Functional diversity can facilitate the collapse of an undesirable ecosystem state

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Abstract

Biodiversity may increase ecosystem resilience. However, we have limited understanding if this holds true for ecosystems that respond to gradual environmental change with abrupt shifts to an alternative state. We used a mathematical model of anoxic-oxic regime shifts and explored how trait diversity in three groups of bacteria influences resilience. We found that trait diversity did not always increase resilience: greater diversity in two of the groups increased but in one group decreased resilience of their preferred ecosystem state. We also found that simultaneous trait diversity in multiple groups often led to reduced or erased diversity effects. Overall, our results suggest that higher diversity can increase resilience but can also promote collapse when diversity occurs in a functional group that negatively influences the state it occurs in. We propose this mechanism as a potential management approach to facilitate the recovery of a desired ecosystem state.

Introduction

In light of global change and biodiversity loss, it is a key challenge to advance our understanding about ecosystem resilience and its relationship with diversity. Resilience is defined as the capacity of ecosystems to absorb changes in the environment without exhibiting large changes in ecosystem state (Holling 1973). Biodiversity among and within species may increase ecosystem resilience (Hughes & Stachowicz 2004; Isbell *et al.* 2015), when species (or genotypes) perform similar functions but respond differently to environmental change (Leary & Petchey 2009). Hence, a key aspect of diversity is variation in functional traits, i.e. the traits that determine how organisms respond to environmental change and affect ecosystem processes (Naeem & Wright 2003; Suding *et al.* 2008). Corresponding research has primarily focused on ecosystems with single equilibria (Yachi & Loreau 1999; Loreau & Mazancourt 2013), but was recently extended to ecosystems with alternative stable states (Dakos *et al.* 2019; Chaparro-Pedraza*et al.* 2021). When such ecosystems experience a change in environmental conditions, higher biodiversity may prevent or delay the shift to an alternative ecosystem state (Figure 1; Chaparro-Pedraza*et al.* 2021). Resilience is particularly crucial in these systems because shifts to alternative states often occur abruptly, are difficult to reverse, and can entail high costs when the ecosystem transitions to a state that is undesired for ecological and/or economic reasons (Scheffer *et al.* 1993; Foley *et al.* 2003; Diaz & Rosenberg 2008).

Ecosystems with alternative stable states are characterized by displaying two or more different states at identical external conditions (Fig. 1a). As an environmental driver increases gradually, the ecosystem shifts abruptly to an alternative state once a threshold, the tipping point, is passed, but recovers to its original state only at lower threshold conditions (Fig. 1a; Scheffer *et al.* 2001). Between these two threshold values, the state of the ecosystem depends on its history, a phenomenon termed hysteresis. A key mechanism behind hysteresis is positive feedback between organisms and their environment (Kéfi *et al.* 2016). For example, in shallow lakes submerged plants and phytoplankton can interact via mutual inhibition (a positive feedback), where macrophytes inhibit phytoplankton by consuming nutrients, while phytoplankton inhibit macrophytes by reducing water clarity (Kéfi *et al.* 2016). At intermediate nutrient concentrations, shallow lakes can thus be in a clear state dominated by submerged plants or in a turbid state dominated by phytoplankton, depending on which of these two functional groups dominated in the past (Scheffer *et al.* 1993).

Effects of diversity on the resilience of systems with alternative stable states were addressed conceptually (Dakos *et al.* 2019) and investigated with mathematical models of predator-prey systems (Ceulemans *et al.* 2019; Chaparro-Pedraza 2021; Wojcik *et al.* 2021) and shallow lakes (Chaparro-Pedraza *et al.* 2021). Two of these studies are particularly relevant here because they analyzed how trait change influences the position of tipping points along an environmental gradient (Chaparro-Pedraza 2021; Chaparro-Pedraza *et al.* 2021). Using three model systems (a population model, a predator-prey model, and a model of a shallow lake ecosystem), the authors report that trait change shifted the transition to an alternative state to a higher level of environmental stress (Chaparro-Pedraza 2021; Chaparro-Pedraza *et al.* 2021). In the shallow lake model system the shifts from a clear to turbid state and back from turbid to clear both occurred at higher nutrient loading when macrophytes varied in shade tolerance (Chaparro-Pedraza *et al.*2021). In this example, diversity was manipulated in one functional group. Yet, multiple functional groups may simultaneously be present, and the effect of diversity on ecosystem resilience may be different if more than one functional group varied in traits.

Studies on systems without alternative stable states have shown that simultaneous changes of diversity in multiple functional groups may lead to complex relationships between diversity and ecosystem processes (Thébault & Loreau 2003; Ceulemans *et al.* 2021). Specifically, diversity of one functional group can enhance (Eisenhauer *et al.*2012; Zhao *et al.* 2019), dampen (Bruno *et al.* 2008), or reverse (Thébault & Loreau 2003) the diversity effects of another functional group. These previous studies focused on trophic and facilitative interactions. It is unclear, however, how simultaneous versus independent changes of diversity play out when functional groups interact via mutual inhibition, an interaction that is characteristic of many ecosystems with alternative stable states (Kéfi *et al.* 2016; Bush *et al.* 2017).

