LETTER

Decomposing multiple dimensions of stability in global change experiments

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Abstract

Ecological stability is the central framework to understand an ecosystem's ability to absorb or recover from environmental change. Recent modelling and conceptual work suggests that stability is a multidimensional construct comprising different response aspects. Using two freshwater mesocosm experiments as case studies, we show how the response to single perturbations can be decomposed in different stability aspects (resistance, resilience, recovery, temporal stability) for both ecosystem functions and community composition. We find that extended community recovery is tightly connected to a nearly complete recovery of the function (biomass production), whereas systems with incomplete recovery of the species composition ranged widely in their biomass compared to controls. Moreover, recovery was most complete when either resistance or resilience was high, the latter associated with low temporal stability around the recovery trend. In summary, no single aspect of stability was sufficient to reflect the overall stability of the system.

Keywords

Biodiversity, biomass, composition, ecosystem functions, fluctuations, recovery, resilience, resistance.

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INTRODUCTION

Ecosystems absorb and respond to multiple types of environmental change, encompassing stochastic to periodic fluctuations as well as pulse and press disturbances. Ecological 'stability' is the core concept describing potential responses to such changes, a concept of central importance for understanding present-day and predicting future ecosystem dynamics. This knowledge is a pre-condition for ecosystem management and environmental policy in the face of rapid environmental change. The scientific approach to stability, however, has been characterised by a multitude of stability measures used, with at times blurred and often non-exclusive definitions (Grimm & Wissel 1997). Important advances were made in defining and understanding these different aspects of stability and their ecological connotations (Pimm 1984; Ives & Carpenter 2007). Still, a recent systematic literature review revealed that the use of different stability aspects varies fundamentally between the scientific literature and policy documents on the one hand, and between empirical and theoretical scientific approaches on the other hand (Donohue *et al.* 2016).

The largest obstacle to understanding 'stability' in ecological systems, however, is the dominance of one-dimensional approaches to environmental change and ecosystem responses. Donohue *et al.* (2016) analysed 354 scientific studies and found that > 90% of these analysed a single stability measure in response to a single aspect of change (e.g. fluctuation or

pulse disturbance or press disturbance). There are examples of more holistic assessments of change and stability, for example, considering mean and variance in drivers of ecosystem responses (Benedetti-Cecchi 2003; Benedetti-Cecchi *et al.* 2006), but the majority of studies focuses on a single stability aspect such as resistance, recovery or resilience in response to a single stressor type. This degradation of stability to a single measure represents an oversimplification likely preventing generalisable findings on stability across ecosystems.

A novel approach to a more holistic scientific concept of stability was initiated by Donohue *et al.* (2013), who addressed the multidimensionality of stability directly. They argue that – instead of analysing single aspects of stability independently – the correlation between different aspects of stability bears the information needed to predict how ecosystems respond to multiple perturbations. The ability of a system to withstand a disturbance, the ability to recover (including the speed of recovery and the maximum degree of recovery after a period of time), the fluctuations over time induced by disturbances and many other aspects of stability can be either correlated (positively, negatively) or independent of each other. When two aspects of stability correlate strongly and positively, they essentially are one dimensional. If the correlation is strong, but negative, then trade-offs exist promoting stability in one aspect at the expense of a second stability aspect. Such trade-offs prevent maximising both aspects of stability at the same time. If the two aspects of stability are

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uncorrelated, describing the community or ecosystem stability requires knowledge on these two orthogonal dimensions, promoting the dimensionality of stability.

However, even this overarching framework needs additional considerations: multiple dimensions of stability will be needed to separate the response framework for the community composition of a certain organism group (compositional stability) and for ecosystem processes performed by that organism group, such as biomass production, resource use or decomposition (functional stability). Compositional stability can beget or reduce functional stability. Empirical and theoretical evidence suggests that more diverse assemblages show more stable productivity over time (Tilman 1996; Yachi & Loreau 1999; Cottingham *et al.* 2001; Hautier *et al.* 2014) because they allow more rapid changes in species composition through asynchronous fluctuations or compensatory dynamics. In these cases, functional and compositional stability are negatively correlated, because the increase in functional stability is a direct consequence of compositional instability reflected by high species turnover (Allan *et al.* 2011) and lower stability at the population level (Tilman 1996). In contrast, responses to press disturbances (rather than fluctuations) often show intricate links between recovery of composition and of functioning (Allison 2004; de Boer *et al.* 2014), where positive correlation between functional and compositional stability arise because functional recovery depends on the recovery of the pre-disturbance composition (Gülzow *et al.* 2017).

Here, we develop an approach on how the analysis of multiple dimensions of stability can be performed on both functional and compositional levels. We use two data-rich freshwater mesocosm experiments that tested the effects of altered light availability on plankton communities at different sites. Both studies used a single disturbance as treatment and quantified the biomass and compositional response across multiple trophic levels. In three Swedish lakes, a single pulse addition of dissolved organic matter (DOM) reduced the light availability to the pelagic communities, whereas in three Austrian freshwater systems, light reduction was achieved by sediment addition (pulse) or intermittent shading treatments (pulse). Both treatments have a strong global change context, as the observed DOM-induced increase in lake colour has been associated with temperature increase (Weyhenmeyer & Karlsson 2009) and altered rainfall patterns (Zhang *et al.* 2010). Increased turbidity and cloudiness also alter the light climate for pelagic communities (Dupont & Aksnes 2013). Both studies initially hypothesised that addition of DOM and sediment, respectively, would influence not only light climate but also other aspects such as resource supply (dissolved organic or inorganic nutrients) – however, light reduction was the predominant effect in both studies, so we constrain the description of the treatment effects to this aspect.

