RESEARCH ARTICLE

Integrating multiple dimensions of ecological stability into a vulnerability framework

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Abstract

1. Ecological stability encompasses multiple dimensions of functional and compositional responses to environmental change. Though no single stability dimension used in isolation can fully reflect the overall response to environmental change, a common vulnerability assessment that integrates simultaneously across multiple stability components is highly desirable for ecological risk assessment.

2. We develop both functional and compositional counterparts of a novel, integrative metric of overall ecological vulnerability (OEV). We test the framework with data from a modularized experiment replicated in five lakes over two seasons, examining functional and compositional responses to both pulse and press disturbances across three trophic groups. OEV is measured as the area under the curve integrated over the entire observation period, with the curve delimiting the difference between the disturbance treatment and undisturbed parallel controls, expressed either as the log response ratio of biomass (functional OEV) or community dissimilarity index (compositional OEV).

3. Both, functional and compositional OEV correlated negatively with functional and compositional 'resistance', 'temporal stability' and 'final/extent of recovery' following both pulse and press disturbances, though less so with 'resilience' following a pulse disturbance. We also found a positive correlation between functional and compositional OEV, which reveals the potential to also evaluate the intricate linkage between biodiversity and functional change.

4. Our findings demonstrate that OEV comprises a robust framework to: (a) capture simultaneously multiple functional and compositional stability components, and (b) quantify the functional consequences of biodiversity change. Our results provide the basis for an overarching framework for quantifying the overall vulnerability of ecosystems to environmental change, opening new possibilities for ecological risk assessment and management.

5. *Synthesis*. Ecological stability comprises multiple dimensions that together encapsulate how ecosystems respond to environmental change. Considering these multiple aspects of stability simultaneously often poses a problem in environmental assessments, which frequently require overarching indicators of risk or vulnerability. While an analysis of multiple dimensions allows for deeper exploration of mechanisms, here we develop and test a new univariate indicator that integrates stability aspects under a broad range of disturbance regimes. Using a modularized experiment in Swedish lakes, we show that this integrative measure captures multiple stability dimensions reflecting compositional and functional vulnerability and their relationships between them.

KEYWORDS
biodiversity, communities, dimensionality, disturbances, ecological risk assessment, ecological stability, ecosystem management, vulnerability

1 | INTRODUCTION

Ecological stability is the general framework for understanding the inherent property of ecosystems to remain unchanged (Pimm, 1991). Over the past decades, ecologists have developed many metrics to describe different aspects of stability such as resistance, engineering resilience, temporal stability and final recovery (Donohue et al., 2016; Kéfi et al., 2019; Hillebrand et al., 2018; Pimm, 1984). However, most studies to date generally focus on describing one single stability component in response to one single disturbance type (Donohue et al., 2016). Recent findings have demonstrated that the ecological stability of a system is multidimensional, where different stability components are more or less correlated with one another (Donohue et al., 2013, 2016; Hillebrand et al., 2018; Yang et al., 2019). These findings suggest that no single component itself reflects the integrated stability of the entire system (Donohue et al., 2013; Yang et al., 2019). Furthermore, the effective dimensionality of stability that emerges from the strength of these relationships can vary depending on the type of disturbance (Donohue et al., 2013; Polazzo & Rico, 2021; Radchuk et al., 2019), the organisms or ecological properties affected (Kéfi et al., 2019) and the spatial and temporal context in which disturbances occur (Clark et al., 2021; Güelzow et al., 2017; Levin, 1992). Thus, it is becoming increasingly clear that a multidimensional analytical approach to the study of stability is needed to reduce the risk of underestimating the overall impact of disturbances. Such multidimensional approach is increasingly important in a world facing rapid and growing environmental change (IPCC, 2013; Millennium Ecosystem Assessment, 2005).

Each stability component is unique in the type of information it provides, and the study of stability cannot therefore be simplified to analysis of a single metric in isolation (Donohue et al., 2016; Ives & Carpenter, 2007; Pimm, 1991; Radchuk et al., 2019). Even so, the need to assess risks and prioritize management actions calls for an integrative measure that effectively captures multiple dimensions of stability in an overall vulnerability metric. Ideally, such a metric would allow comparison of the impact of different disturbances with different trajectories, such as pulse disturbances (changes with finite duration) and more consistent press disturbances. There is clear indication that both pulse (e.g. fires, floods, heat waves and storms; IPCC, 2013; Stockwell et al., 2020) and press (e.g. species loss, biological invasions, acidification; Donohue et al., 2016; IPBES, 2019) disturbances are becoming more frequent and intense across the globe. Even though pulse disturbances are temporally constrained, there is increasing evidence that they may be at least as important in driving long-term community dynamics compared to press disturbances (Jentsch et al., 2007; Lawson et al., 2015; Urrutia-Cordero et al., 2020) and can have long-lasting, persistent effects even after the disturbance per se has ended (Hillebrand et al., 2018).

To be fully operational, an integrative vulnerability metric should work not only for pulse and press perturbations, but also enable exploration and quantification of links between functional and compositional change. The links between functional and compositional change could, for example, be explored where it is possible to compute both functional and compositional counterparts of the same vulnerability metric, and examine their interrelationships (see,

e.g. this principle used for other stability components in Hillebrand et al., 2018 and White et al., 2020). Understanding these interrelationships is important because biodiversity change in terms of species composition (i.e. compositional turnover) is a major mechanistic basis to explain the relationship between species richness and functional stability over time (Cleland, 2011). In contrast, it is less clear how biodiversity changes modulate stability components other than temporal variability (Ives & Carpenter, 2007). Recent results from mesocosm experiments testing the impacts of pulse disturbances revealed that multiple functional and compositional stability components may be coupled (Hillebrand et al., 2018). More generally, a recent meta-analysis spanning 508 field experiments globally distributed across marine, terrestrial and freshwater ecosystems found that functional recovery from pulse disturbances can be achieved with or without compositional recovery (Hillebrand & Kunze, 2020). These results strongly indicate the need to integrate both functional and compositional responses in the study of the overall ecological vulnerability (OEV) of a system if we are to understand and predict the broader consequences of biodiversity change for ecosystems (Pimm et al., 2019).

Here, we develop an analytical framework that integrates multiple dimensions of stability for pulse and press disturbances into a single integrated metric, which we call OEV, from which we can quantify both its functional and compositional counterparts. We then test both functional and compositional counterparts of this metric by analysing the responses of three trophic groups of organisms (i.e. lake zoo-, phyto- and bacterioplankton) to the same pulse (presence of a planktivorous fish) and press (reduced light availability) treatments, both in isolation and combination, in 10 outdoor mesocosm experiments replicated across both space (five Scandinavian lakes) and time (two seasons). OEV was measured as the area under the curve integrated over the entire observation period, with the curve delimiting the difference between the disturbed treatment and parallel undisturbed controls under ambient conditions, expressed either as the log response ratio of biomass (functional OEV) or community similarity index (compositional OEV) between the disturbance treatment and the control (Table 1; Figure 1a–f). A major advantage of the framework is that it enables the quantification of OEV for both function and composition regardless of either disturbance or community type, while simultaneously integrating across multiple dimensions of stability.

We first assessed the capacity of OEV to integrate across multiple dimensions of stability to both pulse (resistance, resilience, temporal stability and final recovery) and press (rate of deviation, temporal stability and extent of recovery) disturbances (Table 1). We predict that both functional and compositional OEV correlate negatively with all of the measured functional and compositional stability metrics for pulse and press disturbances. We then investigated the functional consequences of biodiversity change by examining how compositional OEV relates to functional OEV across both pulse and press disturbances. Finally, we test the potential of our framework to reflect the overall functional and compositional vulnerability of each trophic group to pulse and press disturbances acting both in isolation and combination across all experiments. We thus exemplify the generality of the metric in the context of a modularized experiment across space and time, thus exposing it to considerable variation in local environmental conditions.