Here we investigate how trait diversity in one, two, or three functional groups influences the resilience of ecosystems that have alternative stable states. We used a mathematical model developed by Bush *et al.* (2017) which describes abrupt oxic-anoxic regime shifts of aquatic ecosystems in response to changes in oxygen diffusivity. In this system, regime shifts are mediated by mutual inhibition of cyanobacteria and two types of sulfur bacteria (sulfate-reducing bacteria and phototrophic sulfur bacteria). The already published model (Bush *et al.* 2017) assumes no trait variation within each of the three functional groups, which is equivalent to there being only one strain in each functional group. We extended this model to include trait variation among multiple strains within each of the three groups of bacteria, and tested if the effect of diversity on resilience depends on (i) the amount of trait variation, and (ii) the combination of functional groups that contain variation. Increased resilience can be considered beneficial when it concerns the desired ecosystem state (oxic), but detrimental when it concerns the undesired state (anoxic). To describe our findings, we use the visualization framework illustrated in Figure 1 and terminology explained in Box 1.

We focused on a model that is simple enough to give generally applicable insights about the biodiversity-resilience relationship, but that is of sufficient complexity and realism to provide testable hypotheses for experiments and suggest novel approaches in ecosystem management. Moreover, by using a model of a specific ecosystem type, we may detect mechanisms that might be overlooked with simpler and more abstract models. We show that diversity can both enhance and reduce resilience depending on which and how many functional groups vary in traits, which illustrates the importance of considering multiple groups and their complex interactions.

Methods and Materials

The study ecosystem

We studied a model of anoxic-oxic regime shifts in aquatic ecosystems in response to changes in oxygen diffusivity. Depletion of oxygen has detrimental effects on the survival of many aquatic organisms, leading to changes in community composition and to a decline in biodiversity (Vaquer-Sunyer & Duarte 2008; Hughes *et al.* 2015). Hypoxic conditions can arise naturally when thermal stratification in summer leads to reduced oxygen diffusivity to deep-water habitats (Wetzel 2001). Anthropogenic increases of nutrients and temperature have enhanced the frequency and duration of low-oxygen episodes (Diaz & Rosenberg 2008; Scavia *et al.* 2014; Jane *et al.* 2021). Moreover, severe hypoxia/anoxia can be difficult to reverse because of feedbacks between organisms and their environment (Diaz & Rosenberg 2008; Conley *et al.* 2009; Bush*et al.* 2017).

Using a mathematical model, Bush *et al.* (2017) described anoxic-oxic regime shifts resulting from interactions among microbial organisms. The model ecosystem contains three functional groups of bacteria (Figure 2; cyanobacteria (CB), sulfate-reducing bacteria (SB), and phototrophic sulfur bacteria (PB)), four chemical substrates (oxygen, phosphorous, reduced sulfur, and oxidized sulfur), and four types of flows/interactions (production, consumption, inhibition, and diffusion); there is also abiotic oxidization of the reduced sulfur.

Critical for the presence of alternative stable states in this system is the mutual inhibition of cyanobacteria and sulfur bacteria due to their intolerance of the chemical substrate that the other produces: cyanobacteria inhibit sulfur bacteria by producing oxygen, whereas sulfate-reducing bacteria inhibit cyanobacteria by producing reduced sulfur, e.g. sulfide (Figure 2). Bush *et al.* (2017) simulated this ecosystem with a set of ordinary differential equations (ODEs) and demonstrated that the state of the system depends on the rate at which oxygen diffuses into (or out of) the system: the oxygen diffusivity. The system is oxic and dominated by cyanobacteria when oxygen diffusivity is high, but anoxic and dominated by the two groups of sulfur bacteria when oxygen diffusivity is low. At intermediate oxygen diffusivity, the system is bistable, i.e. either oxic or anoxic depending on whether cyanobacteria or sulfur bacteria dominated in the past (Bush *et al.* 2017).

The Bush *et al.* model (2017) assumes zero diversity within each of the three functional groups. There is, however, empirical evidence of intra- and inter-specific variation in tolerance (Rolfe *et al.*1978; Knoll & Bauld 1989; Miller & Bebout 2004; Ramel *et al.*2015). Furthermore, experimental evolution studies demonstrated considerable and rapid increases in tolerance of bacteria (Martín-Clemente *et al.* 2019; Schoeffler *et al.* 2019).

The model and our extension of it

Bush *et al.* (2017) has an accessible and complete description of the model of the ecosystem, including rate equations, parameter values, and initial conditions. Our implementation of the model is documented in the *microxanox* R package (R Core Team 2021; Krug & Petchey 2022), which has two vignettes (a user guide and a partial reproduction of the analyses in Bush *et al.* (2017)). The R code to run, analyze, and visualize the numerical experiments of our study is available in a repository of supplementary content (Petchey *et al.* 2022), which also includes all variables and parameter values.

We extended the Bush *et al.* model (2017) by modelling multiple strains per functional group. Each of the strains of a functional group has its own parameter set and state variable. For example, a system with nine strains per functional group has 27 state variables for the strains, and four for the chemical substrates. Other than having potentially different parameter values for maximum growth rate and tolerance, the dynamics of the strains in a functional group were described by the same equations. We adjusted the chemical substrate ODEs to correctly account for the number of strains, by summing their substrate consumption and production.

Creating and varying within functional group diversity

We generated diversity within functional groups by creating multiple strains that differed in maximum growth rate and in tolerance to the respective inhibiting substrate (sulfide tolerance of cyanobacteria, and oxygen tolerance of sulfate-reducing bacteria and phototrophic sulfur bacteria). We assumed a trade-off between the two traits, in line with empirical studies that report a negative correlation between maximum growth rate and resistance to environmental stress in microbial organisms (Ferenci 2016). For simplicity, we used a linear trade-off between $\log_{10}$-transformed trait values, with among strain variation distributed evenly on a log-scale (see Supplementary Report Section 3 for more information). In the main text, we report results for nine strains in each functional group. Results were relatively robust to changes in the number of strains, although some effects of strain number were observed at high levels of trait diversity (see Supplementary Report Section 7).