For each experiment, we quantified four different aspects of stability for both function (biomass production) and structure (composition) (Table 1, Fig. 1a): resistance (ability to withstand the change); resilience (speed of recovery from change in the sense of engineering resilience, Pimm 1984); recovery success at the end of the experiment; and temporal stability as the inverse of the variability around compositional and functional trends during the recovery phase. Backed-up by

expectations derived from simulations (Data S1), we tested three hypotheses on the differences between trophic groups in each of the stability aspects, on bivariate relationships between functional and compositional domains of the same stability aspect, and on bivariate relationships between different stability aspects in functional and compositional domains.

H1: Different trophic groups show different stability responses to perturbations. We expect reduction in light availability to mainly have a negative impact on primary producers (low resistance) but not so much for heterotroph bacteria or zooplankton (high resistance). We further expect resilience and recovery to be enhanced by short generation times (bacteria & phytoplankton vs. metazoan zooplankton). We compared the magnitude of each stability aspect against benchmark values (Table 1) and tested for difference in each stability aspects between trophic groups across sites and experiments.

H2: Across the different trophic groups, compositional stability and functional stability show positive correlations. We analysed the correlation between the compositional and functional response to disturbance separately for each stability aspect. Based on Data S1, we expect a positive correlation between compositional and functional stability, and interpret the absence of such a correlation as a reflection of compensatory community dynamics after the disturbance.

H3: Within the functional and compositional domain, stability aspects are correlated with each other. Based on Data S1, we expect positive correlations between resistance and recovery as well as between resilience and recovery, as both smaller initial changes and more rapid resilience will allow more complete recovery (or even overcompensation). However, resistance and resilience should be negatively correlated (Data S1), as a stronger impact gives more room for resilience. Temporal stability is expected to correlate positively with resistance and recovery, but is negatively related to resilience (Fig. 1b).

METHODS

Mesocosm design and sampling

Sweden

During the summer of 2013, mesocosm experiments were performed in three Swedish lakes: Ekholmssjön (59 °52′45” N-17 °03′10” E), Hålsjön (59 °49′0′N-17 °13′46” E) and Edasjön (59 °48′15” N-17 °54′8” E). The experimental set up consisted of 12 500-L mesocosm bags in each lake filled with surface lake water, as described in detail by Lebret *et al.* (2017). In each lake, a water colour gradient was created by the addition of three levels of humic substance (HuminFeed® Humintech GmbH, Grevenbroich, Germany) in triplicate, low (3 mgL^{-1}), medium (6 mgL^{-1}) and high (12 mgL^{-1}), leading to increased water colour by 50, 100 and 180%, respectively, compared to a no-addition control. Water colour was measured as absorbance at 420 nm in a 5-cm quartz cuvette using a spectrophotometer (Lambda35, Perkin Elmer) after filtering through a GF/C glass fibre filter. The experiments were run for 32 days, and samples were collected on days 0 (before addition), 1, 2, 4, 8, 16 and 32.

Table 1 Stability measures addressed in this study, with mathematical definition and interpretation

Measure	Timing	Function F	Interpretation	Composition C	Interpretation
a: Resistance	Initial sampling after disturbance	Measured as initial log response ratio $$a = \ln\left(\frac{F_{dist}}{F_{con}}\right)$$	Benchmark: 0 = maximum resistance if dist = con $a < 0$ = low resistance through underperformance $a > 0$ = low resistance through overperformance	Measured as initial similarity $$a = \text{sim}\left(\frac{C_{dist}}{C_{con}}\right)$$	Fixed range 0–1. Benchmark: 1 = maximum resistance as dist = con $a < 1$ = low resistance
b: Resilience	Intermediate samplings	Measured as slope of regression of relative function over time: $$\ln\left(\frac{F_{dist}}{F_{con}}\right) = i + b * t,$$ where i = intercept, t = time	Benchmark: 0 = threshold, indicating no recovery $b > 0$ (more rapid) recovery; $b < 0$ = further deviation from control[1]	Measured as slope of regression of similarity over time: $$\text{sim}\left(\frac{C_{dist}}{C_{con}}\right) = i + b * t,$$ where i = intercept, t = time	As for function
c: Recovery	Final sampling	Measured as final log response ratio $$c = \ln\left(\frac{F_{dist}}{F_{con}}\right)$$	Benchmark: 0 = maximum recovery where dist = con c < 0 incomplete recovery c > 0 overcompensation	Measured as final similarity $$c = \text{sim}\left(\frac{C_{dist}}{C_{con}}\right)$$	Fixed range 0–1. Benchmark: 1 = maximum recovery when dist = con; $c < 1$ incomplete recovery
d: temporal stability	Intermediate samplings	Measured as inverse standard deviation of residual around resilience (see b) $$d = \left(\frac{1}{\text{sd}(\text{resid}_b)}\right)$$	No benchmark, larger d corresponds to lower fluctuations around trend	Measured as inverse standard deviation of residual around resilience (see b) $$d = \left(\frac{1}{\text{sd}(\text{resid}_b)}\right)$$	As for function

