CONCEPTS & SYNTHESIS

Partitioning species contributions to ecological stability in disturbed communities

Charlotte Kunze[1] | Dominik Bahlburg[2,3] | Pablo Urrutia-Cordero[4,5] |
Maren Striebel[1] | Egle Kelpsiene[6] | Silke Langenheder[7] |
Ian Donohue[8] | Helmut Hillebrand[1,9,10]

[1]Institute for Chemistry and Biology of the Marine Environment (ICBM), School of Mathematics and Science, Carl von Ossietzky Universität Oldenburg, Oldenburg, Germany

[2]Forest Biometrics and Forest Systems Analysis, Technical University Dresden, Tharandt, Germany

[3]Department of Ecological Modelling, Helmholtz Centre for Environmental Research Leipzig/Halle, Leipzig, Germany

[4]Department of Biology/Aquatic Ecology, Lund University, Lund, Sweden

[5]IMDEA Water Institute, Madrid, Spain

[6]Department of Biochemistry and Structural Biology, Lund University, Lund, Sweden

[7]Limnology, Department of Ecology and Genetics, Uppsala University, Uppsala, Sweden

[8]School of Natural Sciences, Trinity College Dublin, Dublin, Ireland

[9]Helmholtz-Institute for Functional Marine Biodiversity at the University of Oldenburg (HIFMB), Oldenburg, Germany

[10]Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research (AWI), Bremerhaven, Germany

Correspondence
Charlotte Kunze
Email: charlotte.kunze@uni-oldenburg.de

Abstract

Ecosystems worldwide are experiencing a range of natural and anthropogenic disturbances, many of which are intensifying as global change accelerates. Ecological responses to those disturbances are determined by both the vulnerabilities of species and their interspecific interactions. Understanding how individual species contribute to the (in-)stability of an aggregated community property, or function, is fundamental to ecological management and conservation. Here, we present a framework to identify species contributions to stability based on their absolute and relative responses to disturbances. Using simulations, we show that these two dimensions enable identification of (de-)stabilizing species and reveal that competitive dominance determines the magnitude of both absolute and relative contributions to stability. Applying our framework to empirical data from a multi-site mesocosm experiment showed that species contributions varied among treatments, sites, and seasons. Despite this dependency on both biotic and abiotic contexts, species contributions were generally constrained by their relative dominance in undisturbed conditions. Rare species contributed positively to stability, while dominant species contributed negatively, indicating compensatory dynamics. Our framework offers an

important step toward a more mechanistic understanding of ecological stability based on species performance.

INTRODUCTION

Ecological stability is the overarching concept capturing an ecosystem's ability to absorb and recover from change, integrating a family of metrics of resistance, resilience, recovery, and spatiotemporal invariance (Donohue et al., 2013; Hillebrand et al., 2018; Kéfi et al., 2019; Urrutia-Cordero, Langenheder, Striebel, Angeler, et al., 2022). Stability can be measured at the level of aggregated functional properties of the community (such as biomass or productivity) on the one hand (i.e., functional stability) and the stability of the community composition on the other (Grimm & Wissel, 1997; Mulder et al., 2004). In diverse systems, overall functional stability and biodiversity tend to be positively correlated, as species-rich communities are often characterized by functional redundancy, that is, the presence of multiple species within a system that perform similar ecological roles or functions, enabling them to effectively mitigate the impacts of disturbances (Urrutia-Cordero, Langenheder, Striebel, Angeler, et al., 2022; Yachi & Loreau, 1999). By contrast, population-level stability might actually decrease with biodiversity (Tilman, 1996). When quantifying biomass change in natural grassland communities, Ladouceur et al. (2022) demonstrated that the effect of compositional change on total aboveground biomass depends on the extent and impact of species entering, leaving, or remaining in communities. As indicated in microbial soil systems, community variability can potentially be predicted from the responses of species to disturbances and their contributions to ecosystem functioning (Orr et al., 2023). Overall, this indicates that variability at the species level and variability at the community level are interlinked (Tilman, 1999; Yachi & Loreau, 1999).

Few studies have measured the influence of individual species on ecosystem stability (see Box 1 for an overview of recent advances). To date, these have involved the assessment of the impact of time-varying species interspecific interactions (and so their correlations) on community sensitivity in deterministic systems (Medeiros & Saavedra, 2023), the assessment of the ecological persistence (i.e., probability of extinction) of individual species and how this relates to feasibility domains (long-term dynamics at the community level) (Allen-Perkins et al., 2023), and the systematic exclusion of species from an experimental community and measuring their contribution as the inverse of the relative consequences of disturbances (White et al., 2020). While excluding species from the community enables determination of both the direct and indirect effects of species absence on the rest of the interaction network, we still lack the ability to measure how much species presence affects the observed community stability through their associated traits and vulnerabilities, determining the direct disturbance effect on species, in addition to their interactions with other species.

Under uneven species abundance distributions, community stability depends greatly on the performance of the dominant species (Grman et al., 2010; Hillebrand et al., 2008; Sasaki & Lauenroth, 2011; Thébault & Loreau, 2006). For example, dominant species, and not diversity, have been found to regulate the temporal stability of total biomass in experimental plant communities (Sasaki & Lauenroth, 2011). Similarly, Grman et al. (2010) showed that stabilizing mechanisms related to the performance of the dominant species were more important than species diversity in a long-term disturbance and fertilization experiment. By contrast, Arnoldi et al. (2019) found that the stability of the community depends not only on the relative abundance of disturbed species (i.e., dominant vs. rare) but also, more generally, on the disturbance type. If the dominant species is resistant to the disturbance, a higher community stability can be expected in less even communities as only rare species suffer (Hillebrand et al., 2008). However, when the dominant species is sensitive to the disturbance, higher dominance is destabilizing and the overall community stability relies instead on compensatory dynamics and thus changes in species interactions and community composition (Grman et al., 2010; Gross et al., 2014; Hillebrand et al., 2008; Sasaki & Lauenroth, 2011).