Functional diversity has multiple components, and we manipulated only one of these, namely the range of trait space represented, which has been termed functional richness (Villéger *et al.* 2008). We compared 20 different amounts of trait diversity ranging from no variation, i.e. all nine strains had the reference trait value (Table 1), to greatest trait variation with the range of trait values according to Table 1. The maximum trait range was selected to ensure that the region of bistability was mostly within the range of oxygen diffusivity values used in Bush *et al.* (2017) when all functional groups contained the maximum amount of variation. The other 18 trait diversity levels were evenly distributed between the no diversity scenario and the greatest amount of diversity. Twenty diversity levels gave sufficient resolution and required reasonable computation time to simulate. A detailed account is in Supplementary Report Section 3.

We also manipulated the combination of functional groups that contained diversity. Specifically, we examined the effect of adding diversity to only one group (either CB, or SB, or PB), simultaneously to two functional groups (CB-SB, CB-PB, and SB-PB), and simultaneously to all three functional groups (CB-SB-PB). This led to 7 combinations * 20 diversity levels, but with seven of these being the same zero diversity in all functional groups, there were 134 diversity scenarios in total.

We have confirmed that when there is no within functional group strain variation, the dynamics of the model are not affected by the number of strains in each of the functional groups. This is a necessary condition for such a model (Moisset de Espanés *et al.* 2021), and gives confidence that our methods and their implementation are correct and robust.

Stable state finding

To investigate the effect of trait diversity on tipping point positions, we parameterized the system according to each of the diversity scenarios described above, and then ran two simulations, one with a stepwise increase and one with a stepwise decrease of oxygen diffusivity. This technique was used to find stable states, rather than to simulate the effects of environmental change per se. At each of 300 values of oxygen diffusivity, ranging from 0 to -8 ($\log_{10}h^{-1}$), we simulated the dynamics for 1,000,000 hours, which was sufficient for the position of the tipping points to stabilize, even though some strain dynamics had not yet completely stabilized (Supplementary Report Section 6.2). At the start of the two simulations, total initial abundance of each functional group was 10^5 cells, equally divided among the strains of each functional group. To avoid very low strain densities which would cause computational problems, we added 1 cell L^{-1} to every biological state variable every 1,000 hours (an alternative approach produced the same results, see Supplementary Report Section 4.3). At the end of each period of constant oxygen diffusivity, the system state was recorded and used as the initial conditions for the simulation at the next step of oxygen diffusivity. This approach for finding stable states differs from the method used by Bush *et al.* (2017). See the Supplementary Report (Section 4) for a detailed description of our rationale for using our approach, and also for evidence of qualitatively similar results produced by both approaches.

We calculated the tipping point position of the oxic to anoxic (anoxic-oxic) transition as the minimum (maximum) level of oxygen diffusivity at which the total density of sulfate-reducing bacteria was more than

1000 abundance units different between the increasing and decreasing oxygen diffusivity simulations. We did not calculate tipping point positions when coexistence patterns were atypical of the classical pattern shown in Figure 1a (e.g. when cyanobacteria coexisted with sulfur bacteria at low oxygen diffusivities; see Results and Supplementary Report Section 10.2 for details). We calculated the effect size of trait variation on tipping point position as the difference in oxygen diffusivity between a tipping point without trait variation and with a given level of trait variation (Fig. 1c-d). A positive effect size indicates increased resilience.

Results

Resilience of the oxic state

The trait diversity effect on the resilience of the oxic state depended on which functional group varied in traits (Fig. 3 a-f, red lines). Resilience increased with increasing trait variation in the group that dominated the oxic state (cyanobacteria; Fig. 3a, b). In contrast, increasing diversity in the two suppressed groups either reduced resilience of the oxic state (sulfate-reducing bacteria; Fig. 3c, d) or had no effect on resilience (phototrophic sulfur bacteria; Fig. 3e, f).

Simultaneous variation in more than one functional group reduced or did not change the diversity effect of individual functional groups (Fig. 3 g-o; red lines). Simultaneous trait variation in cyanobacteria and sulfate-reducing bacteria (Fig. 3g) led to smaller diversity effects than variation in only one of these two groups; the negative diversity effect of sulfate-reducing bacteria outweighed the positive diversity effect of cyanobacteria when trait variation was low, but the effect of cyanobacteria diversity prevailed at high trait variation (Fig. 3b, d, h). Diversity in the phototrophic sulfur bacteria did not change the diversity effects of other functional groups (Fig. 3 i-o).

Resilience of the anoxic state

The diversity effect on the resilience of the anoxic state also differed among groups (Fig. 3 a-f, blue lines). The two groups that dominated the anoxic state had contrasting diversity effects on its resilience: increasing diversity in the sulfate-reducing bacteria increased the resilience of the anoxic state (Fig. 3 c, d), whereas increasing diversity in the phototrophic sulfur bacteria decreased resilience (Fig. 3e, f). Diversity in the suppressed group (cyanobacteria) had no effect on resilience when diversity was low but slightly reduced resilience when diversity was high (Fig. 3 a, b).