The table specifies the following information for each measure: when it is measured (Timing), how it is measured and how it can be interpreted (Interpretation). Measurements are given separately for functional (F) and compositional (C) stability. The letters a–d correspond to Fig. 1, dist are the disturbed treatments, con marks the control. Benchmark values and ranges are given if possible, benchmarks being either a maximum or a threshold value.
[1]If the response to disturbance is not a decrease but an increase in the function (i.e. i = positive), then a more negative slope corresponds to a faster recovery (i.e. higher resilience).
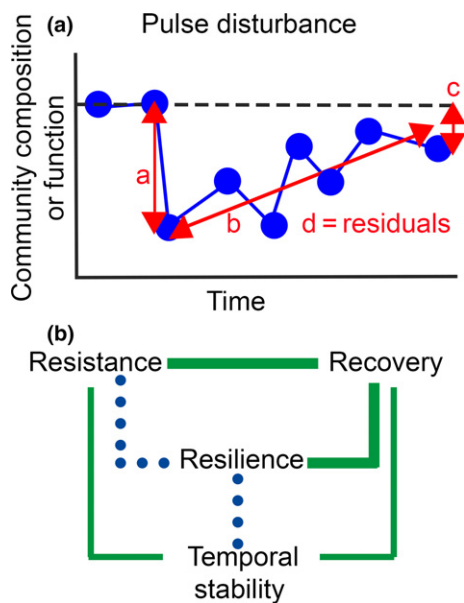
Figure 1 (a) Graphical representation of the four stability measures analysed (a = resistance, b = resilience, c = final recovery, d = temporal stability). Table 1 details the calculations. (b) Predicted relationships between stability measures based on pulse disturbance simulations (Data S1). Green solid lines show predicted positive relationships, blue dotted lines show negative relationships.

Details of the analyses are given in Data S2. In short, bacterial abundances were measured in each mesocosm using flow cytometry. The phytoplankton biomasses were determined by measuring chlorophyll a concentration according to Jespersen & Christoffersen (1987) for each sampling day. The bacterial community composition was assessed by amplicon sequencing of the 16S rRNA region (Sinclair *et al.* 2015). The eukaryotic phytoplankton community was determined using the chloroplast sequences from the 16S rRNA sequencing (Eiler *et al.* 2013). The zooplankton community composition was assessed microscopically to the genus level, and biovolume was calculated using genus-specific relationships between length and biovolume (Bottrell *et al.* 1976; Johansson *et al.* 1976; Ruttner-Kolisko 1977).

Austria

This experiment was conducted using three natural plankton communities from the Danube floodplain area close to Vienna, Austria, differing in their disturbance history. A highly disturbed community was collected from the River Danube, an intermediate disturbed community was collected from 'Kühwörter Wasser' and an intermittently disturbed community from 'Schwarzes Loch'. All communities were incubated in Lake Lunz, a 33 m deep, oligotrophic lake in Lower Austria to ensure similar temperature and light conditions for all treatments. The mesocosms were cylindrical plastic bags (white PE-foil, Renoplan), sealed at the bottom (conical end) and opened

to the atmosphere, with a diameter of 0.8 m and a depth of 1.5 m, enclosing *c*. 750 L water. We filled the mesocosms by pumping the water and installed them on floating frames which were connected to each other and fixed with anchors to the bottom of the lake. Compared to an undisturbed control, we reduced the light availability (by 50%) either by covering the mesocosms with neutral grey filters for 3 days (Chris James Lighting filters, HahneLicht) or by adding sediment to the mesocosm and mixing them twice a day using a disc (Striebel *et al.* 2013). The sediment from an oligotrophic lake (Lake Lunz) was dried and sieved, rinsed with HCL and water, and finally autoclaved with H_2SO_4 and rinsed with water to reduce the amount of nutrients added with the sediment (2 µg P L^{-1}). Light reductions were performed for a high nutrient treatment (15 µg P l^{-1}, 108.3 µg N l^{-1} and 75.3 µg Si l^{-1} added on the first day of disturbance and one-third of this amount every following day, mimicking a flood event) and a no-addition low-nutrient treatment.

Sampling was performed at 0.5 m depth at the beginning of the experiment (the day of filling) and every 3 days after that for 20 days. Phytoplankton samples were preserved with Lugol's solution and counted using an inverted microscope (Utermöhl 1958) to determine cell numbers and biovolume (Hillebrand *et al.* 1999). Zooplankton samples were taken with a 55-µm net (*c*. 95 L sample volume) and preserved with formaldehyde. Both groups were separated at genus level.

Analyses of stability

For both functional and compositional responses to the treatments, resistance, resilience, recovery and temporal stability were calculated for each replicate mesocosm in both studies. We present definitions for each of these measures for both functional and compositional stability that can be used for all trophic groups (Table 1, Fig. 1). We defined resistance as the ability to withstand the perturbation, that is, the difference between perturbed community and the control community at the first sampling after the treatment (Fig. 1a). Communities and functions that changed less directly after the treatment were considered as being more resistant. Measured as log response ratios (LRR) for functions, benchmark resistance, *a*, equals 0 (no change from the control), $a < 0$ indicates low resistance. Initially increased functions is possible ($a > 0$, Table 1), but still reflects low functional resistance, such that absolute values of *a* were partly used in statistical tests as described below. Compositional stability was based on the abundance-based similarity between control and disturbed communities, using the Bray–Curtis index (Bray & Curtis 1957). Values between 0 and 1 are possible. Maximum resistance corresponds to a similarity of 1 (100% similarity between control and treatment), values $\ll 1$ reflect low resistance.