2 | MATERIALS AND METHODS

2.1 | Experimental data

We used data from a modularized lake mesocosm experiment done with the newly established SITES AquaNet infrastructure (see Urrutia-Cordero, Langvall, et al., 2021 for a detailed description of the infrastructure). The modularized experiment comprised of 10 individual experiments performed in five different lakes in Sweden over two seasons. Each experiment lasted 28 days. Five experiments (one in each lake) started in June 2017 (hereafter, 'Spring' experiments), and the remaining five in August 2017 ('Summer' experiments). The lakes (Feresjön, Bolmen, Erssjön, Erken and Stortjärn) span along a latitudinal and climatic gradient in Sweden, thus differing considerably in local environmental conditions such as temperature, nutrient status and humic content (Table S1).

Each experiment consisted of 16 mesocosms (polyethylene enclosures, 0.8 m diameter, 1.5 m height, 700 L volume; Cipax AB) filled with 550 L unfiltered water from the lake in which they were located. The mesocosms were deployed under water (except the top 30 cm) using ropes attached to a jetfloat facility (Jetfloat International Gmbh). Each experiment comprised of four treatments, each replicated four times, resulting in 160 unique experimental units: (a) no experimental disturbance; (b) a pulse disturbance in the form of fish addition, where we added two juvenile crucian carp *Carassius carassius* (mean $\pm$ SD length: 5.77 $\pm$ 0.74 cm) to the mesocosms for the first 7 days of the experiment; (c) a press disturbance in the form of constant shading, where we placed a dark polyester mesh on top of the mesocosms reducing incoming light by approximately 50%; and (d) the pulse and press disturbances combined. We used a transient presence of a top consumer as pulse disturbance because small water bodies and lakes can experience fish colonization and extinction and/or transient migratory patterns leading to sudden changes in fish predation pressure on zooplankton communities (Brönmark et al., 2014). In addition, changing temperatures and heat waves directly affect predation and reproduction rates of planktivorous fishes, with subsequent cascading effects on lower trophic levels (Hansson et al., 2013; Jeppesen et al., 2014). The press disturbance aimed to mimic increased light limitation experienced by boreal and subarctic lakes as a result of increased precipitation and associated cloud cover from climate change (Weyhenmeyer et al., 2016). Furthermore, a reduction of light availability is one of the most important consequences of 'lake browning' from the discharge of terrestrially derived humic substances (Karlsson et al., 2009; Kritzberg et al., 2019).

We sampled each mesocosm six times, on days 1 (just before the experimental treatments were applied), 4, 7, 9, 14 and 28. We measured: (a) zooplankton biomass (function), using light

TABLE 1 Description and measurement of functional and compositional stability for both pulse and press disturbances. Measurement timing indicates when during the experiment each stability aspect was measured.

Response types	Estimation descriptors	Stability metrics for pulse perturbations		
		Overall ecological vulnerability	**Resistance**	**Final recovery**
Function	Measurement timing	Entire experimental period	Sampling after pulse disturbance	Final sampling
	Calculation of raw values	Area Under the Curve (AUC) of the absolute of the log response ratio between the disturbed function and control function by taking 0 as a benchmark	Absolute of the log response ratio between the disturbed function and control function	Absolute of log response ratio between disturbed function and control function
	Equation	$\text{OEV} = \text{AUC}\left(\text{abs}\left(\ln\left(\frac{Fdis}{Fcon}\right)\right)\right)$	$\text{RST} = \ln\left(\frac{Fdis}{Fcon}\right)$	$\text{FR} = \ln\left(\frac{Fdis}{Fcon}\right)$
	Standardization	—	Positive RST values are transformed to negative	Positive FR values are transformed to negative
	Interpretation	Values are ≥ 0. Larger values indicate greater destabilization across the entire time series	Values are ≤ 0. The more negative the value the less resistance, with maximum resistance = 0	Values are ≤ 0. The more negative the value the less final recovery, with maximum recovery = 0
Composition	Measurement timing	Entire experimental period	Sampling after pulse disturbance	Final sampling
	Calculation of raw values	Area Under the Curve (AUC) of the dissimilarity between disturbed composition and control composition by taking 0 as a benchmark	Inverse dissimilarity (akin to similarity) between disturbed composition and control composition	Inverse dissimilarity (akin to similarity) between disturbed composition and control composition
	Equation	$\text{OEV} = \text{AUC}\left(\text{dissim}\left(\frac{Cdis}{Ccon}\right)\right)$	$\text{RST} = \text{dissim}\left(\frac{Cdis}{Ccon}\right) * -1$	$\text{FR} = \text{dissim}\left(\frac{Cdis}{Ccon}\right) * -1$
	Standardization	—	—	—
	Interpretation	Values are ≥ 0. Larger values indicate greater destabilization across the entire time series	Values are bounded between 0 and 1, with maximum resistance = 1. Larger values indicate higher resistance	Values are bounded between 0 and 1, with maximum recovery = 1. Larger values indicate higher final recovery

microscopy; (b) phytoplankton biomass (function), derived from chlorophyll *a* analyses; (c) bacterial abundance (function), using flow cytometry; (d) zooplankton community composition (genus level), using light microscopy; and (e) phytoplankton and (f) bacterial community composition derived from 18S and 16S rRNA amplicon Illumina sequencing at the ASV level respectively. Because the original compositional dataset derived from 18S rRNA amplicon Illumina sequencing included eukaryotes other than phytoplankton, prior to our analyses we removed other taxa than phytoplankton from that dataset. See Urrutia-Cordero, Langenheder, et al. (2021) for further details on the methods during sampling and sample analyses and mesocosm performance. The study was approved by Uppsala animal ethics committee (permission number 5.8.18-03672/2017).

		Stability metrics for press perturbations			
Resilience	**Temporal stability over recovery trend**	**Overall ecological vulnerability**	**Extent of recovery**	**Rate of deviation**	**Temporal stability over deviation trend**
Samplings from the measurement of initial stability to final stability	Samplings from the measurement of resistance to final recovery	Idem as pulse	Idem as final recovery for pulse	Entire experimental period	Entire experimental period
Slope of the regression of the log response ratio over the recovery trend	Log $(x + 1)$ of the inverse standard deviation of the residuals around RSL	Idem as pulse	Idem as final recovery for pulse	Slope of the regression of the log response ratio over total impact	Log $(x + 1)$ of the inverse standard deviation of the residuals around RD
$RSL = \dfrac{\ln\left(\frac{Fdis}{Fcon}\right) - i}{t}$ $i =$ intercept, $t =$ time	$TSrt = \ln\left(\left(\frac{1}{sd(residRSL)}\right) + 1\right)$	Idem as pulse	Idem as final recovery for pulse	$RD = \dfrac{\ln\left(\frac{Fdis}{Fcon}\right) - i}{t}$ $i =$ intercept, $t =$ time	$TSdt = \ln\left(\left(\frac{1}{sd(residRD)}\right) + 1\right)$
Positive RSL values (slopes > 0) are converted to negative, if the disturbed function further deviates from the control over the recovery trend. All negative RSL values (slopes < 0) are converted to positive, except if the disturbed function further deviates from the control over time	—	Idem as pulse	Idem as final recovery for pulse	Positive RD values (slopes > 0) are converted to negative	—
Values can be positive (true recovery) or negative (further deviation from control conditions), with no trend = 0	Values are ≥ 0. Larger values indicate higher temporal stability (i.e. lower fluctuations around the trend)	Idem as pulse	Idem as final recovery for pulse	Values ≤ 0. The more negative the value the more deviation from control conditions over time, with no trend = 0	Values are ≥ 0. Larger values indicate higher temporal stability (i.e. lower fluctuations around the trend)
Samplings from the measurement of initial stability to final stability	Samplings from the measurement of resistance to final recovery	Idem as pulse	Idem as final recovery for pulse	Entire experimental period	Entire experimental period
Slope of the regression of inverse dissimilarity (akin to similarity) over the recovery trend.	Log $(x+1)$ of the inverse standard deviation of the residuals around RSL	Idem as pulse	Idem as final recovery for pulse	Slope of the regression of inverse dissimilarity (akin to similarity) over the entire time series	Log $(x+1)$ of the inverse standard deviation of the residuals around RD
$RSL = \dfrac{\left(dissim\left(\frac{Cdis}{Ccon}\right) * -1\right) - i}{t}$ $i =$ intercept, $t =$ time	$TSrt = \ln\left(\left(\frac{1}{sd(residRSL)}\right) + 1\right)$	Idem as pulse	Idem as final recovery for pulse	$RD = \dfrac{\ln\left(\frac{Cdis}{Ccon}\right) - i}{t}$ $i =$ intercept, $t =$ time	$TSdt = \ln\left(\left(\frac{1}{sd(residRD)}\right) + 1\right)$
—	—	—	—	—	—
Values can be positive or negative, with no trend = 0. Larger values indicate higher resilience	Values are ≥ 0. Larger values indicate higher temporal stability (i.e. lower fluctuations around the trend)	Idem as pulse	Idem as final recovery for pulse	Values ≤ 0. The more negative the value the more deviation from control conditions over time, with no trend = 0	Values are ≥ 0. Larger values indicate higher temporal stability (i.e. lower fluctuations around the trend)