When more than one functional group varied in traits, their effects were either additive (cyanobacteria and sulfate-reducing bacteria) or one group erased the diversity effect of another group (Fig. 3 g-o, Supplementary Report Section 12). Specifically, variation in sulfate-reducing bacteria erased the diversity effect of phototrophic sulfur bacteria (Fig. 3 l, m), and variation in phototrophic sulfur bacteria erased the (small) diversity effect of cyanobacteria (Fig. 3 i, k).

Dynamics of strains and substrates

Trait variation led to compositional turnover along the oxygen diffusivity gradient when a functional group was on the collapse trajectory (see Box 1 for explanation of terms). Less tolerant strains were replaced by more tolerant strains as the concentration of the inhibiting substrate increased (Fig. 4). On the trajectory of decreasing oxygen diffusivity, the ecosystem was initially dominated by the cyanobacteria strain with lowest sulfide tolerance and highest maximum growth rate (Fig. 4a). As oxygen diffusivity declined, more tolerant strains of cyanobacteria replaced the fastest growing strain until the strain with highest sulfide tolerance dominated. Subsequently, the cyanobacteria collapsed, probably due to their reduced capacity to suppress the sulfur bacteria, and simultaneously the ecosystem shifted from oxic to anoxic (Fig. 4 d, e). Prior to the tipping point, the most tolerant strains of the two sulfur bacteria groups slightly increased in abundance, in particular in the sulfate-reducing bacteria (Fig. 4b). However, once the system shifted to anoxic, the sulfur bacteria strains with lowest tolerance and highest maximum growth rate dominated (Fig. 4 b, c).

Strain dynamics were similar on the trajectory of increasing oxygen diffusivity (Fig. 4). Replacement of less tolerant by more tolerant strains in both groups of sulfur bacteria was followed by the collapse of the phototrophic sulfur bacteria. Then sulfate-reducing bacteria collapsed, simultaneously with the shift from anoxic to oxic and the rise of the least tolerant cyanobacteria strain. In contrast to the trajectory of decreasing oxygen diffusivity, the switch from least to most tolerant strains occurred over a comparatively broad range of oxygen diffusivity.

The strain dynamics deviated from this pattern when there was medium to high variation in only the phototrophic sulfur bacteria. In this case, all three functional groups coexisted at low levels of oxygen diffusivity likely because high maximum growth rates in the phototrophic sulfur bacteria led to lower sulfide concentrations (Supplementary Report Section 10.2). The same pattern occurred for simultaneous variation in phototrophic sulfur bacteria and cyanobacteria, albeit only on the trajectory of increasing oxygen diffusivity (Supplementary Report Section 10.2).

Mechanisms of the functional diversity effects

At low levels of trait variation, the diversity effects were driven entirely by the most tolerant strains. At higher levels of trait variation, however, strains with low tolerance (and high maximum growth rate) also contributed to the diversity effects in five of the seven combinations (Supplementary Report Section 11). For example, in the sulfate-reducing bacteria, absence of strains with high maximum growth rates led to reduced production of sulfide and therefore to coexistence with cyanobacteria at low oxygen diffusivity. That is, high maximum growth rates often had ecosystem-level consequences.

Discussion

Using a model of anoxic-oxic regime shifts, we found three key results: first, not all functional groups had positive diversity effects on the resilience of their preferred ecosystem state (Fig. 3a-f). Second, the effect of diversity was often smaller or absent when a functional group was on the recovery trajectory rather than on the collapse trajectory (Figure 3a-f). And third, diversity effects were often reduced or erased when multiple groups varied in traits, except when a functional group had no individual effect on resilience (Figure 3g-o). From a management perspective, our results suggest that higher biodiversity in a functional group that dominates a desired ecosystem state may prevent or delay the shift to an undesired state but does not necessarily promote recovery. A more promising approach to facilitate recovery may be to identify functional groups in the undesired state (here: phototrophic sulfur bacteria) that promote their own collapse and therefore the recovery of the desired state.

Diversity did not always increase resilience

Greater diversity in cyanobacteria or sulfate-reducing bacteria increased the resilience of the state they dominated, whereas greater diversity in phototrophic sulfur bacteria reduced resilience of their preferred state (Figure 3a-f). These contrasting diversity effects reflect differences in interactions: whereas cyanobacteria and sulfate-reducing bacteria interact in a strictly antagonistic way, phototrophic sulfur bacteria have both positive and negative effects on the other two functional groups (Figure 2). By oxidizing sulfide, phototrophic sulfur bacteria indirectly increase the level of oxygen because the lower sulfide concentration (i) promotes cyanobacteria and therefore oxygen production, and (ii) leads to less oxygen consumption during abiotic oxidation of sulfide (Supplementary Report Section 10.1). Via these two pathways, phototrophic sulfur bacteria deteriorate their own environment and promote the shift to the oxic state. High diversity in this group even resulted in failure to exclude cyanobacteria likely because the fastest-growing strain lowered the sulfide concentration to such an extent that cyanobacteria were able to grow despite low oxygen diffusivity (Supplementary Report Section 10.2).

Stimulating the growth of groups that have negative diversity effects may be used as a management tool to promote the recovery of a desired ecosystem state. Such an approach would require identifying functional groups that co-dominate an undesired ecosystem state and negatively affect it. Microbes may be particularly useful for this approach because (i) they often dominate undesired ecosystem states (e.g. turbid lake state, anoxic state), and (ii) they often interact via modification of the chemical environment (Ratzke *et al.* 2018; Ratzke & Gore 2018), including even microbes that drive themselves extinct by deteriorating their environment (Ratzke *et al.* 2018).