Resilience (*b*) was measured for functions as the slope of the log-transformed difference (LRR) between perturbed and control biomass over time (Fig. 1b). Given the log-transformed response variable, the recovery trend was linearised even when growth after disturbance was exponential, so that we were able to use linear regression. $b = 0$ characterises the lack of resilience; $b < 0$ indicates that the treatment further deviates from the control over time (NB: if low resistance is

characterised by LRR> 1, $b > 0$ corresponds to the lack of resilience instead). This change in difference between perturbed communities and the controls reflects the 'engineering' aspect of resilience (Pimm 1984) in contrast to Holling's resilience concept (Holling 1973). For composition, resilience was reflected correspondingly by the slope of similarity between treatment and control, with the same benchmarks.

Recovery, *c*, measured the degree of functional or compositional restoration at the end of the experiments (Fig. 1a, Table 1), which was quantified as LRR ($c = 0$ means full recovery, that is, same function in treatment and control). Compositional recovery was measured by similarity and thus $c = 1$ means full recovery.

The temporal stability, *d*, was measured as the inverse of the standard deviation of residuals around *b* described above, over time (Fig. 1a, Table 1). This measure of stability is especially useful to measure the response to single disturbances, whereas other measures are often used when monitoring stability over long time periods in fluctuating or multiple disturbance settings, for example, the inverse of the coefficient of variation. Using the residuals of the regression for resilience avoids mixing the speed of recovery with the variation around this trend, which is a useful feature in systems undergoing shifting baselines (Guiz *et al.* 2016).

Functional stability was assessed by bacterial abundance (Swedish lakes), phytoplankton and zooplankton biomass (the latter only measured on the final day in the Swedish experiment, restricting stability to final recovery). Compositional stability was measured on relative proportions of taxa for bacteria (only Sweden), phytoplankton and zooplankton. We performed the same analyses on the simulated data (Data S1) in order to specify expectations for the statistical analyses.

Statistical analyses

We used one-way *t*-tests to analyse whether resistance, resilience and recovery were significantly different from their benchmark values (see Table 1). For these analyses, we pooled the different disturbance intensities in the Swedish experiments and the different nutrient levels in the Austrian experiments. All analyses were performed in R (R Development Core Team 2015).

We tested for different stability responses between trophic groups (H1) by a general linear mixed model using lme4 (Bates *et al.* 2015). Organism group was added as a fixed factor, the error structure of the data was represented by study (Austria/Sweden) and site nested within study (lakes within Austria and Sweden) as random factors. For functional resistance and recovery, we used the absolute values of LRR in order to test whether the absolute magnitudes differed between organism groups rather than the sign of the deviation from the control.

H2 and H3 explicitly address the question whether there are predisposed associations between different aspects of stability which are not contingent upon details of the study. Therefore, both hypotheses were tested across experiments, organisms and locations. Nonparametric correlations (Spearman R) were used to detect bivariate relationships between the same stability aspect measured for composition and function (testing H2)

as well as between different stability aspects within compositional and functional stability respectively (testing H3). In order to avoid inflation of degrees of freedom by using multiple trophic groups per experimental replicate, we compared observed correlations coefficient with critical tabulated values for $N = 42$ (number of independent experimental units) and report adjusted P-values (p_{adj}). For H2, we tested the correlation between compositional stability and the absolute value of the respective functional stability aspect, as both negative and positive deviations from control biomass reflected low resistance or recovery. For H3, we kept the sign of functional resistance and recovery as negative or positive deviations corresponded to the sign of the other metrics (Table 1).

RESULTS

Differences between trophic groups (H1)

In Swedish and Austrian sites, treatment effects on functions differed between sites within the studies and between organism groups (Data S2). Functional resistance immediately after the disturbance was negative for phytoplankton (reduction in biomass) for all sites except one, but significantly < 0 only for one site in each experiment (Data S2: Fig.S2.1, Table S2.1). Bacteria significantly increased in biomass after the disturbance in Edasjön (resistance > 0) and zooplankton significantly decreased in one Austrian site. The other sites showed non-significant and diverging resistance, leading to high variance in resistance across sites and a significant difference between organism groups (Table S2.2.).

Functional resilience tended to be positive across sites, but was significantly > 0 only for phytoplankton in Edasjön. For zooplankton, resilience was significantly negative in the low disturbance Austrian site (Table S2.1), that is, deviated further from the control during the course of the experiment. Final recovery was complete for most functions at the end of the experiment (recovery not different from 0), with few exceptions (Table S2.1). Bacteria tended to show more complete functional recovery than zooplankton and phytoplankton (Table S2.2). Temporal functional stability differed little between studies and sites, but was higher for zooplankton than phytoplankton.