2.2 | Calculation of OEV

We quantified the OEV of a system to a pulse, press and the combination of both disturbances by measuring the area under the curve (AUC) over the entire time series of the functional log response ratio (functional OEV) or community similarity index (compositional OEV) between the disturbance treatment and the undisturbed control (Table 1; Figure 1a–f). We created plots for each mesocosm time series based on the log response ratio of biomass/abundance and community similarity index relative to mean control conditions (Figures S1–S3). To derive the log response ratio (LRR) from each mesocosm for functional OEV, we used the mean of the four replicated control functional values (total community biomass/abundance) as a benchmark for each sampling point
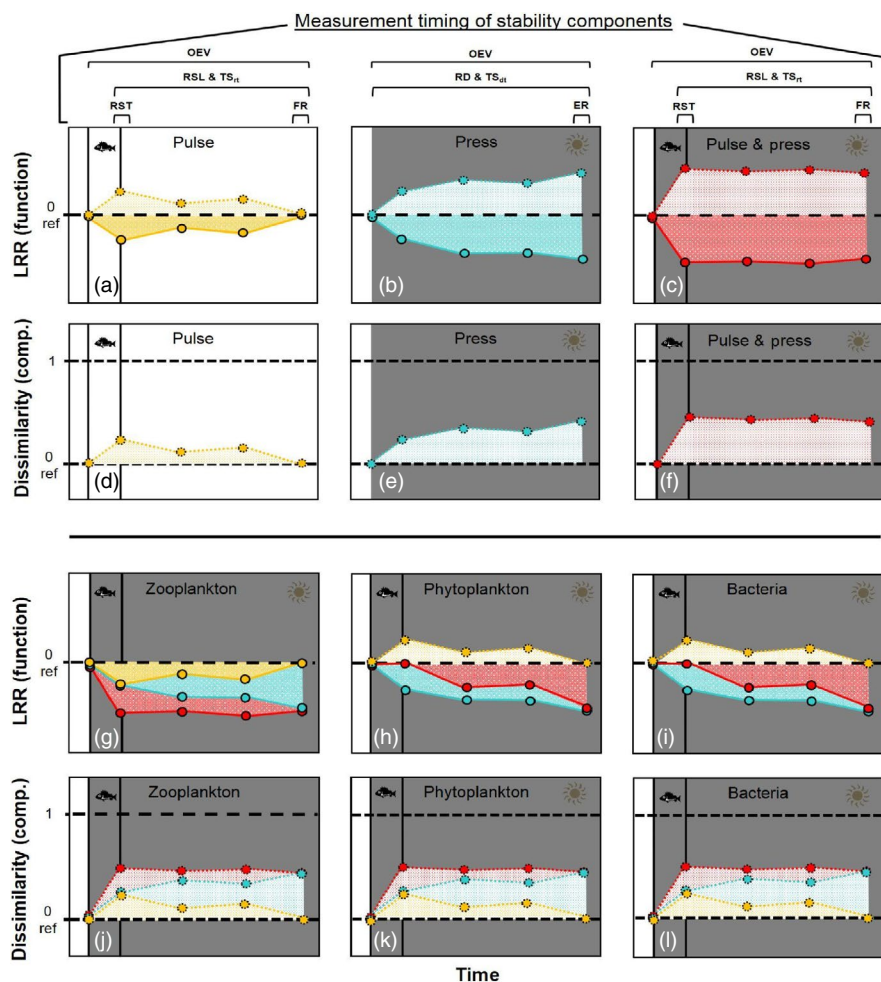
FIGURE 1 Conceptual illustration of the measurement of overall ecological vulnerability (OEV) and its relationship with other stability components. (a–f) OEV is measured as the area under the curve (AUC) over the entire time series of the functional log response ratio (a–c) (functional OEV) or (d–f) community dissimilarity index (compositional OEV) between a disturbed treatment and an undisturbed control. Yellow, blue and red backgrounds denote the AUC (light colours if positive responses, darker colours if negative) for pulse, press and combined pulse and press treatments respectively. The vertical black lines delimit the duration of the pulse disturbance (here, fish presence), whereas the dark grey background represents the duration of the press perturbation (here, shading). Other stability components are: RST = Resistance, FR = Final recovery, RSL = Resilience, TS_{rt} = Temporal stability over recovery trend, RD = Rate of deviation, TS_{dt} = Temporal stability over deviation trend and ER = Extent of recovery. (g–l) Expected responses of different trophic groups. If pulse and press disturbances have both a negative effect on a function (g; zooplankton), we predict greater OEV when both perturbations act in concert than separately (AUC red > AUC blue or AUC yellow). If pulse and press perturbations have opposing impacts on a function (h–i; phytoplankton and bacteria), we expect lower overall vulnerability when both disturbances act in concert than the sum of the two separately (AUC red < AUC blue + AUC yellow). For compositional responses, we expect greater overall vulnerability when both perturbations act in concert than separately (AUC red > AUC blue or AUC yellow) regardless of the trophic level (j–l)

(LRR = ln(treatment unit/control mean)). To estimate the variability within the control treatment, we ran the same calculations by comparing each control replicate value against the control mean within each sampling point (LRR = ln(control unit/control mean)). To derive compositional responses (for compositional OEV), we calculated the Bray–Curtis dissimilarity (Bray & Curtis, 1957) for each treatment mesocosm from the mean value compared to each of the four control replicates. Again, we did the same for each control replicate as mean dissimilarity to the other replicates to benchmark the variability within the control treatment without disturbances. Once we obtained these standardized time series

based on the log response ratio and community dissimilarity index for each mesocosm (Figures S1–S3), we calculated AUC using the 'pk.calc.auc' function from the PKNCA package (Denney et al., 2015) in R (version 4.0.0; R Core Team, 2020). For functional responses (functional OEV), a log response ratio of zero indicates no deviation from control conditions, thus the AUC is calculated with zero as a benchmark. For compositional responses (compositional OEV), dissimilarity values of 0 and 1 represent, respectively, a total compositional convergence or divergence relative to control conditions, thus AUC is also calculated with 0 as a benchmark (Figure 1d–f).