Diversity effects were often smaller or absent on recovery trajectories

In two functional groups, the effect of trait diversity on resilience was very small (cyanobacteria; Figure 3b) or absent (phototrophic sulfur bacteria; Figure 3 f) when the group was on the recovery trajectory rather than on the collapse trajectory. For example, except for very high diversity levels, cyanobacteria diversity had no effect on the shift from the anoxic to the oxic state likely due to the abrupt change of the inhibiting substrate: sulfide was maintained by sulfate-reducing bacteria at a constantly high level such that not even the most tolerant cyanobacteria strain was able to grow (Figure 4a, e). At the tipping point to the oxic state, sulfide dropped abruptly to a level at which all cyanobacteria strains would be able to grow, resulting in immediate dominance of the strain with lowest sulfide tolerance and highest maximum growth rate (Figure 4a). Previous work showed that evolutionary trait change can even delay recovery when organisms adapt to the alternative state and then have reduced performance once environmental conditions return to original (Chaparro-Pedraza *et al.* 2021). Our study adds a further mechanism for why diversity might not aid recovery of a suppressed group: the greater abruptness of change of the inhibiting substrate on recovery trajectories might hinder attempts to restore ecosystems by introducing tolerant strains.

Diversity effects were often reduced or erased when multiple groups varied in traits

Antagonistic diversity effects were to be expected in a system where organisms interact via mutual inhibition. Surprisingly, however, opposing diversity effects were not necessarily caused by groups that dominated alternative ecosystem states but also by two groups that dominated the same state and interacted via facilitation. Contrary to other examples where functional groups that interact via facilitation enhance each other's diversity effects (Eisenhauer *et al.* 2012), variation in sulfate-reducing bacteria erased the diversity effect of phototrophic sulfur bacteria. Apparently, when both groups varied in traits, the positive effect of sulfate-reducing bacteria on sulfide outweighed the negative effect of phototrophic sulfur bacteria, precluding the earlier shift to the oxic state. Simultaneous variation did usually not alter diversity effects when a functional group had no diversity effect on resilience, which was often the case on recovery trajectories. If it is a general phenomenon that diversity plays out less on recovery trajectories, the positive diversity effect on resilience of the dominant group would not be dampened by diversity in the suppressed group. Collectively, our results illustrate that predicting the outcome of simultaneous diversity effects of multiple functional groups can be difficult in systems where organisms interact via a multitude of complex interactions.

In natural systems, the alternative states of an ecosystem are often dominated by functional groups that strongly differ in intra- and interspecific diversity, and in how quickly new variation arises. In some of the most prominent examples of ecosystems with alternative states, macro-organisms dominate the desired state and micro-organisms the undesired state. For example, benthic macro-organisms and bacteria dominate the oxic and anoxic state of coastal ecosystems, respectively (Diaz & Rosenberg 2008), and macrophytes and phytoplankton dominate the clear and turbid state of shallow lakes, respectively (Scheffer et al. 1993). Prokaryotic and eukaryotic micro-organisms are both characterized by tremendous diversity (de Vargas et al. 2015; Locey & Lennon 2016), including diversity in functional traits (Litchman & Klausmeier 2008;

Escalas et al. 2019). Furthermore, microorganisms might adapt more rapidly to new environmental conditions than macro-organisms due to their short generation times, high population sizes, and low complexity (Orr 2000; Barraclough 2015). Such greater standing variation and higher ability to adapt to stressful conditions of micro-organisms may pose an additional challenge to reversing shifts to an undesired ecosystem state dominated by micro-organisms.

Ecology, evolution, or both?

The observed replacement of strains along the gradient of oxygen diffusivity may be interpreted as changes in the abundances of species (an ecological process) or of genotypes (an evolutionary process). Furthermore, models such as ours are interpreted in both of two ways (Govaert *et al.* 2019): as representing ecological processes (Ceulemans *et al.* 2019; Wojcik *et al.* 2021) or eco-evolutionary feedbacks (Jones *et al.* 2009). To be clear, this modelling approach only includes sorting of standing heritable variation. Including mutation and recombination could be a useful next step to investigate how these evolutionary processes influence regime shifts. Chaparro-Pedraza et al. (2021) used a quantitative genetics approach to show that changes in macrophyte shade tolerance can shift the tipping point between the clear and turbid state of a lake to higher levels of stress. Despite its different approach, our study yielded similar results for two of the three functional groups. This gives some credence to interpreting models such as ours as usefully informing about the effects of evolution on ecosystem resilience.

Limitations and future directions

Naturally, our model is a simplification of natural ecosystems with assumptions that might have influenced our results. The model system focuses on three groups of bacteria; however, other functional groups (e.g. eukaryotic phytoplankton, colorless sulfur bacteria) might also have relevant effects on oxic-anoxic regime shifts (Lavik *et al.*2009). We demonstrated that including more than two functional groups can reveal counter-intuitive diversity effects; expanding models such as ours to include even more functional groups may therefore give further useful insights into the response of ecosystems to environmental change. Furthermore, we did not vary the values of parameters other than those of maximum growth rate and environmental tolerance. For the remaining parameters we used the same values as Bush *et al.* (2017) because the authors found high consistency of their modelling results and empirical observations. Also, we did not vary the shape of the trade-off between environmental tolerance and maximum growth rate. We speculate that such changes to the trade-off would have altered the pattern of strain replacement but not the position of tipping points.