In contrast to these divergent responses of functional stability, the compositional responses to the treatments were stronger in magnitude and more consistent across experiments and sites (Fig. S2.2). Directly after the pulse, bacterial, algal and zooplankton composition significantly differed from control (Table S2.1, resistance < 1 in all lakes in both countries), but with different magnitude between organism groups and sites (Table S2.2). In contrast to expectations, the composition did not recover but moved further away from the control over the time course of the experiment (resilience significantly < 0 for all groups in all Swedish lakes and in the Austrian lakes, except for zooplankton at the low disturbance site). In consequence, we found a wide range of recovery (similarity between 0.1 and 0.9) at the end of the experiments, but final recovery remained significantly < 1 across organisms and sites (Table S2.1). The temporal stability of the composition was

lower for phytoplankton than for bacteria (Swedish sites) or zooplankton (Austrian sites).

Differences between compositional and functional stability (H2)

Correlations between functional stability and compositional stability differed between stability measures (Fig. 2). Higher compositional resistance and recovery (closer to maximum of 1) was associated with almost perfect functional stability resistance and recovery (LRR close to maximum) respectively (Fig. 2a and c). However, if compositional resistance or recovery were weak ($\ll 1$), the corresponding functional stability aspect deviated from 0 as the biomass was either higher or lower than the biomass of the control. Consequently, compositional resistance and recovery were positively correlated with the corresponding absolute values of functional resistance and recovery (resistance: $R = 0.44$; recovery $R = 0.44$, $p_{adj} < 0.001$ in both cases).

In contrast, resilience was not correlated between function and composition ($R = -0.03$, $p_{adj} > 0.8$), that is, an experimental unit showing high functional resilience did not necessarily show a fast compositional resilience. Likewise, the stability of biomass over time was not significantly related to the stability of composition over time ($R = 0.22$, $p_{adj} > 0.2$).

Differences between stability aspects (H3)

The correlations between different stability aspects in functional and compositional space ranged from significantly negative over non-significant to significantly positive relationships (Fig. 3). Resistance and resilience were negatively correlated for functions ($R = -0.65$, $p_{adj} < 0.001$), but uncorrelated for composition ($R = -0.01$) (Fig. 3a). High functional resistance ($c.$ 0) did not require resilience, resulting in resilience close to 0, whereas weak resistance (strong deviation from control) allowed for fast recovery (positive slopes if resistance < 0, negative slopes if resistance > 0) resulting in a negative relationship between functional resistance and resilience.

Functional resistance and recovery were unrelated ($R = 0.03$) in contrast to compositional resistance and recovery, which showed a significant positive correlation ($R = 0.57$, $p_{adj} < 0.001$) (Fig. 3b). Weak deviation of composition directly after the disturbance led to higher composition recovery at the end of the experiment. In contrast, functional resistance did not predispose the degree of functional recovery at the end. Functional overcompensation (recovery > 0) was common in the mesocosms and independent of an initial positive (resistance > 0) or negative (resistance < 1) response. High compositional resistance stabilised the temporal dynamics of communities ($R = 0.42$, $p_{adj} < 0.01$), but functional resistance was not associated with functional temporal stability ($R = -0.02$, Fig. 3c).

Resilience and final recovery showed strong positive relationships (Fig. 3d), in correspondence to our simulations (Data S1), which indicated that faster recovery will result in more complete recovery or even overshooting ($R = 0.54$, $p_{adj} < 0.001$ for functions, $R = 0.71$, $p_{adj} < 0.001$ for composition). Resilience was not significantly correlated with temporal stability, neither for function ($R = -0.04$) nor for composition ($R = 0.26$, $p_{adj} > 0.1$, Fig. 3e). For composition, higher
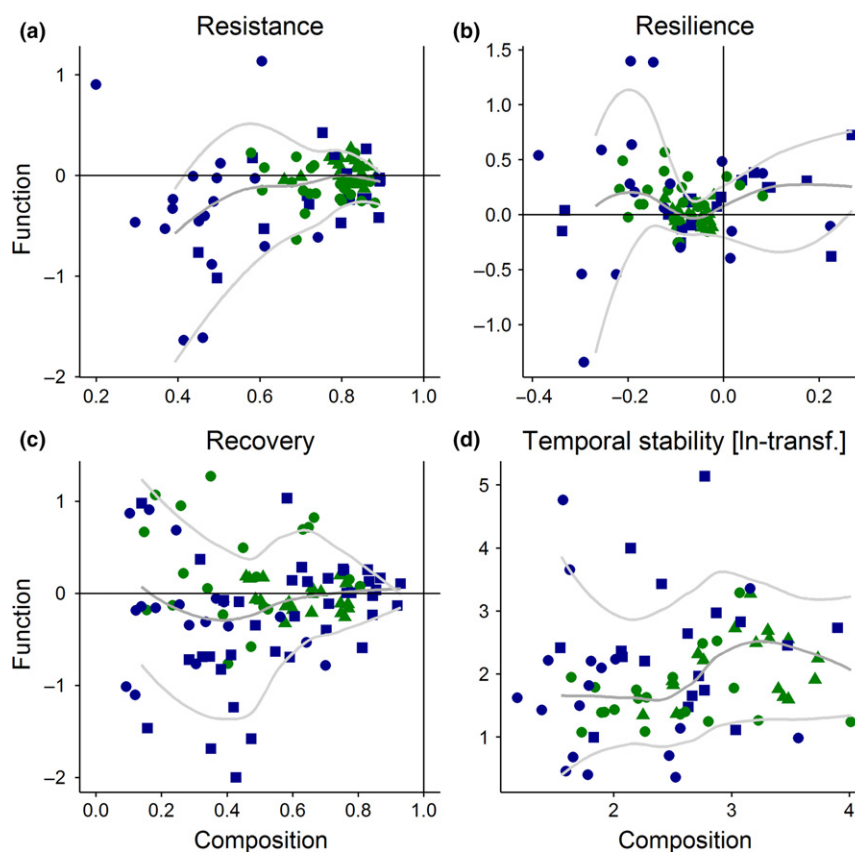
Figure 2 Relationship between functional and compositional aspects of stability in mesocosm experiments (Austria = blue symbols, Sweden = green symbols) for three organism groups (circles = phytoplankton, squares = zooplankton, triangles = bacteria). Each dot is a replicate from the two experiments. Dark grey lines present the median, grey lines the 10 and 90% quantiles for the functional variable. (a) Resistance (significant Spearman rank correlation, $R = -0.44$, $p_{adj} < 0.001$), (b) Resilience, (c) Recovery (significant Spearman rank correlation, $R = -0.44$, $p_{adj} < 0.001$), (d) Temporal stability. Neither resilience nor temporal stability was significantly correlated between function and composition ($p_{adj} > 0.2$).