Aside from individual species performances, stability can also emerge as a community property, that is, from bilateral interactions or through network properties (McCann, 2000). Abundant literature shows that the architecture of a network can affect its stability, with trophic networks generally being stabilized if many weak and compartment interactions prevail, whereas

BOX 1   Overview table of recent studies that measured the influence of individual species on ecosystem stability

Summary	Stability metrics	Applications/limitations
Allen-Perkins et al. (2023)		
Introduction of new metrics that provide insights into the vulnerability of species to extinction (persistence of individual species) within ecological communities and allow to predict and explore short-term ecological dynamics. The framework was tested to predict short-term changes in species' relative abundances during 7 years in a Mediterranean grassland.	Set of metrics that are based on the shape of the feasibility domain (FD): species' probability of exclusion, species exclusion ratio at the community level, and the asymmetry index. The FD describes the necessary conditions for maintaining positive long-term abundance for all species and requires information on the structure of species interactions and growth rates in ecological communities.	Intra- and interspecific pairwise species interactions are estimated by relating individual reproductive success to the number of potentially competing individuals within communities. The concept is yet limited to systems with similar population dynamics and responses to external disturbances as the ones tested, for example, annual plant communities, coral reef fishes, tropical trees, and plant–pollinator mutualistic systems.
Arnoldi et al. (2019)		
Study relating species abundance to species variability contribution in three different disturbance regimes: the immigrational type, the environmental type, and the demographic type. The disturbance regime determines species-specific contributions to the variability distribution, in a way that allows both common and rare species to drive community-wide variability patterns and thus lead to opposite diversity–stability patterns.	Stability is defined as the inherent ability of a dynamical system to tolerate disturbances. It is measured as community-wide variability constructed from the variance of species time series. Species contribution to variability is assessed as the variability that is induced by disturbing a single species.	Restricted to systems near equilibrium.
Medeiros and Saavedra (2023)		
Theoretical framework for assessing the impact of fluctuating interspecific effects over time on the sensitivity of a community to disturbances. They use synthetic time series generated from population dynamics models and experimental predator–prey time series to show how to identify community states where species interactions (and so their correlations) have either a weak or strong impact on community sensitivity, for example, based on the abundance of the prey.	Community sensitivity (measured as the volume expansion rate of disturbed abundances) is decomposed into contributions of individual species and species correlations by converting the time-varying Jacobian matrix into a time-varying covariance matrix.	The concept is limited to deterministic dynamics (e.g., fixed points, transient dynamics, limit cycles, and chaotic dynamics) and does not address cases where communities undergo non-equilibrium dynamics.
Medeiros et al. (2022)		
Framework ranking the species of a community according to their sensitivity to small pulse disturbances under non-equilibrium dynamics. Interestingly, the most sensitive species were not always the ones with the most rapidly changing or lowest abundance.	Sensitivity rankings are inferred from the time-varying Jacobian matrix (1) as eigenvector ranking and (2) by computing an expected sensitivity value.	Sensitivity ranking requires the Jacobian matrix of the community, an initial covariance matrix of the disturbances in time, and the timescale of the disturbances. This information is difficult to obtain for natural communities and is estimated here from time series of species abundance data.

Summary	Stability metrics	Applications/limitations
White et al. (2020)		
Experimental study systematically excluding grazer species from an intertidal community to measure their contribution to ecological stability. Individual species have the capacity to simultaneously stabilize and destabilize ecosystems along different dimensions of stability. Their contribution differs between compositional and functional (biomass) stability.	Species contribution to stability is assessed as the inverse of the relative consequences of disturbances in the absence of a focal species. They assessed different components of ecological stability using metrics of resistance, resilience, recovery time, reactivity, and (spatial and temporal) variability of the function and composition, respectively.	The approach measures species' "gross" contribution as it determines both the direct and indirect effects of species absence on the rest of the interaction network.

mutualistic network stability profits from highly connected, nested structures (Gross et al., 2009; McCann et al., 1998; Thébault & Fontaine, 2010). Another insight from the recurrent and long-standing diversity–stability debate is that even in the absence of interactions between species, community properties will be more stable if more independently fluctuating species are included, which has become known as the insurance or portfolio aspect of stability (Cottingham et al., 2001; Doak et al., 1998; Yachi & Loreau, 1999). The more asynchronously species fluctuate in time, the higher is the stabilizing effect of diversity (Hautier et al., 2014; Loreau & de Mazancourt, 2013).

In natural systems, the statistical averaging effect—which implies that the variability of a community metric will be lower than the variability of the individual species due to averaging across species (Cottingham et al., 2001; Doak et al., 1998)—co-occurs with compensatory dynamics, where the increase in one species' density offsets the decrease in the density of other species (Gonzalez & Loreau, 2009; Micheli et al., 1999). Such compensatory dynamics often derive from species interactions, for example, in the form of competitive release through the decline of a dominant competitor. Consequently, "emergent" stability dimensions at the community level will be influenced by species identities, as their interaction and tolerance traits (sensu Bauer et al., 2021) will predispose the probability for compensatory dynamics.

The potential influence of individual species, both through their own traits and through their network of interactions, highlights the need for an integrated approach to identify species contributions to stability. The potential of such a decomposition can be seen in the biodiversity–ecosystem functioning literature, where the ability to identify species contributions to community performance has become a major cornerstone of

our understanding of net biodiversity effects (Bannar-Martin et al., 2018; Loreau & Hector, 2001).

Here, we introduce an analytical framework that quantifies species net contributions to functional stability (i.e., the stability of total community biomass) in disturbed communities by discriminating between changes in their biomass and proportion. This way, we can measure their absolute and relative contributions to functional stability, respectively. We use this approach to identify which species stabilize and which species destabilize community properties such as biomass. In what follows, we (1) show that this framework can identify particularly sensitive or tolerant species with known competitive abilities in simulated communities, (2) demonstrate that the method can identify (de-)stabilizing species in natural manipulated communities following experimental pulse and press disturbances and illuminate underlying processes such as compensatory dynamics, and (3) show that emergent patterns are similar in our simulations and empirical data.

METHODS

General framework

We base our framework on species-specific responses in a community exposed to a disturbance, in comparison with their performance in an undisturbed control community. A disturbance is defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resource, substrate availability, or the physical environment" (White & Pickett, 1985). This disturbance can be discrete with a defined start and end (pulse) or have more long-lasting and consistent effects on dynamics and conditions (press). We use the integrative

metric of overall ecological vulnerability (OEV; Urrutia-Cordero et al., 2022) to calculate differences between species responses in the disturbed community and the undisturbed control community (as response ratio [RR]) over time as the foundation of our framework. Specifically, OEV is estimated for each population individually as the integral (area under the curve [AUC]) of population density or biomass in comparison with the control and represents a measure of instability that integrates multiple dimensions of post-disturbance stability. So far, OEV and AUC have been used for community metrics such as total biomass production or the similarity of disturbed to undisturbed community composition (Urrutia-Cordero et al., 2022). Here, we transfer this approach to single species. Thereby, the response of the disturbed species is normalized to its response in the undisturbed control community, and the AUC of this deviation from control is directly proportional to the total effect size of the disturbance. The AUC is large if fluctuations are strong, the ability to withstand the disturbance (resistance) is weak, the speed of recovery (resilience) is slow, recovery remains incomplete, or transition to an alternate state occurs (see Box 2 for a definition of these concepts; Donohue et al., 2013; Hillebrand et al., 2018; Urrutia-Corderoet al., 2022; Urrutia-Cordero, Langenhederet al., 2021). In addition to capturing stability beyond single dimensions, the advantage of the AUC approach lies in its versatility as it allows comparison of ecosystem responses to varying disturbances (e.g., press, pulse disturbances, and fluctuations). For a pulse disturbance, the AUC reflects the initial response, the recovery trajectory, and the ability to recover in comparison with the control, whereas for a press disturbance and fluctuating multi-pulse systems, the AUC equates to the total amount of departure from the control (see Urrutia-Cordero, et al., 2022).