An interesting avenue for future studies would be the analysis of transient dynamics, that is, the response of the system to temporal environmental change. Because we addressed questions about alternative stable states, we focused on responses of stable states, and therefore ran simulations for 1,000,000 hours at each level of oxygen diffusivity. However, in natural systems environmental conditions would not remain constant over such long timescales, and new trait variation could arise by mutation and recombination. Most of our results remained qualitatively similar when we reduced simulation length to 10,000 hours, but a further reduction in simulation length considerably changed the results (Supplementary Report Section 6). Investigation of transient dynamics in a model of shallow lakes showed that the capacity of evolution to prevent a regime shift depended on the relative rates of environmental change and trait change (Chaparro-Pedraza *et al.*2021). It would be interesting to test with our system if the capacity of functional diversity to increase resilience is contingent on a slow rate of environmental change. Possibly, however, the rate of change is less influential in systems such as ours because sorting of standing variation might allow a faster response to environmental change than if relevant variation has yet to arise.

Conclusions

Our results illustrate that greater trait diversity of the functional group that dominates a desired ecosystem state may increase the ability of the system to absorb environmental change before tipping to the alternative, undesired state. However, once the system has shifted to an undesired state, recovery of a desired ecosystem state might be more easily achieved by managing functional groups that dominate the undesired state than by managing groups that dominate the desired state. Trying to facilitate recovery by bringing in more stress tolerant strains of the functional group that dominates the desired state might be unsuccessful because of the abrupt change of the inhibiting substrate on the recovery trajectory. A more promising management approach could be to stimulate the growth of functional groups that co-dominate the undesired state but have negative effects on it. To identify such groups, it is useful to consider more than two functional groups in models of systems with alternative stable states. Collectively, our results highlight the importance of considering multiple interacting groups when predicting the response of ecosystems with alternative states to environmental change.

Acknowledgements

Statement is on the title page, or one after that.

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Table 1: Range of growth rates and tolerances. Without trait variation, all strains of a functional group had the reference trait value. With trait variation, the trait values of the strains varied around the reference trait value. Here we give the range of growth rates and tolerances when trait variation was at its maximum and for the results displayed in Figure 4. The maximum amount of variation was set to a range so that the region of bistability was usually within the range of oxygen diffusivity values used in Bush *et al* (2017). Tolerance is given as the concentration of the inhibiting substrate where growth rate is reduced by 50%.

Trait	Functional group	Reference trait value	Range for maximum trait variation (min, max)	Range for results in Figure 4 (min, max)
Maximum growth rate (h^{-1})	Cyanobacteria	0.05	0.0489, 0.0511	0.0490, 0.0510
Maximum growth rate (h^{-1})	Sulfate-reducing bacteria	0.1	0.0936, 0.1068	0.0943, 0.1061
Maximum growth rate (h^{-1})	Phototrophic sulfur bacteria	0.07	0.0656, 0.0748	0.0660, 0.0742
Sulfide tolerance (µM)	Cyanobacteria	300	335.2, 268.5	331.3, 271.7
Oxygen tolerance (µM)	Sulfate-reducing bacteria	100	383.2, 26.1	332.6, 30.1
Oxygen tolerance (µM)	Phototrophic sulfur bacteria	100	383.2, 26.1	332.6, 30.1

Box 1: Glossary of terms.

Term	**Definition**
Resilience	Ability of the ecosystem to absorb a change in oxygen diffusivity without tipping to the alternative ecosystem state.
Resilience of the oxic state	Ability of the ecosystem to absorb a decrease in oxygen diffusivity without shifting from oxic to anoxic. Resilience is therefore higher when the *oxic-anoxic* tipping point is at lower oxygen diffusivity.
Resilience of the anoxic state	Ability of the ecosystem to absorb an increase in oxygen diffusivity without shifting from anoxic to oxic. Resilience is therefore higher when the anoxic-oxic tipping point is at higher oxygen diffusivity.
Dominant group	Functional group that dominates a given ecosystem state (oxic state: cyanobacteria; anoxic state: sulfate-reducing bacteria and phototrophic sulfur bacteria).

Term	**Definition**
Suppressed group	Functional group that is inhibited in a given ecosystem state and therefore has zero or low abundance (oxic state: sulfate-reducing bacteria and phototrophic sulfur bacteria; anoxic state: cyanobacteria).
Collapse trajectory	Trajectory with increasingly unfavourable conditions for a given functional group, leading to its collapse. (cyanobacteria: trajectory of decreasing oxygen diffusivity; sulfur bacteria: trajectory of increasing oxygen diffusivity)
Recovery trajectory	Trajectory with increasingly favourable conditions for a given functional group, leading to its recovery. (cyanobacteria: trajectory of increasing oxygen diffusivity; sulfur bacteria: trajectory of decreasing oxygen diffusivity)

Figure legends:

