sulfur bacteria. To investigate this possible causality for the responses depending on the direction of environmental change, the model of Bush et al (2017) has been reduced to balance processes and interaction responsible for both regime shifts.

## The balanced, symmetric model

An implementation of the models ordinary differential equations, parameter values and initial conditions used by Bush et al (2017) can be found the R package microxanox {Citation}. This open -access package was used as the foundation stoned due to its transparency and flexibility, enabling exchanging parameter values and ordinary differential equations conveniently. My Documentation: sym microxanox,R vignette?

Raises t question whether cyano are responsible for all resilience, which hysteresis are is from whom, sym axis balanced model

Detrimental for the dominating regime is thus which substrate is higher concentrated, directly decided by the productivity of groups dominating the surroundings(Bush et al. 2017). (The ecosystem displays hysteresis, hence the dominance in different layers is determined by the community composition of the close environment, as this decides on the substrate diffusivity meaning which group is more inhibited by the surrounding substrate.)

dchieving a symmetric model system exhibiting regime shifts requires three substantial steps. First, clarification and definition of a symmetric model. Symmetry can be applied from a numeric point of view. In the balanced system, the oxic and the anoxic regime are each dominated by one functional group, which are affected by similarly built ODEs: Cyanobacteria produce oxygen and sulfur-reducing bacteria produce reduced-sulfur, both substrates which inhibit the competing group. Furthermore, the substrates impact on the regimes is balanced: Phosphorus nourishes one functional group dominating each regime and the abiotic oxidation cycle removes both substrates (i.e. oxygen and reduced sulfur) from the biogeochemical cycle. Second, the parameter trait values of involved functional groups are equalized. Here, the sulfur-bacteria were adjusted to be identical to the cynaonobacteria. And third, parameters describing chemical substances are adjusted as hyperparameters by the trial-and-error method to eventually bring the system to exhibit shifts upon gradual change of environmental stressors. Especially increasing the abiotic oxidation rate was crucial for the balanced system to display hysteresis behaviour. Finally, these manipulations converted the asymmetric model of Bush et al (2017) to a balanced, symmetric ecosystem model.