temporal stability was associated with higher recovery ($R = 0.42$, $p_{adj} < 0.01$). The same was true for functional stability, but only if the absolute recovery (deviation from zero) was used as both negative or positive deviations of the function from the control led to low temporal stability ($R = 0.37$, $p_{adj} < 0.01$).

DISCUSSION

Using two similar, but independent, mesocosm experiments, we showed that ecological stability, the ability of a system to absorb and respond to changing conditions, must be analysed as a multidimensional construct. The initial changes introduced by the treatment as well as the recovery trajectory differed between trophic groups (H1), between functional and compositional response variables (H2), and for different aspects of stability (H3). Thus, no single aspect of stability would have been able to reflect the response to the environmental change introduced by the treatment. At the same time, the four aspects were not truly orthogonal either, indicating links predisposed by the definition of the different metrics and associations arising from community dynamics. These results achieve scientific relevance in light of the fact that the far majority of global change studies analyses only one of the many different aspects of stability (Ives & Carpenter 2007), as

revealed by recent systematic literature analysis (Donohue *et al.* 2016). This study thus contributes to the emerging evidence that a recasting of stability as a concept is needed in order to summarise the response of an ecosystem to changing conditions.

Function and composition

In the simplified ecosystems represented by the mesocosms, we found that if the composition largely withstands or recovers from a disturbance, the function it performs (in our case, the biomass produced) will be very close to the control as well. These positive correlations were also predicted by the simple simulation model where – as in the data – a strong immediate or lasting impact of the disturbance on the composition immediately after the disturbance (low compositional resistance) or at later time (low compositional recovery) was associated with larger functional consequences of this change. The empirical data, however, revealed additionally that the sign of the functional deviation from the control was unpredictable at low compositional stability: the median functional stability was constant across a wide range of compositional resistance and recovery, but the variance increased with low compositional stability leading to higher, lower or the same functioning as the control.
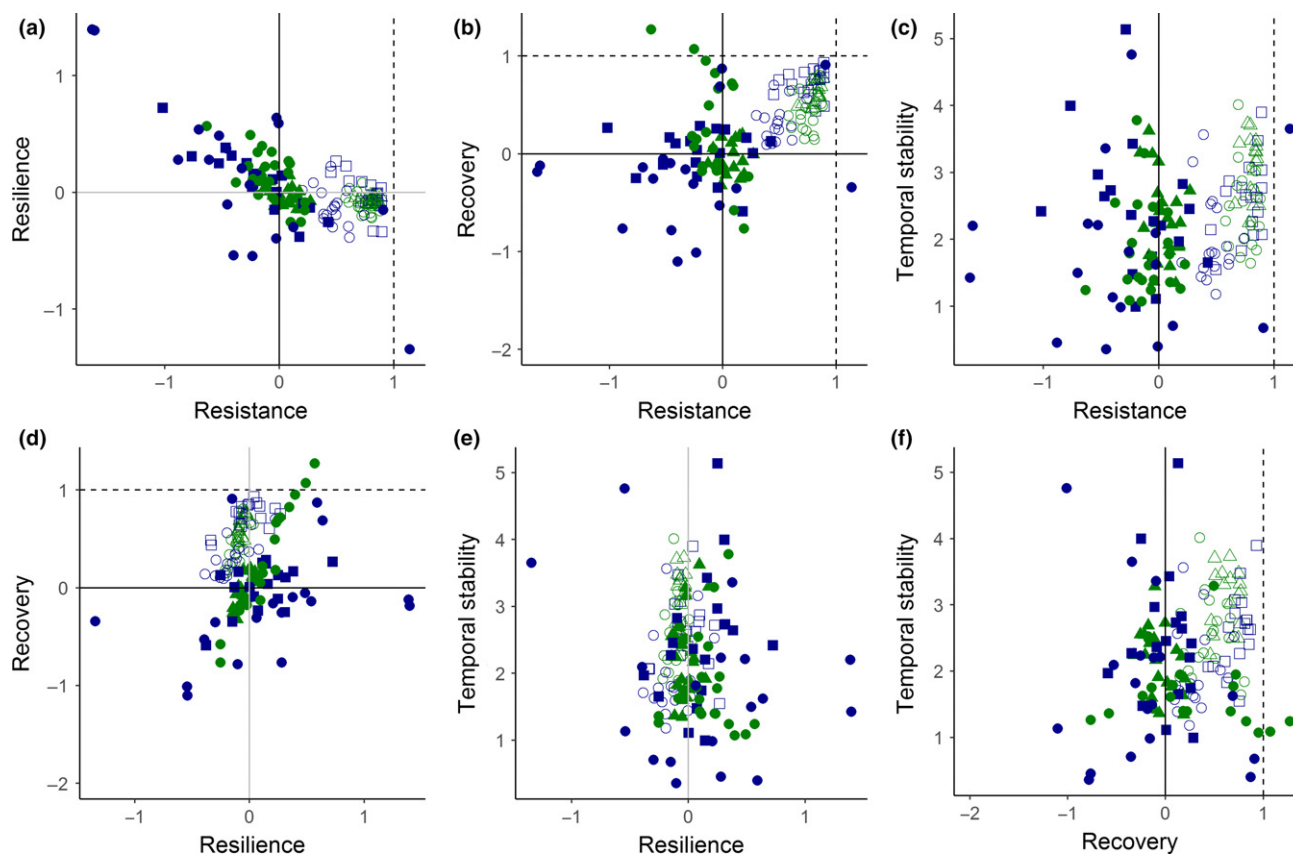
Figure 3 Bivariate relationship between different aspects of stability in mesocosm experiments (Austria = blue symbols, Sweden = green symbols) for three organism groups (circles = phytoplankton, squares = zooplankton, triangles = bacteria). Each dot is a replicate from the two experiments. For each pair of stability measures, the compositional stability is depicted by open symbols, the functional stability by closed symbols. Horizontal and vertical black lines delimit maximum values for functional stability (solid) and compositional stability (dashed). Grey lines indicate zero resilience, that is, delimit further deviations from control from experimental units recovering. Significant correlations were found for functional resistance and resilience (a, $R = -0.65$, $p_{adj} < 0.001$), compositional resistance and recovery (b, $R = 0.54$, $p_{adj} < 0.001$), compositional resistance (c, $R = 0.42$, $p_{adj} < 0.001$). Resilience and final recovery showed strongest positive relationships (d, $R = 0.54$ for functions, $R = 0.71$ for composition, both $p_{adj} < 0.001$). Finally, higher recovery was associated with higher temporal stability for composition (f, $R = 0.42$, $p_{adj} < 0.001$) and function ($R = 0.37$, $p_{adj} < 0.01$).