Specifically, our framework comprises two dimensions: species' relative and absolute contributions to functional stability, that is, the stability of emerging community functions such as biomass or abundance (Figure 1a). This is because a species can contribute positively to stability after disturbances, where community biomass declines, in two ways (Figure 1b): First, the biomass of a species' population may increase despite the disturbance inflicting mortality on other species, as its traits allow it to tolerate or even benefit from the disturbance. Second, a species can be affected negatively, but to a lesser extent than other species. In the first case, we would see an increase in the absolute biomass and relative proportion of the species, and in the latter case, a decrease in absolute biomass but an increase in its relative proportion (Figure 1b). We therefore calculate the AUC of the species-specific responses by comparing both the species biomass and species proportion in a disturbed community with those in an undisturbed control.

The original OEV approach uses the log response ratios (LRRs) of biomass in the natural log of treatment over control biomass. However, single species can become locally extinct, which would result in an undefined LRR (as ln(0) is not defined), even though the contributed instability of that species is potentially large. Therefore, we use standardized RRs instead. First, we calculate the biomass RR as the difference in species-specific biomass between treatment and control divided by the summed biomass of the same species in treatment and control for each single time point (Table 1, Figure 1a). If RR equals zero, the species was unaffected by disturbance at this time point; a negative RR reflects biomass decline; and a positive RR reflects biomass increase for this species post-disturbance. Second, we determine Δpi, the species-specific difference in proportion between treatment and control (Table 1). Similar to RR, negative values of Δpi reflect declines in proportion, while positive values reflect increases in proportion for this species post-disturbance. These species-specific responses in disturbed communities are net responses as they integrate both species sensitivities and the outcomes of interactions. For absolute contribution to stability, we then calculate the AUC of RR over time, and for the relative contribution to stability, the AUC of Δpi. A negative AUC reflects a higher sensitivity of the species to the disturbance, and a positive AUC, a species benefiting from the disturbance. It should be noted that AUC over time can be calculated only if species are present on at least two occasions. This might exclude very rare species from the analysis, which might be present in only one sampling.

Distinguishing positive and negative deviations from the control as well as absolute and relative biomass or abundance creates four potential categories (Figure 1b). These categories appear as sectors when plotting the absolute and relative contributions to community stability: If species benefit from the disturbance and increase in proportion and absolute biomass, they contribute positively to the functional stability of the community in relative and absolute terms (Sector I). Species in Sector II are affected negatively by the disturbance, but less so than the other species. These species have a positive relative contribution to stability but a negative absolute contribution. Species in Sector III suffer from the disturbance by decreasing in both biomass and proportion. They are, therefore, more sensitive than the average species and contribute negatively to stability. Sector IV covers species that benefit from the disturbance in absolute terms but still decline in proportion as other species benefit even more. This outcome is potentially less relevant if the response is to a mortality-inducing disturbance.

BOX 2   Glossary of used terms and abbreviations

Term	Definition
AUC	Area under the curve
Disturbance	Changes to the biotic or abiotic environment that affect the structure and dynamics of ecosystems (White & Pickett, 1985). This disturbance can be discrete with a defined start and end (pulse) or have more long-lasting and consistent effects on dynamics and conditions (press).
Ecological stability	Ecological stability is the overarching concept capturing an ecosystem's ability to absorb and recover from change, integrating a family of metrics of resistance, resilience, recovery, and spatiotemporal invariance (Donohue et al., 2013; Hillebrand et al., 2018; Kéfi et al., 2019; Urrutia-Cordero, Langenheder, Striebel, Angeler, et al., 2021).
Functional redundancy	Functional redundancy describes the ability of a community to maintain the functionality of a particular process despite the loss of species (under disturbance) because other species can compensate by performing similar ecological functions, making species redundant for a particular process (Yachi & Loreau, 1999).
Functional stability	Stability of the aggregated functional properties of the community (such as biomass or productivity) (Hillebrand et al., 2018).
Resistance	Ability to withstand disturbance (Pimm, 1984).
Resilience	Ability to recover from disturbance; also measured as the rate of recovery (Hillebrand et al., 2018; Pimm et al., 2019).
Recovery	The ability to return to undisturbed/pre-disturbance conditions following a disturbance (Hillebrand et al., 2018).
Temporal stability	Stability (or variability) over time, often estimated as temporal variation around the recovery trend (resilience) (Hillebrand et al., 2018).
OEV	Overall Ecological Vulnerability, an integrative metric of instability based on the area under the curve (Urrutia-Cordero et al., 2021).

Measuring species contributions under different types of environmental changes

Before applying our framework to data, we can consider what a typical outcome for pulse and press disturbance might look like. First, we consider a pulsed mortality event of limited duration (Figure 1c). In our empirical example, this is the temporary introduction of a non-selective consumer into the system, but other common examples are fires, storms, or floods (Hillebrand & Kunze, 2020). Here, we expect direct detrimental effects on aggregate community functions (such as biomass), as most species would suffer from this additional mortality. That is, most species are in Sectors II and III according to our scheme (Figure 1c). Of these, some species suffer more than the average species (red species in Figure 1c) and can be characterized as destabilizing, while others suffer less and thus increase in proportion—they show a positive relative contribution to stability. A few species may even increase in biomass—and thereby in proportion—and are thus stabilizing by compensating for the biomass loss in

other species, due to, for example, traits enabling avoidance of the consumer (Figure 1c, Sector I).

A press disturbance represents a lasting impact such as warming, salinity stress, or, as in our empirical example, a longer term chronic reduction in resources (Figure 1d). Here, we can expect both winners (e.g., species with lower resource demands) and losers, the latter being vulnerable and declining in both absolute and relative terms (Figure 1d, red species). Stabilizing species may either increase in both absolute and relative terms (blue species), compensating for the loss of other species, or contribute only relatively to stability (gray species).

Whereas we restrict our simulations to these more typical cases where the average response to disturbance is negative (a reduction in abundance or biomass), our framework can equally be applied to disturbances that trigger biomass production, such as a nutrient pulse (see Appendix S1: Figure S6). In this case, the interpretation of sectors would switch as stabilizing properties are proportional to the change relative to an undisturbed community.

Model simulations

We constructed a five-species Lotka–Volterra species competition model and included scenarios with press, pulse, and combined disturbances as well as control runs without any disturbance. In the model, the change of biomass for each species is described as

$$\frac{dB_i}{dt} = r_{\max} B_i \left(1 - \frac{\sum_{j=1}^{5} \alpha_{i,j} B_j}{K} \right), \qquad (1)$$

where B_i corresponds to the species-specific biomass, $r_{\max}$ is the maximum growth rate, K is the carrying capacity, $\alpha_{i,j}$ is the competition strength between species i and species j, and B_j is the biomass of species j.