2.3 | Calculation of individual stability components for pulse and press disturbances

We calculated multiple stability components for pulse disturbances following the analytical framework of Hillebrand et al. (2018), which we extended to also include the measurements of stability for press disturbances (Table 1; Figure 1). We calculated four stability components for each mesocosm that received a pulse disturbance (Table 1). 'Resistance' is the initial response to the pulse, and was calculated as the difference between the disturbed community and the control community at the sampling when the pulse disturbance ceased (i.e. at day 7). 'Resilience' is the rate of recovery from the pulse disturbance, and was measured as the slope of the linear regression of the difference between the disturbed community and the control community after the pulse disturbance ceased (i.e. from sampling days 7 to 28). Linear regression was used due to the recovery trend being linearized based on the log-transformed response variable. 'Temporal stability' over the recovery trend was measured as the log $(x + 1)$ of the inverse of the standard deviation of model residuals of the linear regression described above for resilience. 'Final recovery' is the final measurable response to the disturbance, and was calculated as the difference between the disturbed community and the control community at the end of the experiment (i.e. at day 28).

For the press disturbance, we calculated three stability components (Table 1): rate of deviation over time, temporal stability over the deviation trend and extent of recovery. The rate of deviation over time and temporal stability over the deviation trend for press disturbances were measured in the same way as resilience and temporal stability for pulse disturbances, except that they are calculated from the commencement of the press disturbance (i.e. over the entire experimental period). Extent of recovery was measured for press disturbances in the same way as final recovery for pulse disturbances.

We restricted our analyses of the combined pulse and press disturbance treatment to stability components for pulse disturbances only because of constraints caused by linearizing the potential deviation trend induced by the press disturbance with the additional presence of a pulse disturbance. Including measurements from the combined pulse and press disturbance treatment in our analyses thus enabled us to explore whether the relationships between stability components for pulse disturbances and the OEV metric differed between systems with and without additional stress by press disturbances.

2.4 | Data analyses

We evaluated how OEV integrates multiple stability components for both pulse and press disturbances separately by exploring relationships between OEV and each stability component using Spearman rank correlations. We did this for both functional and compositional counterparts of OEV. We also used Spearman rank correlations to examine the relationships between functional and compositional OEV, and explore the functional consequences of biodiversity change within trophic groups of organisms. Functional stability components were

standardized prior to analysis (Table 1). Because initial functional responses to disturbances (resistance) can be positive or negative, either negative or positive functional resilience values can indicate functional recovery. For example, a positive slope over the recovery trend (i.e. a positive resilience value) indicates recovery only if the resistance value of the same mesocosm was negative, whereas a negative slope (i.e. a negative resilience value) would denote further deviation from control conditions. Consequently, functional resilience values that were positive (slopes >0) were converted to negative if the disturbed function deviated further from the control over the recovery trend and vice versa. Analysed functional resilience values could, therefore, be either positive, indicating ongoing recovery, or negative, indicating further deviation from control conditions, with zero indicating no recovery (Table 1). Similarly, positive resistance and final recovery values were transformed to negative, such that all resistance and final recovery values were integrated in the same negative scale with zero representing maximal stability (Table 1). Unlike functional components, compositional stability components did not require prior standardization because they all integrate within the same scale from 0 to 1 (Table 1).

We tested the applicability of OEV to depict overall functional or compositional vulnerability of each of the organism groups to pulse or press disturbances, both in isolation and combination (Figure 1e–l). We used linear mixed models (LMMs) to test for disturbance effects across all experiments on the functional and compositional OEV of each trophic group. We included trophic group and experimental treatment (nested within community type) as fixed explanatory variables and lake and season (nested within lake) as random components in all models. For each LMM, we square root transformed the response variable (functional and compositional OEV) in order to achieve normality in the distribution of the residuals of the models after exploration with q–q plots. Having square root transformed OEV values also aided in visualizing patterns emerging in the correlation plots given the range in the original OEV values. All analyses were run with the 'lmer' function (package: LMERTEST) and figures were created with 'ggplot2' (Wickham, 2016) in R (version 4.0.0; R Core Team, 2020).

3 | RESULTS

3.1 | Integration of multiple stability components into overall functional and compositional vulnerability

Both functional and compositional OEV showed a negative correlation with all stability components except for resilience following our pulse disturbance (Figure 2; Table S2). For functional aspects, we found similarly strong relationships between OEV and resistance, the rate of deviation for press disturbances, temporal stability and final/extent of recovery (Figure 2a; Table S2, $p < 0.001$ in all cases, $-0.829 \geq \text{rho} \geq -0.542$). For compositional aspects, correlations between OEV and both resistance and final/extent of recovery were similarly strong as for functional aspects (Figure 2; Table S2, $p < 0.001$ in both cases, $-0.885 \geq \text{rho} \geq -0.742$). Compositional OEV also correlated significantly with the compositional rate of deviation

for press disturbances (Figure 2; Table S2, $p = 0.004$, rho = −0.265) and temporal stability (Figure 2; Table S2, −0.438 ≥ rho ≥ −0.279).

3.2 | Linkages between functional and compositional vulnerability

The correlation between functional and compositional OEV was significant across all communities and all treatments (Figure 3; Table S3, $p < 0.001$ in all cases, 0.709 ≥ rho ≥ 0.530). We found, however, that high compositional OEV could be associated with either high or low functional OEV, whereas low compositional OEV was associated only with low values of functional OEV (Figure 3). Correlations between functional and compositional aspects of OEV also varied among the biological communities under scrutiny, with significant positive correlations for all perturbed treatments in zooplankton communities (Figure 3; Table S3, $p < 0.001$ in all cases, 0.825 ≥ rho ≥ 0.503) compared to phytoplankton and bacterial communities (Figure 3; Table S3, almost no significant correlations).

3.3 | Overall functional and compositional vulnerability to pulse and press disturbances

Though OEV revealed a strong overall vulnerability for each of zoo-, phyto- and bacterioplankton communities in response to our experimental perturbations across all sites and seasons, we found differences in responses among the three trophic groups we examined

(Table 2). Zooplankton displayed the strongest functional vulnerability across all disturbance types (pulse and press) followed by the phyto- and bacterioplankton (Figure 4; Table 2, $p ≤ 0.001$, larger negative estimate in Bact vs. Zoop than Phyto vs. Zoop).

Functional OEV to the pulse perturbation was greatest in the zooplankton, followed by the phytoplankton (Figure 4; Table 2, larger significant difference between the pulse treatment and control in zooplankton compared to phytoplankton), whereas the pulse perturbation had no effect on the functional OEV of the bacterioplankton (Figure 4; Table 2). For compositional OEV, zooplankton composition was most vulnerable, followed by that of bacterio- and phytoplankton (Figure 4; Table 2, larger significant difference between pulse treatment and control in zooplankton compared to bacteria and then phytoplankton).

The phytoplankton were functionally vulnerable to the press perturbation across all sites and seasons (Figure 4; Table 2, significant difference between the press treatment and control), whereas there were no significant effects on the functional vulnerability of the zoo- or bacterioplankton (Table 2). Moreover, our press perturbation had no effect on the compositional OEV of any of our focal trophic groups (Table 2).