In contrast to resistance and recovery, which can be seen as relatively static aspects of stability directly after the disturbances and at the end of the experiment, respectively, the more dynamic aspects (resilience and temporal stability) did not show significant correlations between function and composition. Thus, the speed of recovery and the fluctuations around the trajectory were not directly related for species composition and biomass production. In fact, compositional resilience was often negative, indicating that composition departed further from the control after the applied disturbances, rather than approaching control levels. In our simple simulations, species trade-offs between growth (r) and equilibrium abundance (K) resulted in positive associations between functional and compositional resilience. In contrast, the experiments highlighted that fast recovery in biomass can be performed by community that increasingly diverged in composition.

Functional recovery after a disturbance is thus predictable only if the composition recovers, whereas in the absence of compositional recovery, functional recovery can vary widely in extent and sign. This decoupling between functional and compositional stability has been found in other studies on

recovery as well (Hoover *et al.* 2014; Johns *et al.* 2014; Gülzow *et al.* 2017). Restoration ecology has provided examples for systems recovering functionally by ecosystem management, although the pre-disturbance composition did not recover (Borja *et al.* 2010). Functional recovery is possible despite persisting shifts in species dominance (Hillebrand *et al.* 2008) or altered community assembly processes (Fukami *et al.* 2005) if the vulnerability of the component species to the disturbance is not related to their functional performance.

The lack of compositional recovery over the many generations of bacterio- and phytoplankton in these experiments opens up the question whether not only the time scale of recovery might differ between functions and composition but also the probability for recovery at all. Generally, we expect a decrease in the disturbance effect with time (i.e. functional recovery), but this might not be true for composition: recovery of the initial community is prevented if the disturbance leads to local extinction of species in systems with low immigration or to altered competitive hierarchies. Examples for such dynamics have been documented for tropical forests (Martin *et al.* 2013), grasslands (Hoover *et al.* 2014) and microbial communities (Berga *et al.* 2012).

Being explicit about functional and compositional stability and their relationship may be a way to integrate different aspects of the entangled discussions about diversity–stability relationships (DSR). Part of the debate stems from different 'stabilities' being used: Elton's (Elton 1958) idea of more diverse assemblages being less invaded focuses on compositional stability, as does the persistence criterion in May's models on food webs with increasing number of species (May 1973). More recent models on DSR focus on the stability of a function (or functional property, often biomass production as in our case) in systems of different species richness (Yachi & Loreau 1999; Cottingham *et al.* 2001; Loreau & de Mazancourt 2013). Here, the fluctuation in the environment has less impact on the functioning if more species coexist, as these allow compositional shifts that sustain the function over time. Thus, the functional stability requires compositional flexibility, as is reflected in the terms 'insurance effect' (Yachi & Loreau 1999) and 'portfolio effect' (Cottingham *et al.* 2001) coined to describe this relationship. Most empirical evidence on positive DSR is about such increases in functional stability with increasing diversity (Tilman 1996; McGrady-Steed & Morin 2000; Borer *et al.* 2012; Gross *et al.* 2014; Hautier *et al.* 2014), but empirical relationships between diversity and compositional stability have been reported as well, with some variation as to the sign and strength of the relationship (Shurin *et al.* 2007). Obviously, the mechanisms by which diversity stabilises functions (often measured as temporal invariance of processes) and composition (often measured as persistence of species and their relative contribution) can – or even must – differ. Disentangling these mechanisms might overcome some of the idiosyncrasy in the DSR debate (Ives & Carpenter 2007).