The model describes a generic community that, with system-specific modifications and traits, could be adapted to describe a natural system. For simplicity, we assumed that the different species differ only in their competitive abilities, while their growth rates $r_{\max}$ and carrying capacity K are constant ($r_{\max} = 0.6$, $K = 10$). We assumed that the strongest competition in this community is intraspecific due to the competition for identical ecological niches among conspecifics. This is implemented by setting competition terms $\alpha_{i,j}$ along the competition matrix diagonal to 1, the maximum value of all $\alpha_{i,j}$. The interspecific competition terms $\alpha_{i,j}$ ($i \neq j$) were drawn from a normal distribution ($\mu = 0.7, \sigma = 0.05$). The low SD greatly reduces the probability of randomly drawing interspecific competition values >1. The exact values have no further specific meaning but were picked to frequently generate community assemblages where each species reaches meaningful biomass at equilibrium, effectively preventing communities with few extremely dominant species.

A higher value of $\alpha_{1,2}$ indicates a larger competition effect by Species 2 on the net growth of Species 1 (maximum growth rate scaled by competitive ability). By contrast, a low $\alpha_{1,2}$ indicates a lower competition effect of Species 2 on the net growth of Species 1. We further assumed that all $\alpha_{i,j} > 0$ and, therefore, predation (e.g., $\alpha_{1,2} > 0$ and $\alpha_{2,1} < 0$) or mutualism (e.g., $\alpha_{1,2} < 0$ and $\alpha_{2,1} < 0$) is not considered. The interactions between two species in the model are not symmetric ($\alpha_{1,2} \neq \alpha_{2,1}$). We calculated the relative competitiveness of species as the inverse of their relative α:

$$\text{Relative competitiveness} = \frac{\text{maximum } \alpha \text{ in community}}{\text{species } \alpha}. \qquad (2)$$

The model system is solved numerically using the fourth-order Runge–Kutta method with time step $\Delta t = 0.5$.

In an undisturbed system, all species grow until they converge toward a species-specific biomass value. The differences between these biomass values can be explained by the competitive abilities of each species within the community. Extinctions can arise stochastically when the randomly drawn competition terms $\alpha_{i,j}$ place the respective species at a disadvantage within the competitive assemblage.

In simulations with disturbances, we used the same model as for the undisturbed systems, but here, the biomass of all species was reduced at time point 150, which ensured that the community had reached its equilibrium before the disturbance was applied (Appendix S1: Figure S1). The mortality was short-term (pulse), lasting (press), or a combination of short-term and lasting (pulse and press). A pulse disturbance in the model simulations was defined as a sudden, singular removal of biomass where the magnitude of mortality depends on each species' sensitivity to the disturbance. A press disturbance was defined as lasting removal of biomass at each time step for 300 time points.

To test how reliably our approach identified a sensitive or tolerant species, we explicitly tested three scenarios for each disturbance type, respectively:

1. All species are equally sensitive to the disturbance, thus losing 50% of their biomass in a pulse or 0.5% per time step in a press scenario.
2. One species in the system is more tolerant to the disturbance; all the others respond equally. The more tolerant species loses only 25% of its biomass in a pulse or 0.25% per time step in a press disturbance scenario, whereas the other species all lose 50% of their biomass in a pulse or 0.5% per time step in a press disturbance scenario.
3. One species in the system is more sensitive to a disturbance; all the others respond equally. This species loses 50% in a pulse or 0.5% per time step in a press scenario, whereas all other species are more tolerant and lose 25% for the pulse disturbance or 0.25% per time step for the press disturbance, respectively.

Individual sensitivities were selected randomly without any consideration of competitive abilities. After the pulse disturbance, the system rebounds and converges to its previous equilibrium. To account for stochasticity when drawing competitive traits, each disturbance scenario was repeated 50 times using the same parameter choices for disturbance intensities and sensitivity values in the various scenarios. Due to parameter selection in our model, species extinctions occurred only rarely, but we kept all model runs including those where species extinctions occurred for a better comparison with the experimental data. All analyses of simulations of model dynamics and empirical data were done using the R
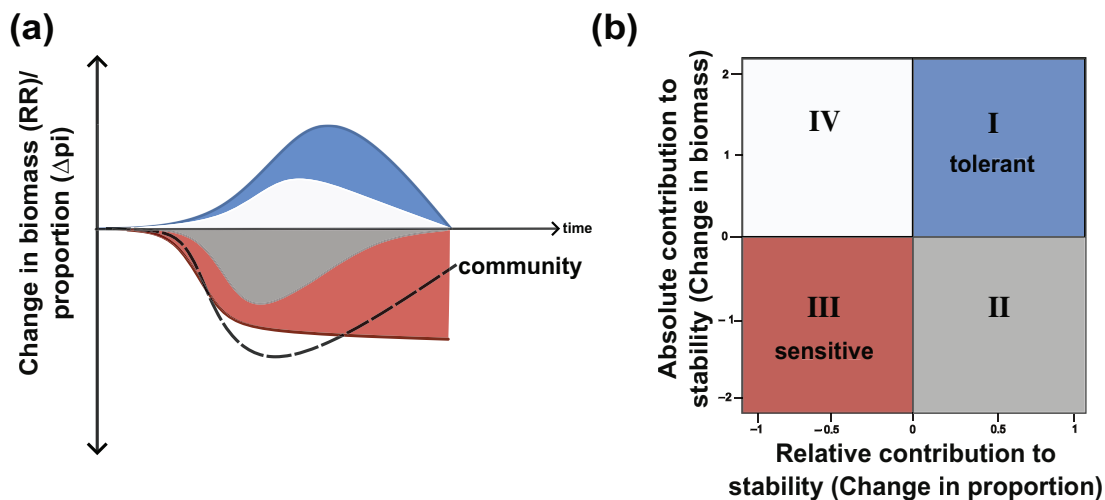
(I) Species benefits and increases in biomass and in proportion after perturbation.

(II) Species suffers in that it decreases in absolute biomass but less so than others and increases in proportion.
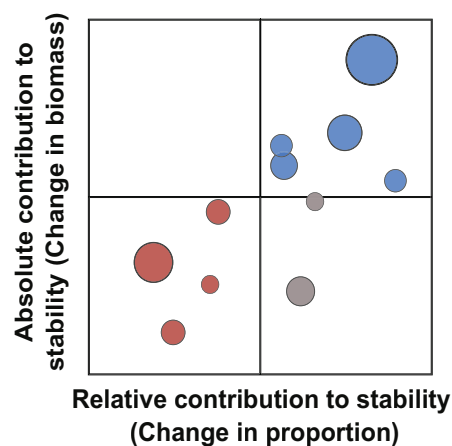
(III) Species suffers from the disturbance by decreasing in biomass, and even more so than the other species.