Even though we did not see significant effects of our press perturbation on the functional vulnerability of zooplankton, the effects of the combined pulse and press perturbations were larger than those of the pulse perturbation in isolation (Figure 4; Table 2, larger significant difference between the combined pulse and press treatment and control compared to the significant difference between pulse treatment and control). We also found significant effects of the
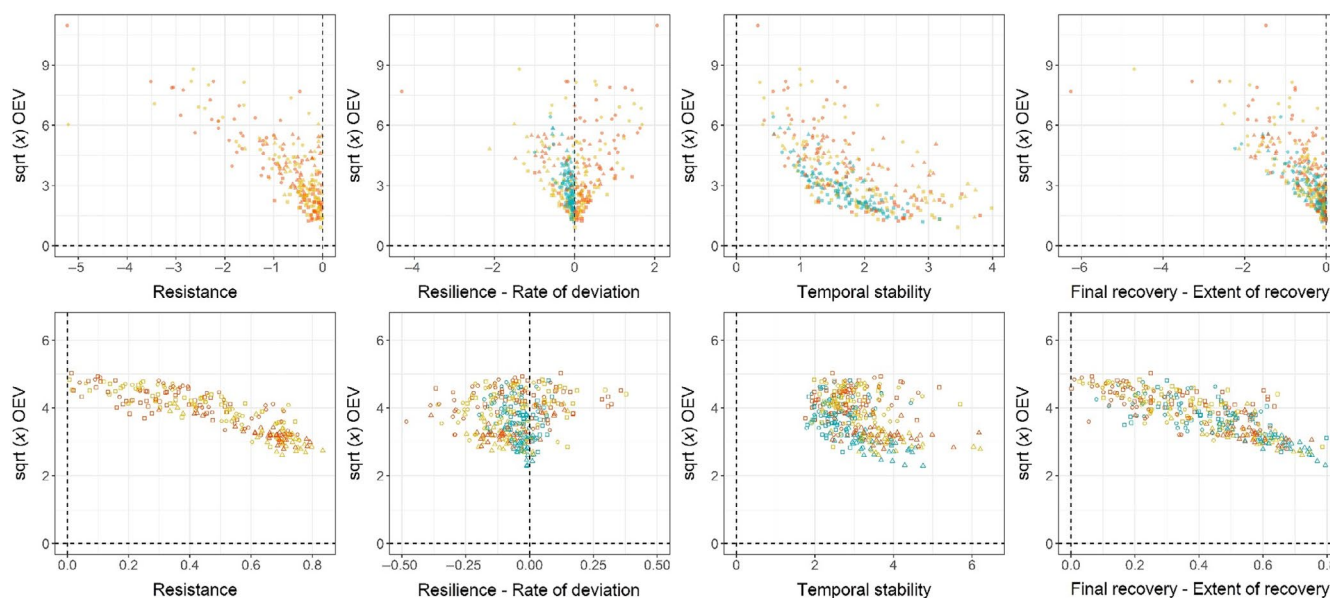

FIGURE 2 Bivariate relationships between each measured stability component and overall ecological vulnerability (OEV) to pulse and press perturbations for (upper panel) functional and (lower panel) compositional stability components. Each sample unit is a mesocosm replicate from one of the 10 experiments from the pulse (yellow), press (blue) and pulse and press (red) perturbation treatments. Circles = zooplankton, triangles = phytoplankton and squares = bacteria. For simplicity, we combined in the same plot data for resilience (RSL) for pulse perturbations and the rate of deviation (RD) for press perturbations (as both stability components represent rates of change over time), temporal stability over the recovery trend for pulse perturbations (TS$_{rt}$) and temporal stability over the deviation trend for press perturbations (TS$_{dt}$), and final recovery for pulse perturbations and extent of recovery for press perturbations
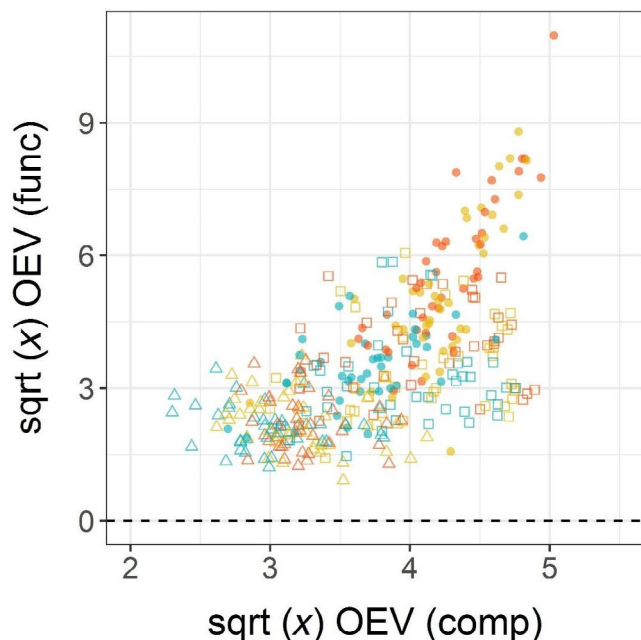
FIGURE 3 Relationship between the compositional and functional aspect of overall ecological vulnerability (OEV). Each sample unit is a mesocosm replicate from one of the 10 experiments from the pulse (yellow), press (blue) and combined pulse and press (red) perturbation treatments. Filled circles = zooplankton, open triangles = phytoplankton and open squares = bacteria. Please see Figure S8 for visualization of patterns separated for the three communities

combined pulse and press perturbation on the functional vulnerability of phytoplankton, which matched well the addition of the effects of the pulse and press perturbations in isolation (Figure 4; Table 2). For compositional aspects, we also observed larger compositional vulnerability to the combined perturbations compared to the pulse and press perturbations in isolation (Figure 4; Table 2), despite no significant effects of shading in isolation in any community (Table 2).

4 | DISCUSSION

Our study reveals several strengths of OEV as a potential management tool for ecological risk assessment. First, a critical advantage of using the OEV metric is its strong connection with a diverse range of stability components for both pulse and press disturbances. While some studies have employed an area under the curve approach to depict certain properties of stability (Todman et al., 2016; Zhang et al., 2010), none have actually evaluated how a metric such as OEV integrates across multiple stability components for both functional and compositional aspects. Functional and compositional OEV correlated negatively with their respective functional and compositional aspects of resistance, temporal stability and final/extent of recovery for pulse and/or press disturbances, but less so with resilience after a pulse. The observed inverse correlations are consistent with our predictions, and indicate that OEV acts as a robust and integrative

metric of multiple dimensions of stability. Indeed, no other stability metric showed such strong relationships with other stability components (Figures S4 and S5). That OEV integrates across multiple dimensions of stability means that if either resistance, temporal stability or final/extent of recovery is low, the OEV of a system to a disturbance is consequently high and vice versa. While each stability component is unique in the type of information delivered (Kéfi et al., 2019) and no single stability metric can reveal the entire complexity of ecological stability (Hillebrand et al., 2018), these findings reveal that OEV integrates multiple dimensions of stability robustly and can thereby offer managers a straightforward and conceptually simple framework for assessing ecological risk. Though we test the applicability of our vulnerability framework in freshwater systems, OEV should also be a good candidate for other systems. However, its potential applicability across ecosystem realms needs to be investigated given that different ecological traits of organisms, as well as changing environmental contexts or disturbance types, have been shown to alter the effective dimensionality of ecological stability (Donohue et al., 2013, 2016; Kéfi et al., 2019; Polazzo & Rico, 2021; Radchuk et al., 2019).

Though we did not find similarly strong correlations between the functional and compositional OEV with functional or compositional resilience from pulse disturbances compared to other stability metrics (Figure 2; Table S2), resilience and OEV were nonetheless interlinked. Communities with high resistance tend to show resilience values around 0, mainly because a community that is barely disturbed initially has little to recover from (Figures S4 and S5). Hence, stratifying the correlative analyses between OEV and resilience with ranks based on resistance values aids in removing the contribution of resistance to the apparent relationship between OEV and resilience. On doing this, we found that communities that initially responded in similar ways to the disturbances (i.e. within the same ranks based on initial stability values) showed overall lower functional and compositional OEV with higher resilience (Figure S6).