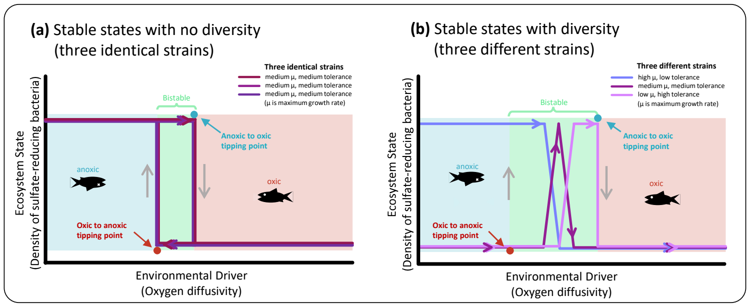
Figure 1. Various complementary visualizations of how diversity could influence the position of tipping points in systems with alternative stable states. **(a, b)** Illustrations of the possible dependence of ecosystem state on an environmental driver **(a)**with no diversity and **(b)** with diversity. The ecosystem illustrated can exist in either an anoxic state with high density of sulfate-reducing bacteria or an oxic state with low density of sulfate-reducing bacteria (other functional groups are omitted for clarity). In the region of bistability (green) the state of the system depends on its history. At tipping points, the ecosystem shifts abruptly (grey arrows) to the alternative state. **(b)** illustrates replacement of less tolerant by more tolerant strains as the environmental driver increases (strain dynamics caused by a decreasing environmental driver are omitted for clarity.) **(c, d)** Two complementary visualizations of the effect of trait variation on resilience. **(c)** The position of the two tipping points at different levels of trait variation. **(d)** The effect size of trait variation on resilience, i.e. on the position of the tipping points. Effect size is the difference in oxygen diffusivity between a tipping point without trait variation and with a given level of trait variation. A positive effect size indicates increased resilience. The depicted example shows a scenario where increasing trait variation increases the resilience of both the oxic and the anoxic state. A non-linear effect and linear effect are shown only to aid understanding. Please see Box 1 for further explanation of terms.

Figure 2. The model ecosystem. We simulated interactions among three functional groups of bacteria. Cyanobacteria inhibit phototrophic sulfur bacteria and sulfate-reducing bacteria by producing oxygen, while sulfate-reducing bacteria inhibit cyanobacteria by producing reduced sulfur. All three groups consume phosphorus. In addition, the two sulfur bacteria groups interact by producing the substrate that the other group consumes: sulfate-reducing bacteria reduce oxidized sulfur to reduced sulfur, while phototrophic sulfur bacteria oxidize reduced sulfur to oxidized sulfur. Reduced sulfur is also oxidized abiotically. Finally, all four chemical substrates diffuse into or out of the system depending on their concentrations. Modified version of Figure 1 of Bush et al (2017).

Figure 3. Effect of trait variation on resilience. As in Figure 1c-d, we here display the effects of trait variation on resilience with two types of visualization which together provide two complementary views of the same data and patterns. The left column of panels shows the position of the tipping points at different levels of trait variation (red: oxic-anoxic tipping point; blue: anoxic-oxic tipping point). Data is missing in panels e, and i, when patterns of coexistence were atypical of the classical pattern shown in Figure 1a (e.g. when cyanobacteria coexisted with sulfur bacteria at low oxygen diffusivities). The amount of trait variation

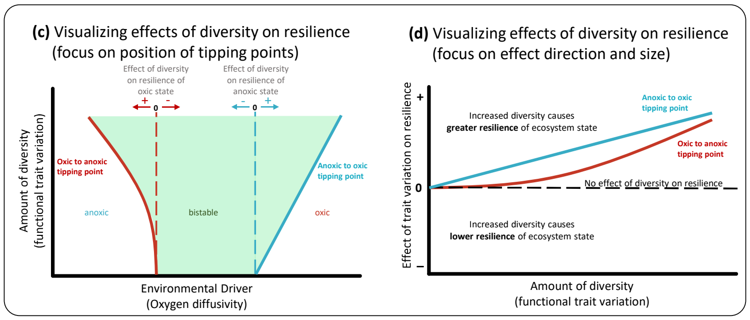
was standardized to range from 0 to 1 by dividing each value of trait variation by the maximum amount of trait variation of the respective functional group. The green area depicts the extent of the region of bistability, the thick grey vertical bars indicate the bounds of oxygen diffusivity analyzed in our simulations. The right column of panels shows the effect size of trait variation on resilience. Effect size is displayed only when the tipping point was within the investigated range of oxygen diffusivity. Figure labels indicate which functional group(s) varied in traits (CB: cyanobacteria, SB: sulfate-reducing bacteria, PB: phototrophic sulfur bacteria). See Figure 1c-d and Box 1 for further explanation of terms.

Figure 4. Relationship of ecosystem state variables and oxygen diffusivity when there is functional diversity among nine strains within each functional group. The range of trait values is given in Table 1. The different strains are shaded differently, so that in each functional group (a-c) the darkest strain is the most tolerant, the lightest the least tolerant. The left column of panels shows the trajectory of decreasing oxygen diffusivity, the right column of panels shows the trajectory of increasing oxygen diffusivity. Points (which often are so close as to appear as thick lines) show the stable state at the end of each period of constant oxygen diffusivity. Thin lines are for visualization only and join the points. Grey arrows show the oxygen diffusivity at which the system shifts, and the direction of the shift. The length of the grey arrows is without meaning.