(IV) This case is included for completeness but captures the unlikely scenario that a species suffers more than others from the disturbance (decrease in proportion), yet increases in absolute biomass.
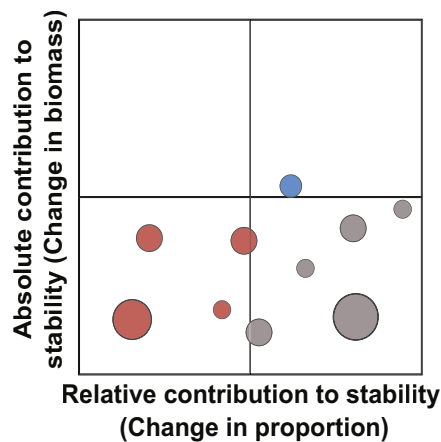
FIGURE 1 (a) Conceptual figure illustrating species-specific responses to a pulse disturbance that reduces community biomass (dashed, black line), (b) the interpretation of our framework showing which species would be displayed in which sector, and (c, d) an exemplary demonstration of the effect of two different environmental drivers, representing a pulse and a press disturbance, on species contribution to stability. (a) Species-specific responses to a disturbance are defined by the area under the curve of their change in relative proportion (Δpi) and their change in absolute biomass (response ratio [RR]). (b) The species-specific net contribution to stability is then captured in a two-dimensional space made up by the area under the curve of the absolute (RR) and relative (Δpi) biomass changes (see Table 1 for calculations). For different environmental drivers, we expect different patterns: (c) Following a mortality pulse, for example, due to non-selective grazer intrusion into a system, we expect a negative overall effect on community biomass, although some species may increase in absolute biomass slightly because of competitive interactions. (d) Following a resource reduction, for example, due to reduced food quality, we expect species responses to differ between those that benefit (because of lower resource demand) and those that suffer. The point size indicates potential differences in species dominance.

TABLE 1 Overview of response variables used for calculating the area under the curve (AUC) as a measure of the absolute (change in biomass) and relative (change in proportion) contributions of individual species to stability.

Measure	Equation	Interpretation
Total biomass	$\text{treat.total} = \sum \text{treat.biomass}$ $\text{con.total} = \sum \text{con.biomass}$	$x > 0$, sum of all species biomass in communities in control and treatment, respectively.
Species biomass contribution per treatment	$\text{treat.pi} = \frac{\text{treat.biomass}}{\text{treat.total}}$ $\text{con.pi} = \frac{\text{con.biomass}}{\text{con.total}}$	$0 < x < 1$, relative species biomass indicating how dominant a species is in the community
Difference in species biomass contribution	$\Delta \text{pi} = \text{treat.pi} - \text{con.pi}$	$x < 0$, the relative species biomass is lower than in the control $x > 0$, the relative species biomass is higher than in the control
Biomass response ratio of species	$\text{RR} = \frac{(\text{treat.biomass} - \text{con. biomass})}{(\text{treat.biomass} + \text{con. biomass})}$	$x < 0$, negative effect of treatment on species biomass $x > 0$, positive effect of treatment on species biomass
AUC for RR and Δpi (change in species biomass and in proportion)	$\text{Relative contribution} = \text{AUC}(\Delta \text{pi})$ $\text{Absolute contribution} = \text{AUC}(\text{RR})$	$x < 0$, negative absolute or relative contribution to stability, respectively $x > 0$, positive absolute or relative contribution to stability, respectively

Abbreviations: AUC, area under the curve; *con*, unmanipulated control; RR, response ratio; *treat*, treatment.

programming language (Version 4.3.2; R Core Team, 2022). For data wrangling, analysis, and visualization, we used packages available within the tidyverse (Wickham et al., 2019), cowplot (Wilke, 2020), ggpmisc (Aphalo, 2021), psych (Revelle, 2022), ggpubr (Kassambara, 2020), sjPlot (Lüdecke, 2021), and here (Müller, 2020). For the calculation of the AUC, we applied the auc() function within the MESS package using linear splines (Ekstrøm, 2022). We calculated the AUC over a time interval of maximum 450 timepoints for model simulations and 28 days for experimental data (see below). As the maximum obtainable AUC is highly dependent on the time interval, the reported values are not biologically meaningful and cannot be compared across studies (see *Discussion* for further details). Moreover, we used Spearman rank correlations to examine relationships between the magnitude of species contributions (i.e., absolute values of relative and absolute contributions) and their relative dominance. For the correlations of simulated data, we combined Sensitivity Scenarios 2 and 3 comprising one sensitive and one tolerant species, respectively. Conceptual figures were created using Inkscape 1.2 (dc2aeda, May 15, 2022).

Experimental study

To test our framework with empirical data, we applied it to published data from experimentally disturbed lake communities (Langenheder et al., 2020; Urrutia-Cordero, Langenheder, Striebel, Eklöv, et al., 2021). The experiments were conducted using the SITES AquaNet mesocosm facilities (https://www.fieldsites.se) in five different lakes in

Sweden, namely, Erken, Feresjön, Erssjön, Stortjärn, and Bolmen, and in two seasons, namely, spring (Experiment 1, starting in June 2017) and summer (Experiment 2, starting in August 2017) (Urrutia-Cordero, Langenheder, Striebel, Eklöv, et al., 2021). Each site consisted of 20 mesocosms, each with a total volume of 700 L (1.5 m deep, 0.8 m diameter), installed on a floating platform. The experiments are especially suitable for our purpose because, on the one hand, its modularized setup comprised 10 independent experiments across a wide range of conditions allowing for high generality, and on the other hand, the design combined a pulse and press type of disturbance, that is, pulsed mortality and reduced resources. The experimental design comprised the following four different treatments; each ran for 28 days and was replicated four times in each lake and season (i.e., total 5 lakes × 2 seasons × 4 treatments × 4 replicates = 160 mesocosms):

1. Undisturbed control.
2. Pulse disturbance, comprising a fish addition treatment, where two small crucian carp (mean length ± SD: 5.77 ± 0.74 cm) were added to the mesocosms for 7 days and removed afterward. The fish addition was expected to result in the mortality of zooplankton through grazing.
3. Press disturbance comprising a shading treatment, where dark mesh was placed on top of the mesocosms to reduce available light. This was done to reduce phytoplankton growth and thus food quantity for zooplankton.
4. Pulse and press disturbance, comprising combined shading and crucian carp addition.

Samples were collected on Days 0 (pre-disturbance), 3, 7, 9, 14, and 28 to capture species (and community)

responses to the disturbances. For lakes Bolmen, Erken, and Störtjan, additional samples were collected on Day 21. In this study, we focused on the zooplankton communities as these were identified consistently to the genus level in the experiment and as they are an ideal model group due to the key roles that they play in aquatic food webs (Lomartire et al., 2021). Zooplankton biomass was examined using light microscopy (400× magnification). Zooplankton identification was at the genus level, but to be consistent with the wording of the simulations, we use "species contribution to stability" here, as for the model. To standardize the data collected in the 10 experiments (5 lakes × 2 seasons) and calculate the correct mean of species responses, missing values of species responses were handled by replacing NAs with zeros. In doing so, we assume that the collected samples are representative of the experimental units and that missing biomass values reflect the absence of the species rather than a collection or recording error.