Our results also show a strong positive relationship between overall compositional and functional vulnerability across all trophic groups. That is, the higher the compositional vulnerability, the greater the functional consequences (Figure 3; Table S3). Thus, OEV emerges as an effective tool to explore the functional consequences of biodiversity change. The trophic group comprising the fewest taxa (i.e. the zooplankton) drove the positive relationship between compositional and functional vulnerability (Figure 3; Table S3). In other words, in more diverse trophic groups (phyto- and bacterioplankton; Figure S7), functional stability (i.e. low functional vulnerability) can be achieved with or without compositional stability (Figure 3). Although further evidence is needed to confirm the mechanism underpinning these patterns, it is likely that this was caused because more diverse communities generally hold higher functional redundancy, and thereby larger potential to experience compensatory dynamics among different taxa that stabilize biomass production at the community level (Allan et al., 2011; Gonzalez & Loreau, 2009).

The utility of the OEV metric is exemplified by results from our modularized experiment. Urrutia-Cordero, Langenheder,

TABLE 2 Results from LMM analyses evaluating the response of zoo-, phyto- and bacterioplankton communities to pulse and press disturbances captured by functional and compositional OEV across all experiments. The degree of variation explained by the fixed effects is indicated by m-R^2, whereas c-R^2 stands for the total variation explained including both fixed and random effects. Black-bolded p-values and black-bolded *p*-values in brackets denote significant effects of the explanatory variables at $\alpha = 0.05$ and $\alpha = 0.1$ respectively. Zoop = Zooplankton, Phyto = Phytoplankton and Bact = Bacterioplankton

Response	m-R^2	c-R^2	Comparison	Expl.	Estimate difference	SE	df	F	p
Function	0.551	0.592	Community versus community	Phyto versus Zoop	−0.714	0.220	464	−3.243	**0.001**
				Bact versus Zoop	−1.456	0.220	464	−6.613	**<0.001**
			Pulse effect (benchmark: control)	Zoop	1.863	0.220	464	8.465	**<0.001**
				Phyto	0.781	0.220	464	3.547	**<0.001**
				Bact	0.346	0.220	464	1.573	0.116
			Press effect (benchmark: control)	Zoop	0.188	0.220	464	0.854	0.394
				Phyto	0.567	0.220	464	2.574	**0.010**
				Bact	0.278	0.220	464	1.262	0.208
			Pulse & press effect (benchmark: control)	Zoop	2.312	0.220	464	10.505	**<0.001**
				Phyto	1.326	0.220	464	6.024	**<0.001**
				Bact	0.344	0.220	464	1.564	0.118
Composition	0.492	0.659	Community versus community	Phyto versus Zoop	0.212	0.083	459	2.536	**0.011**
				Bact versus Zoop	−0.708	0.083	459	−8.465	**<0.001**
			Pulse effect (benchmark: control)	Zoop	0.523	0.083	459	6.244	**<0.001**
				Phyto	0.145	0.083	459	1.738	**(0.083)**
				Bact	0.221	0.083	459	2.642	**0.008**
			Press effect (benchmark: control)	Zoop	−0.021	0.083	459	−0.252	0.801
				Phyto	0.057	0.083	459	0.691	0.489
				Bact	0.008	0.083	459	0.103	0.918
			Pulse & press effect (benchmark: control)	Zoop	0.563	0.083	459	6.729	**<0.001**
				Phyto	0.169	0.083	459	2.022	**0.044**
				Bact	0.248	0.083	459	2.966	**0.003**

et al. (2021) describe the outcome of the experiments in the form of the direct measured response variables for each taxonomic group (biomass/abundance and community turnover) and presents statistical analyses across sites and seasons. Urrutia-Cordero, Langenheder, et al. (2021) also extend on discussions on the observed response differences across disturbance types and communities. The modularized multitrophic structure of this experiment thus represents an ideal test case to illustrate how functional and compositional OEV could be applied to experiments if we want to compare different types of disturbances, different local ecosystems and different trophic groups. Specifically, we found strong differences in the overall vulnerability of zoo-, phyto- and bacterioplankton to both pulse and press disturbances across sites and seasons, with zooplankton communities being the most vulnerable community to the pulse disturbance and phytoplankton communities to the press disturbance. Although each analytical approach is different in the type of information provided, we show that an important advantage of using functional and compositional OEV as response variables (as shown in this study) is the possibility to also investigate the linkage between its functional and compositional counterparts, as well as with other stability metrics in a relatively straightforward way.

It is important to stress that OEV does not give the direction of the response, though this information can also be obtained. For functional OEV, the difference between the area with positive sign and the area with negative sign from the LRR time series (Figures S1–S3) would be indicative of the direction of the response across the entire experimental period. For compositional OEV, one can take the initial dissimilarity values as a benchmark and do the same procedure by taking the area above and below that benchmark. Furthermore, our analytical framework should work not only for experimental settings, but also for ecological risk assessments based on natural observations when it is possible to obtain baselines derived from pre-disturbance conditions (Wright et al., 2015) or from comparable undisturbed whole ecosystems (Wilkinson et al., 2018). Our findings should, therefore, provoke discussions on which stability metrics should be measured and prioritized for ecological risk assessments. Understanding the connection of other known metrics with OEV can also help us reveal under which circumstances each of these other metrics best represent the OEV of a system. Generating such understanding is important because ecological risk assessments might need to rely on information provided by a stability metric that is simpler to measure over a time
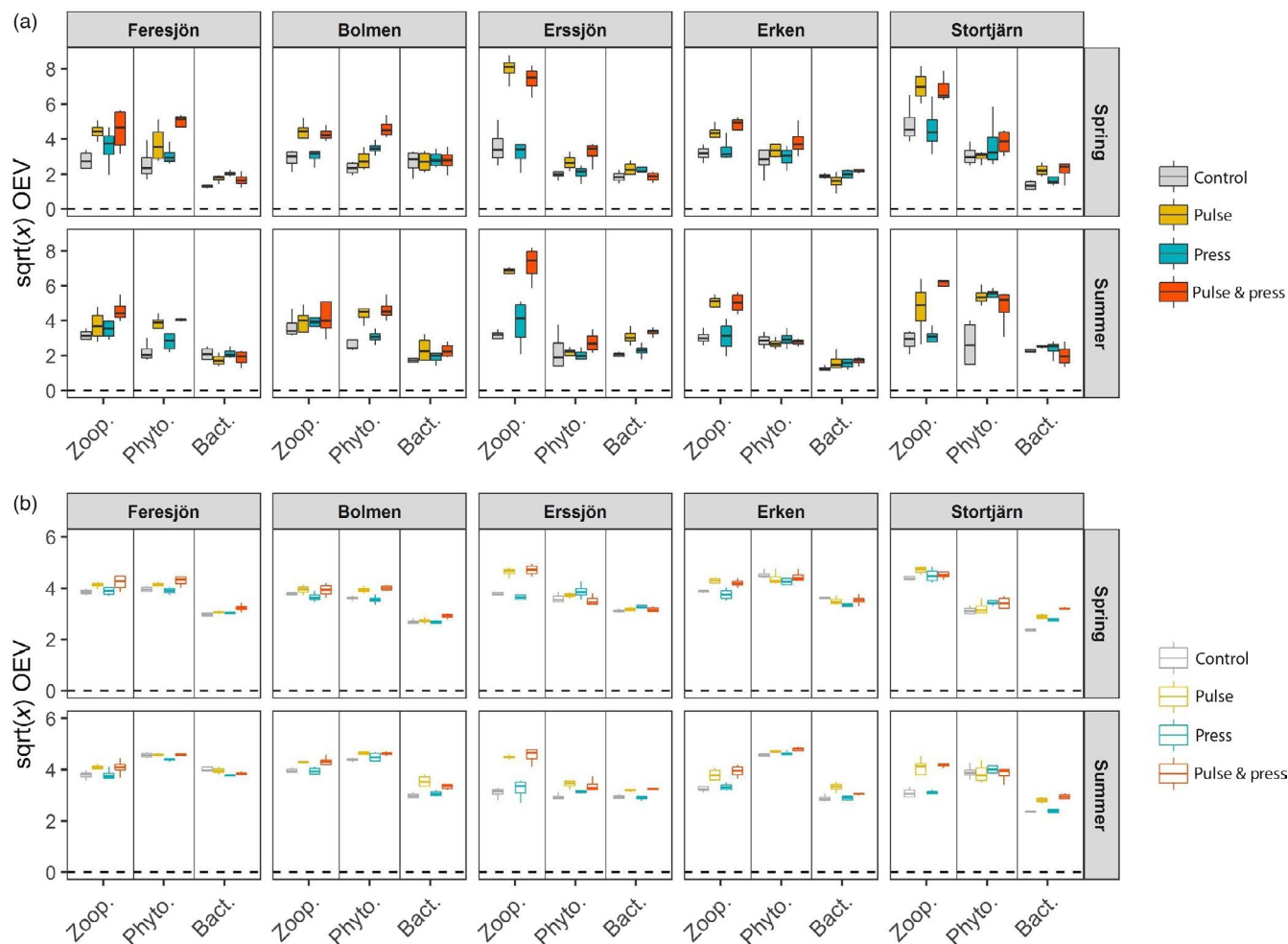
FIGURE 4 Overall ecological vulnerability (OEV) to pulse and press perturbations in zoop-, phyto- and bacterioplankton communities for all experiments. Boxplots show the minimum, first quartile, median, third quartile and maximum total impact values for functional (a) and compositional (b) responses. OEV values are sqrt(x) transformed in order to aid visual comparisons across trophic levels and experiments