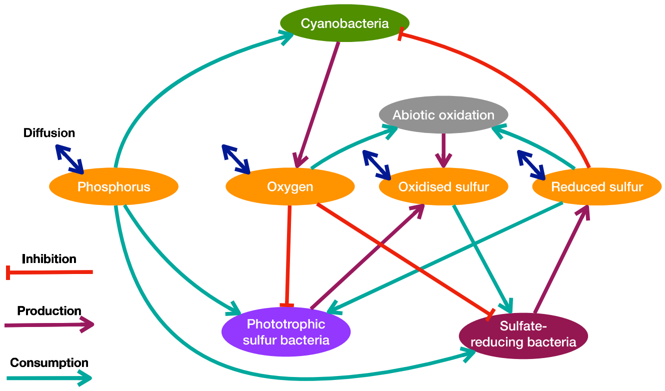
(a) Stable states with no diversity (three identical strains)

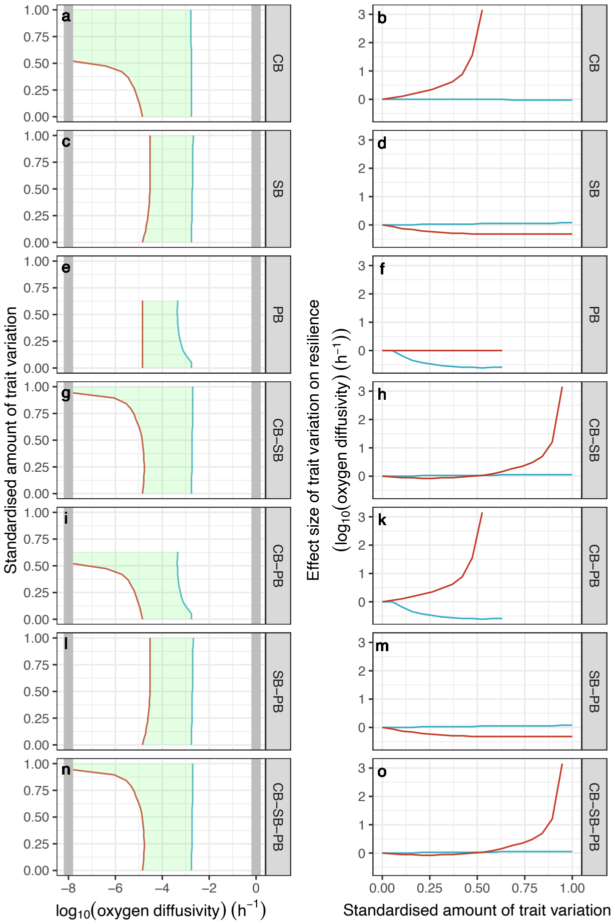
(b) Stable states with diversity (three different strains)



(c) Visualizing effects of diversity on resilience (focus on position of tipping points)

(d) Visualizing effects of diversity on resilience (focus on effect direction and size)


Cyanobacteria
Diffusion
Abiotic oxidation
Phosphorus
Oxygen
Oxidised sulfur
Reduced sulfur
Inhibition
Production
Consumption
Phototrophic sulfur bacteria
Sulfate-reducing bacteria


a
b
c
d
e
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i
k
l
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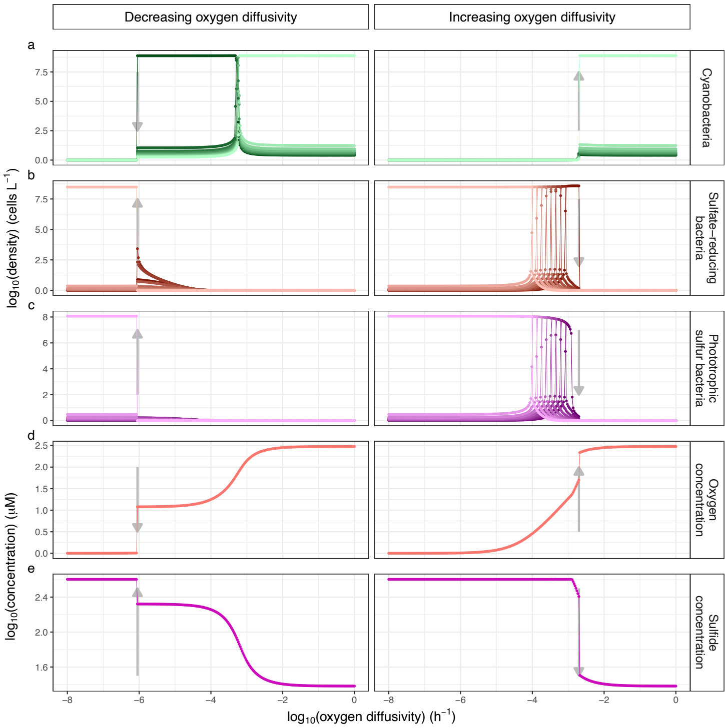
o
CB
SB
PB
CB–SB
CB–PB
SB–PB
CB–SB–PB
1.00
0.75
0.50
0.25
0.00
3
2
1
0
−8
−6
−4
−2
0
0.00
0.25
0.50
0.75
1.00
Standardised amount of trait variation
$\log_{10}$(oxygen diffusivity) (h^{-1})
Effect size of trait variation on resilience ($\log_{10}$(oxygen diffusivity) (h^{-1}))
Standardised amount of trait variation


Decreasing oxygen diffusivity
Increasing oxygen diffusivity
a
b
c
d
e
Cyanobacteria
Sulfate−reducing bacteria
Phototrophic sulfur bacteria
Oxygen concentration
Sulfide concentration
$\log_{10}$(density) (cells L^{-1})
$\log_{10}$(concentration) (µM)
$\log_{10}$(oxygen diffusivity) (h^{-1})
0.0
2.5
5.0
7.5
0
2
4
6
8
0.5
1.0
1.5
2.0
1.6
2.4
−8
−6
−4
−2
0