Species contributions to stability were determined in each replicate mesocosm from species-specific changes in biomass and proportion over time, respectively. To estimate the likelihood of a species contributing to stability in the same way among all lakes and seasons and thus being displayed in the same sector (Figure 1), we build individual linear models for each disturbance type and dimension using the lmer() function within the lme4 package (Bates et al., 2015). We used lake and season as random effects in our model and removed the intercept to test each species against zero (H0: species is not affected by disturbance and maintains initial biomass and proportion).

For a comparison of community dynamics between our model simulations and the experimental data, we analyzed how species relative dominance constrains species contributions to stability in both simulations and experimental data. While the model created dominance patterns based on competitiveness, we did not have the means to measure competitiveness directly in the experiment. Therefore, we used species relative dominance in the undisturbed control and compared this with species contributions to stability using Spearman rank correlations.

RESULTS

Model simulations

Simulations show that our framework can reliably identify both sensitive (Scenario 2) and tolerant (Scenario 3) species, by determining the absolute and relative contributions to stability (Figure 2). In Scenario 1, all species were negatively affected and decreased in biomass to the same extent. Therefore, they showed no shift in proportion but contributed negatively to absolute stability (Figure 2a). In Scenario 2, the single more robust species increased in both biomass and proportion and showed positive absolute and relative contributions to stability compared with other species that decreased in biomass (Figure 2b). In Scenario 3, the sensitive species showed negative absolute and relative contributions to stability, whereas all other species benefited from the reduction in their competitor (Figure 2c).

As expected, our simulations did not contain any species that increased in biomass but decreased in proportion (Sector IV in Figure 1b), but most species showed either an increase or decrease in both proportion and biomass (Sectors I and III in Figure 1b). Only rarely did we find species that suffered from the disturbance but less than others (Sector II), likely due to use of the dichotomous categories "sensitive" and "tolerant" in our model.

Whereas the detection of the species contributing to (in-)stability was consistently possible independent of the simulation run, the magnitude and direction of their relative and absolute contributions to (in-)stability varied (Figure 2b,c). These differences reflected the relative dominance of the species and thus their competitiveness (Figure 3; Appendix S1: Figure S2). When all species were equally sensitive (Figure 3a, Scenario 1), the least dominant species showed lower absolute reductions in biomass, while no differences occurred for the more dominant species. The relative change in biomass was, as expected from the scenario, close to zero, but again, the least dominant species showed a deviant response as it benefited from the reduction in the other, more competitive species and therefore decreased less in biomass and thus increased in proportion. Similarly, the single tolerant species (Figure 3b, Scenario 2) could show a larger absolute contribution to stability than already dominant species, as the latter were closer to their carrying capacity and thus could gain less biomass. This eventually also restricts the maximum obtainable gain in proportion for dominant species, which reduces their relative contribution to stability. The results for absolute biomass change were similar in the scenario with a single sensitive species: if the sensitive species was rare, that is, competitively inferior, it suffered even larger losses than when the sensitive species was competitively more dominant (Figure 3c, Scenario 3).

For disturbances involving a pulse component, species relative and absolute contributions to stability were consistently related to species dominance (Table 2). When all species were equally sensitive (Scenario 1), species absolute and relative contributions to stability decreased with dominance (for all disturbance types) as the least dominant/competitive species showed lower absolute reductions in biomass as the other species were competitively superior.

Similarly, species contributions to stability declined with relative dominance for the one tolerant species (Scenario 2). In contrast, species contributions to stability increased with relative dominance for the one sensitive species (Scenario 3), because of a competitive advantage of the more dominant species (Figure 3c). As dominance was determined mainly by the relative positioning of competitive abilities (Pearson correlation, $R = 0.83$, $p < 0.05$), we observed very similar patterns when comparing species contributions to stability as a function of their relative dominance to their relative competitiveness (Appendix S1: Figure S2).

Mesocosm experiments

Across experiments and treatments, zooplankton taxa were generally distributed among three of the four sectors of our framework (Figure 4) since we—as expected—did not find species that showed a negative relative contribution but a positive absolute contribution to stability (i.e., species that increase in biomass but decrease in proportion; Sector IV in Figure 1b). In contrast to the simulations, where this outcome did not occur, empirical taxa frequently showed a positive relative contribution but a negative absolute contribution to stability (Sector II; Figure 4). Thus, across disturbance types and lakes, species could be mapped into those benefiting from the disturbance (Sector I), those being sensitive (Sector III), and those being sensitive but less than others (Sector II). While each of these sectors was populated in each lake and season, the number and the identity of species present in each sector varied among lakes, seasons, and disturbance types. In contrast, species contributions to stability were highly context-dependent, such that the same species was stabilizing in one context and destabilizing in another.