series (e.g. resistance or final recovery), and thus a priori knowledge of its relation with OEV can potentially provide complementary information of OEV to disturbances. Therefore, our results suggest that OEV may comprise a useful and complementary addition to the ecological information provided by other metrics, including early warning indicators, which can detect non-existent or miss existing nonlinear ecosystem transitions (Burthe et al., 2016). Refining our ability to deal with the uncertainty of ecological vulnerability and risk is badly needed for sound management.

AUTHORS' CONTRIBUTIONS

H.H., S.L., M.S., P.E. and D.G.A. had the original idea of implementing the SITES AquaNet infrastructure; P.U.C., S.L., H.H., M.S., S.B. and P.E. contributed to network-level coordination of experimental designs, sample collection, method standardization and/or staff management; S.L., P.U.C., H.L., L.-A.H., E.K., L.P. and M.L. contributed to site-level coordination of experimental performance, data collection and/or staff management; P.U.C., H.H., I.D., S.L. and M.S. framed the original idea and data analyses of this study; P.U.C. conducted the data analyses with input from H.H., I.D., S.L., S.B. and M.S.; P.U.C. wrote the paper with contributions from all authors. All authors read and approved the final manuscript.

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REFERENCES

Allan, E., Weisser, W., Weigelt, A., Roscher, C., Fischer, M., & Hillebrand, H. (2011). More diverse plant communities have higher functioning over time due to turnover in complementary dominant species. *Proceedings of the National Academy of Sciences of the United States of America*, 108, 17034–17039. https://doi.org/10.1073/pnas.1104015108

Bray, J. R., & Curtis, J. T. (1957). An ordination of upland forest communities of southern Wisconsin. *Ecological Monographs*, 27, 325–349.

Brönmark, C., Hulthén, K., Nilsson, P. A., Skov, C., Hansson, L.-A., Brodersen, J., & Chapman, B. B. (2014). There and back again: Migration in freshwater fishes. *Canadian Journal of Zoology*, 92, 467–479. https://doi.org/10.1139/cjz-2012-0277

Burthe, S. J., Henrys, P. A., Mackay, E. B., Spears, B. M., Campbell, R., Carvalho, L., Dudley, B., Gunn, I. D. M., Johns, D. G., Maberly, S. C., May, L., Newell, M. A., Wanless, S., Winfield, I. J., Thackeray, S. J., & Daunt, F. (2016). Do early warning indicators consistently predict nonlinear change in long-term ecological data? *Journal of Applied Ecology*, 53, 666–676. https://doi.org/10.1111/1365-2664.12519

Clark, A. T., Arnoldi, J.-F., Zelnik, Y. R., Barabas, G., Hodapp, D., Karakoç, C., König, S., Radchuk, V., Donohue, I., Huth, A., Jacquet, C., Mazancourt, C., Mentges, A., Nothaaß, D., Shoemaker, L. G., Taubert, F., Wiegand, T., Wang, S., Chase, J. M., ... Harpole, S. (2021). General statistical scaling laws for stability in ecological systems. *Ecology Letters*, 24, 1474–1486. https://doi.org/10.1111/ele.13760

Cleland, E. E. (2011). Biodiversity and ecosystem stability. *Nature Education Knowledge*, 3, 14.

Denney, W., Duvvuri, S., & Buckeridge, C. (2015). Simple, automatic noncompartmental analysis: The PKNCA R package. *Journal of Pharmacokinetics and Pharmacodynamics*, 42, 11–107.

Donohue, I., Hillebrand, H., Montoya, J. M., Petchey, O. L., Pimm, S. L., Fowler, M. S., Healy, K., Jackson, A. L., Lurgi, M., McClean, D., O'Connor, N. E., O'Gorman, E. J., & Yang, Q. (2016). Navigating the complexity of ecological stability. *Ecology Letters*, 19, 1172–1185. https://doi.org/10.1111/ele.12648

Donohue, I., Petchey, O. L., Montoya, J. M., Jackson, A. L., McNally, L., Viana, M., Healy, K., Lurgi, M., O'Connor, N. E., & Emmerson, M. C. (2013). On the dimensionality of ecological stability. *Ecology Letters*, 16, 421–429. https://doi.org/10.1111/ele.12086

Gonzalez, A., & Loreau, M. (2009). The causes and consequences of compensatory dynamics in ecological communities. *Annual Reviews in Ecology, Evolution and Systematics*, 40, 393–414. https://doi.org/10.1146/annurev.ecolsys.39.110707.173349

Güelzow, N., Muijsers, F., Ptacnik, R., & Hillebrand, H. (2017). Functional and structural stability are linked in phytoplankton metacommunities of different connectivity. *Ecography*, 40, 719–732. https://doi.org/10.1111/ecog.02458

Hansson, L.-A., Nicolle, A., Granéli, W., Hallgren, P., Kritzberg, E., Persson, A., Björk, J., Nilsson, P. A., & Brönmark, C. (2013). Food chain length alters community response to global change in aquatic systems. *Nature Climate Change*, 3, 228–233.

Hillebrand, H., & Kunze, C. (2020). Meta-analysis on pulse disturbances reveals differences in functional and compositional recovery across ecosystems. *Ecology Letters*, 23, 575–585. https://doi.org/10.1111/ele.13457

Hillebrand, H., Langenheder, S., Lebret, K., Lindström, E., Östman, Ö., & Striebel, M. (2018). Decomposing multiple dimensions of stability in global change experiments. *Ecology Letters*, 21, 21–30. https://doi.org/10.1111/ele.12867

IPBES. (2019). *Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services*. IPBES Secretariat.

IPCC. (2013). *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, Cambridge University Press.