Multiple dimensions of stability

The degree of correlation between the four different metrics of stability differed between negative, positive and uncorrelated, especially in the functional realm of analysis. Some of these correlations reflect relationships that arise from the definition of the metrics and their calculation (as indicated by the simulations). The most prominent associations expected from the model existed between resistance, resilience and recovery. The simulations suggest that a system that withstands the perturbance opens little scope for fast recovery rates being measured (negative resistance–resilience correlation), whereas fast-recovering systems are prone to achieve high final recovery (positive resilience–recovery correlation). In the model, initial stability was also positively related to final stability (positive resistance–recovery correlation). In the empirical data, some of these predictions were significantly reflected, but some important deviations point to community dynamics that enlarged the dimensionality of stability. In line with model predictions, we found positive associations between resilience and recovery for both functions and composition as well between resistance and recovery. The latter was constrained to composition, however, indicating that functional recovery can occur independently of the initial resistance. Conversely, the predicted negative association between resistance and resilience was found only for functional stability, whereas the initial compositional resistance did not predict

the rate of change in the community composition after the disturbance. These deviations from predicted correlations are important to consider in the assessment of overall stability as they reflect ecological interactions beyond the simplified expectation of return to initial state.

This conclusion is reinforced by analysing the temporal stability around these recovery dynamics. The temporal stability of composition was high if resistance or final recovery of the composition was high, but no relationship between functional stability over time and the corresponding functional resistance or recovery were found. Temporal fluctuations in composition increased if the system was more strongly affected (low resistance) and if it did not recover (low recovery), but the speed of recovery (resilience) was unrelated to the variation around this trend.

The lack of correlations in these cases and especially in the functional stability aspects sustains the idea on the multidimensional nature of stability (Donohue *et al.* 2016). Others have also found decoupling between different aspects of stability, for example, in grasslands following drought (van Ruijven & Berendse 2010) or intertidal communities following heat stress (Allison 2004). The disconnection between, for example, resistance and resilience, is not surprising per se, given that trade-offs might preclude optimising traits related to tolerant or resistant to a perturbation compared with traits related to fast recovery. Therefore, the component species of an assemblage will contribute differently to the different aspects of stability, and thus species identity and dominance will play an important role for overall stability (Hillebrand *et al.* 2008).

Despite this view being commonly accepted in ecology, the way we address stability in most studies does not reflect these ideas. The observed variety of links between stability aspects and stability domains indicates that stability neither collapses to a single dimension nor does it represent an n-dimensional space if n metrics are quantified.

Outlook

Understanding stability in the face of environmental change requires being explicit about the relationship between functional and compositional stability and between different phases of the response reflected by different stability aspects. This conclusion from the analysis of two freshwater mesocosm studies is based on a simple one-time application of a treatment. The multidimensional nature of stability becomes even more important if multiple changes are ongoing, that is, if multiple stressors interact (Folt *et al.* 1999; Sundbäck *et al.* 2007; Flöder & Hillebrand 2012) or environmental change consists of different timing and directionality of changes in several factors (Donohue *et al.* 2016).

Following Donohue *et al.* (2013), it seems feasible to achieve a more holistic understanding of system stability by quantifying species-specific contributions to one or more different components of stabilisation. Such a trait–stability relationship would mirror the trait–functioning relationships which have been established to explain biodiversity effects on ecosystem functions such as productivity (Reiss *et al.* 2009; Loreau 2010). Although the conceptual framework for such trait-based analyses of multiple dimensions of stability has

been laid out, few empirical analyses show the feasibility of an approach addressing species contributions to community-level stability (Supp & Ernest 2014; Baert *et al*. 2016).

One future avenue of research needs to be disentangling species contributions to multiple stability aspects. The biodiversity–ecosystem functioning literature has been very successful in establishing metrics for species-specific contributions to functions, which allow calculating expected functioning for different species compositions as well as interpreting deviations from these expected functions as being based on interactions between species. Currently, a framework for such species-specific contributions to stability has not been fully developed, but stepping stones have been created. Using the Price equation from evolutionary biology, Fox (2010) partitioned the contribution of species to community variability after species loss. Leibold *et al*. (2017) adopted this view in their approach to community assembly and the functioning of ecosystems ('CAFÉ'). Thereby, ecology might overcome the present situation where stability is discussed as an epiphenomenon rather than from the underlying community dynamics.

AUTHOR STATEMENT

HH designed the study, conducted all analyses on the data and wrote the manuscript with substantial input from all co-authors. KL, MS, EL, SL and ÖÖ provided the data from the mesocosm studies and discussed the aim and approach of the analysis. ÖÖ provided the simulations.

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