For example, *Bosmina* showed a consistently significant negative absolute contribution to stability across all disturbance types (Appendix S1: Table S1). However, it differed in its relative contribution to stability among lakes and seasons (Figure 4; Appendix S1: Table S1). In contrast, both the relative and absolute contributions of *Keratella* varied among disturbance types, lakes, and seasons (Appendix S1: Table S1). In Lake Erken, *Keratella* was tolerant to disturbances involving a pulse (pulse and the combination of pulse and press) and showed both positive absolute and relative contributions to stability (Figure 4, Sector I), but it was sensitive to the press disturbance (but less so than others), showing negative absolute and positive relative contributions to stability (Figure 4, Sector II). Overall, none of the 20 taxa showed consistently both significant absolute
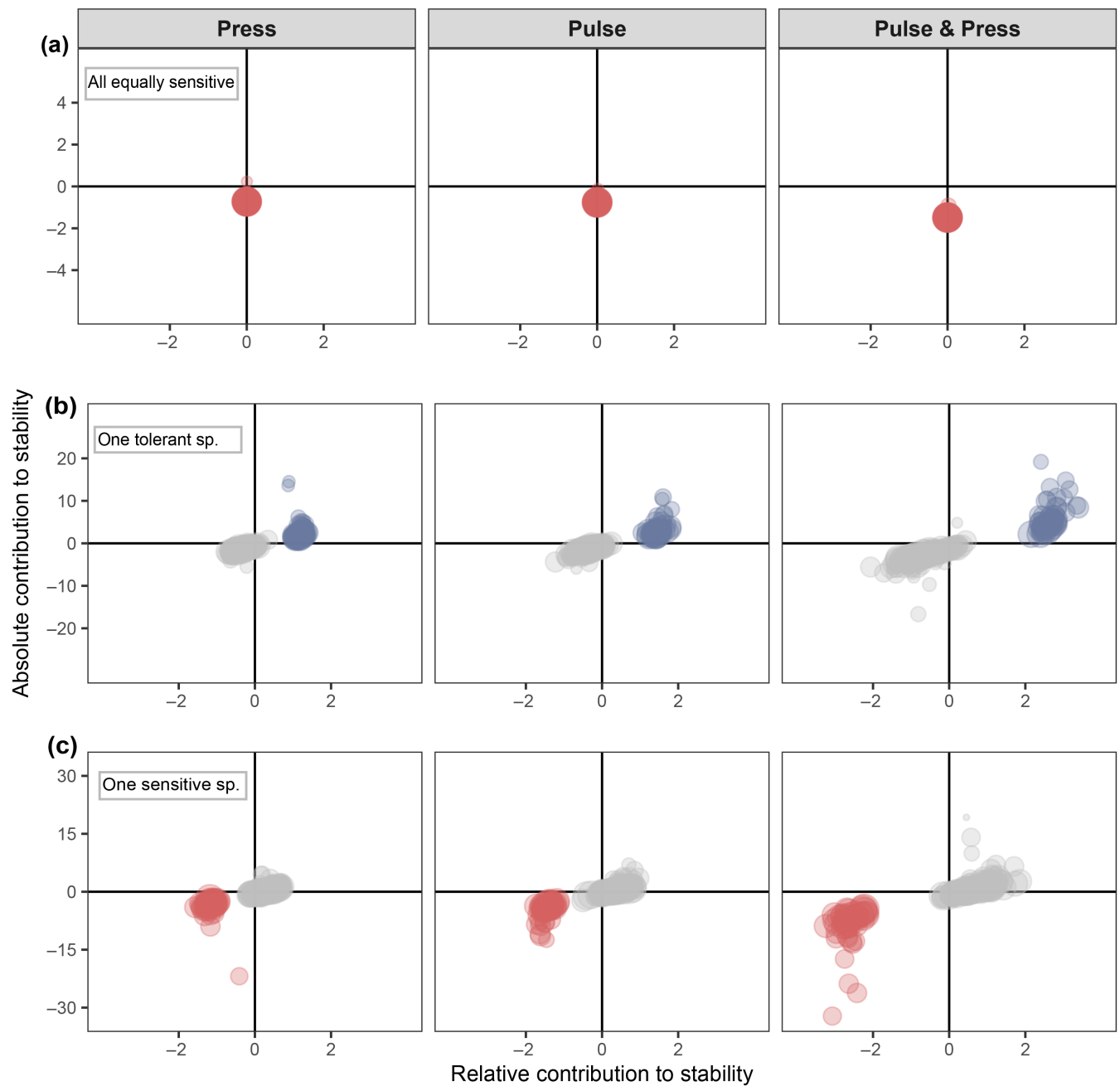
and relative contributions to stability (Appendix S1: Table S1).

A key aspect of this variation in species relative and absolute contributions to stability (across lakes and seasons) in the mesocosm experiments stems from variation in species dominance (Figure 5). Most species showed a negative response to the disturbance. Only a few, initially rare species were able to gain biomass, while the relatively dominant species decreased in biomass, resulting in a negative absolute contribution to stability. The relative contribution of species to stability showed similar trends compared with their absolute contribution. Species that were dominant in the undisturbed control decreased in proportion in the treatments, while rare and less dominant species increased in proportion and thus showed positive relative contributions. This was consistent with the results of our simulations.

Moreover, similar to the empirical data, in our simulations, species contributions to stability declined with increasing relative dominance of the one tolerant species (Scenario 2) or equally sensitive species (Scenario 1; Figure 3). In the empirical data, species relative contribution to stability was consistently and significantly correlated with their relative dominance and decreased with increasing relative dominance across all disturbances. Similarly, species absolute contributions to stability decreased with increasing dominance for disturbances involving a mortality pulse (Table 2; Figure 5). Solely, for the press disturbance treatment, we find a slightly positive correlation between the absolute contribution to stability and relative dominance ($R = 0.082$, $p = 0.38$). This suggests that dominant species were not as severely affected by the press disturbance as for the pulse or pulse and press combination disturbances.

DISCUSSION

Our conceptually simple framework enables quantification of species net contributions to the functional stability of a community based on changes in their absolute and relative biomass. While the framework is applicable to different organism groups and ecosystems, it requires (1) the comparison of disturbed communities with undisturbed ones and (2) temporal data on the course of post-disturbance dynamics. It is, therefore, restricted to manipulative studies such as experimental and field studies with a wide range of disturbance types. However, we also discuss below how it can potentially be extended to observational data. Before we address the extension of our framework, we discuss the results of our simulations and empirical analysis, especially with respect to the generality of our approach.

FIGURE 2 Contribution of individual species to functional stability in simulated communities, reflected in their absolute and relative contributions to stability after experiencing a pulse, a press, or a combined pulse and press disturbance under scenarios where all species have the same sensitivity to the disturbance (Scenario 1) (a), one species is more tolerant to the disturbance (Scenario 2) (b), and one species is more sensitive to the disturbance (Scenario 3) (c). Each point represents one species in one model run; relative dominance is indicated by point size. More sensitive species are highlighted in red, and more tolerant species in blue; all other species are colored gray.

Simulations

We first tested our approach with simulated data with known presence of sensitive and tolerant species. Our framework reliably identified both the single sensitive (Scenario 2) and tolerant (Scenario 3) species. The sensitive species was always characterized by negative absolute and relative contributions to stability, whereas the