Ives, A. R., & Carpenter, S. R. (2007). Stability and diversity of ecosystems. *Science*, 317, 58–62. https://doi.org/10.1126/science.1133258

Jentsch, A., Kreyling, J., & Beierkuhnlein, C. (2007). A new generation of climate-change experiments: Events, not trends. *Frontiers in Ecology and the Environment*, 5, 365–374.

Jeppesen, E., Meerhoff, M., Davidson, T. A., Trolle, D., Søndergaard, M., Lauridsen, T. L., Beklioglu, M., Brucet, S., Volta, P., González-Bergonzoni, I., & Nielsen, A. (2014). Climate change impacts on lakes: An integrated ecological perspective based on a multi-faceted approach, with special focus on shallow lakes. *Journal of Limnology*, 73, 88–111. https://doi.org/10.4081/jlimnol.2014.844

Karlsson, J., Bystrom, P., Ask, J., Ask, P., Persson, L., & Jansson, M. (2009). Light limitation of nutrient-poor lake eco-systems. *Nature*, 460, 506–509.

Kéfi, S., Domínguez-García, V., Donohue, I., Fontaine, C., Thébault, E., & Dakos, V. (2019). Advancing our understanding of ecological stability. *Ecology Letters*, 22, 1349–1356. https://doi.org/10.1111/ele.13340

Kritzberg, E. S., Hasselquist, E. M., Škerlep, M., Löfgren, S., Olsson, O., Stadmark, J., Valinia, S., Hansson, L.-A., & Laudon, H. (2019). Browning of freshwaters: Consequences to ecosystem services, underlying drivers, and potential mitigation measures. *Ambio*, 49, 375–390. https://doi.org/10.1007/s13280-019-01227-5

Lawson, C. R., Vindenes, Y., Bailey, L., & van de Pol, M. (2015). Environmental variation and population responses to global change. *Ecology Letters*, 18, 724–736. https://doi.org/10.1111/ele.12437

Levin, S. A. (1992). The problem of pattern and scale in ecology: The Robert H. MacArthur award lecture. *Ecology*, 73, 1943–1967.

Millennium Ecosystem Assessment. (2005). *Ecosystems and human well-being: Synthesis*. Island Press.

Pimm, S. L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321–326. https://doi.org/10.1038/307321a0

Pimm, S. L. (1991). *The balance of nature? Ecological issues in the conservation of species and communities*. University of Chicago Press.

Pimm, S. L., Donohue, I., Montoya, J. M., & Loreau, M. (2019). Measuring resilience is essential to understand it. *Nature Sustainability*, 2, 895–897. https://doi.org/10.1038/s41893-019-0399-7

Polazzo, F., & Rico, A. (2021). Effects of multiple stressors on the dimensionality of ecological stability. *Ecology Letters*, 24, 1594–1606. https://doi.org/10.1111/ele.13770

R Core Team. (2020). *R: A language and environment for statistical comput-ing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Radchuk, V., Laender, F. D., Cabral, J. S., Boulangeat, I., Crawford, M., Bohn, F., Raedt, J. D., Scherer, C., Svenning, J.-C., Thonicke, K., Schurr, F. M., Grimm, V., & Kramer-Schadt, S. (2019). The dimen-sionality of stability depends on disturbance type. *Ecology Letters*, *22*, 674–684. https://doi.org/10.1111/ele.13226

Stockwell, J. D., Doubek, J. P., Adrian, R., Anneville, O., Carey, C. C., Carvalho, L., De Senerpont Domis, L. N., Dur, G., Frassl, M. A., Grossart, H.-P., Ibelings, B. W., Lajeunesse, M. J., Lewandowska, A. M., Llames, M. E., Matsuzaki, S.-I., Nodine, E. R., Nõges, P., Patil, V. P., Pomati, F., ... Wilson, H. L. (2020). Storm impacts on phyto-plankton community dynamics in lakes. *Global Change Biology*, *26*, 2756–2784. https://doi.org/10.1111/gcb.15033

Todman, L. C., Fraser, F. C., Corstanje, R., Deeks, L. K., Harris, J. A., Pawlett, M., Ritz, K., & Whitmore, A. P. (2016). Defining and quan-tifying the resilience of responses to disturbance: A conceptual and modelling approach from soil science. *Scientific Reports*, *6*, 28426.

Urrutia-Cordero, P., Langenheder, S., Striebel, M., Eklöv, P., Angeler, D. G., Bertilsson, S., Csitári, B., Hansson, L.-A., Kelpsiene, E., Laudon, H., Lundgren, M., Osman, O. A., Parkefelt, L., & Hillebrand, H. (2021). Functionally reversible impacts of disturbances linked to spatial and tem-poral dependencies. *Ecology*, e03283. https://doi.org/10.1002/ecy.3283

Urrutia-Cordero, P., Langvall, O., Blomkvist, P., Angeler, D. G., Bertilsson, S., Colom Montero, W., Eklöv, P., Aagaard Jakobsen, N., Klemedtsson, L., Laudon, H., Liljebladh, B., Lundgren, M., Parkefelt, L., Kelpsiene, E., Pierson, D., Rankinen, J., Striebel, M., Tranvik, L. J., Weslien, P., ... Langenheder, S. (2021). SITES AquaNet: An open infrastructure for mesocosm experiments with high frequency sensor monitoring across lakes. *Limnology and Oceanography Methods*, *19*, 385–400.

Urrutia-Cordero, P., Zhang, H., Chaguaceda, F., Geng, H., & Hansson, L.-A. (2020). Climate warming and heat waves alter harmful cyano-bacterial blooms along the benthic-pelagic interface. *Ecology*, *101*, e03025. https://doi.org/10.1002/ecy.3025

Weyhenmeyer, G. A., Müller, R. A., Norman, M., & Tranvik, L. J. (2016). Sensitivity of freshwaters to browning in response to future climate change. *Climatic Change*, *134*, 225–239. https://doi.org/10.1007/s10584-015-1514-z

White, L., O'Connor, N. E., Yang, Q., Emmerson, M. C., & Donohue, I. (2020). Individual species provide multifaceted contributions to the stability of ecosystems. *Nature Ecology & Evolution*, *4*, 1594–1601. https://doi.org/10.1038/s41559-020-01315-w

Wickham, H. (2016). *ggplot2: Elegant graphics for data analysis*. Springer-Verlag.

Wilkinson, G. M., Carpenter, S. R., Cole, J. J., Pace, M. L., Batt, D. B., Buelo, C. D., & Kurtzwei, J. T. (2018). Early warning signals precede cya-nobacterial blooms in multiple whole-lake experiments. *Ecological Monographs*, *88*, 188–203. https://doi.org/10.1002/ecm.1286

Wright, A. J., Ebeling, A., de Kroon, H., Roscher, C., Weigelt, A., Buchmann, N., Buchmann, T., Fischer, C., Hacker, N., Hildebrandt, A., Leimer, S., Mommer, L., Oelmann, Y., Scheu, S., Steinauer, K., Strecker, T., Weisser, W., Wilcke, W., & Eisenhauer, N. (2015). Flooding distur-bances increase resource availability and productivity but reduce stability in diverse plant communities. *Nature Communications*, *6*, 6092. https://doi.org/10.1038/ncomms7092

Yang, Q., Fowler, M. S., Jackson, A. L., & Donohue, I. (2019). The predict-ability of ecological stability in a noisy world. *Nature Ecology and Evolution*, *3*, 251–259. https://doi.org/10.1038/s41559-018-0794-x

Zhang, B., Dengac, H., Wang, H., Yin, R., Hallett, P. D., Griffithsd, B. S., & Daniell, T. J. (2010). Does microbial habitat or community structure drive the functional stability of microbes to stresses following re-vegetation of a severely degraded soil? *Soil Biology and Biochemistry*, *42*(5), 850–859. https://doi.org/10.1016/j.soilbio.2010.02.004

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