tolerant species always showed positive contributions. While the sign of the contribution was consistently as expected, the magnitude was not uniform and depended on species' competitive abilities. Interestingly, species contributions declined with relative dominance as the least dominant species benefited from the reduction in other, more competitive species for disturbances involving a pulse (Scenarios 1 and 2). This strong signal of
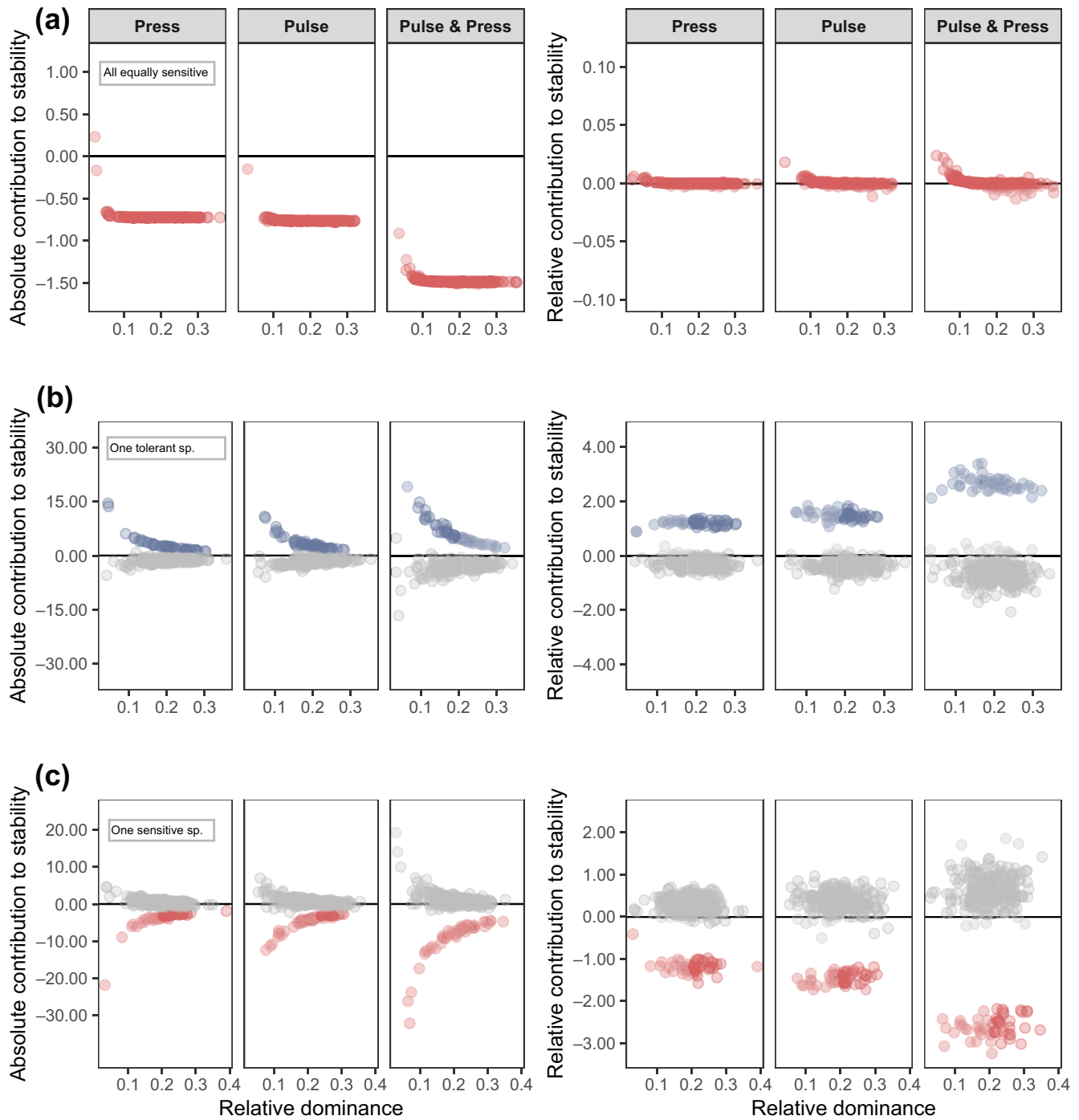
FIGURE 3 The absolute and relative contributions of species to stability in simulated communities as a function of their relative dominance in the control. Low values of relative dominance indicate that species are less dominant than the others in their respective community. Simulated communities experienced pulse, press, or combined pulse and press disturbances under scenarios where all species have the same sensitivity to the disturbance (Scenario 1) (a), one species is more tolerant to the disturbance (Scenario 2) (b), and one species is more sensitive to the disturbance (Scenario 3) (c). Each point represents one model run. Negatively affected species are highlighted in red, and species that are more tolerant in blue; all other species are colored gray.

compensatory dynamics in the simulations is partly enforced by the fact that dominant (competitive) species were already close to their carrying capacity, thus reducing their ability to increase in biomass in contrast to rare

species. In contrast, species contributions for the one sensitive species (Scenario 3) increased with relative dominance as species that were initially rare (weak competitors) suffered larger biomass losses than competitively

TABLE 2 Spearman rank correlation coefficients for species relative dominance and their absolute or relative contributions to stability across different disturbance scenarios in simulations and empirical data, respectively.

Disturbance	Sensitivity scenario (simulations)	Model simulations				Mesocosm experiments			
		Absolute contribution to stability		Relative contribution to stability		Absolute contribution to stability		Relative contribution to stability	
		R	p	R	p	R	p	R	p
Press						0.08	0.38	−0.41	**<0.01**
	All equally sensitive	−0.3	**<0.01**	−0.5	**<0.01**				
	One tolerant sp.	−0.82	**<0.01**	0.16	0.26				
	One sensitive sp.	0.71	**<0.01**	−0.27	0.057				
Pulse						−0.32	**<0.01**	−0.51	**<0.01**
	All equally sensitive	−0.28	**<0.01**	−0.53	**<0.01**				
	One tolerant sp.	−0.88	**<0.01**	−0.29	**<0.05**				
	One sensitive sp.	0.9	**<0.01**	0.37	**<0.01**				
Pulse and press						−0.36	**<0.01**	−0.56	**<0.01**
	All equally sensitive	−0.41	**<0.01**	−0.59	**<0.01**				
	One tolerant sp.	−0.77	**<0.01**	−0.26	0.066				
	One sensitive sp.	0.83	**<0.01**	0.21	**0.14**				

Note: For the sensitivity scenarios "one tolerant" and "one sensitive" of the simulations, we only applied the correlations to the one sensitive/tolerant species. Significant correlations ($p < 0.05$) are indicated in bold.

superior species and thus showed negative absolute and relative contributions.

Mesocosm experiment

Applying our approach to a multi-site mesocosm experiment with pulse and press disturbances, we were able to identify (de-)stabilizing species at each site and in each season. Most species showed a clear distinction by contributing negatively or positively to stability (Sectors I and III in Figure 1). Across cases, 46.9% of species showed a negative absolute but positive relative contribution (Sector II in Figure 1), which characterizes species that suffer from the disturbance but less than other species. No species appeared in Sector IV, as expected.

While this distribution of species across sectors allows identification of the (de)stabilizing species for each single experiment, use of a multi-site experiment allowed us to analyze the consistency of species contributions across 10 different environmental and biotic contexts (5 lakes × 2 seasons). In total, 43.3% of the analyses showed a significant contribution; that is, the species showed a significant relative and/or absolute contribution to stability independent of lake and season (52 out of 120 cases, i.e., 2 dimensions × 3 disturbances × 20 taxa).

Of these, none of the 20 genera contributed consistently significantly in terms of both absolute and relative terms across disturbances (Appendix S1: Table S1). However, 10 out of 20 taxa showed consistently significant absolute contribution across disturbances. In conclusion, most species showed context-specific contributions to stability.

Context specificity includes both the different abiotic conditions for the 10 experimental runs, and the surrounding community composition. The latter biotic component of context specificity has been stressed in network theory showing that the stability of a network can be influenced by its architecture. Trophic networks tend to be more stable when many weak and compartmented interactions prevail, while mutualistic networks benefit from highly interconnected and nested structures (Gross et al., 2009; McCann et al., 1998; Thébault & Fontaine, 2010).

Our analyses indicate that the high context specificity we observed also reflects the dominance of species. Dominance patterns varied among experiments, as divergent abiotic conditions and co-occurring zooplankton taxa led to different relative proportions for each species in the communities (Urrutia-Cordero, Langenheder, et al., 2021). As we derived empirical dominance from the undisturbed controls, it can be interpreted as an analog to the competitiveness in our simulations.
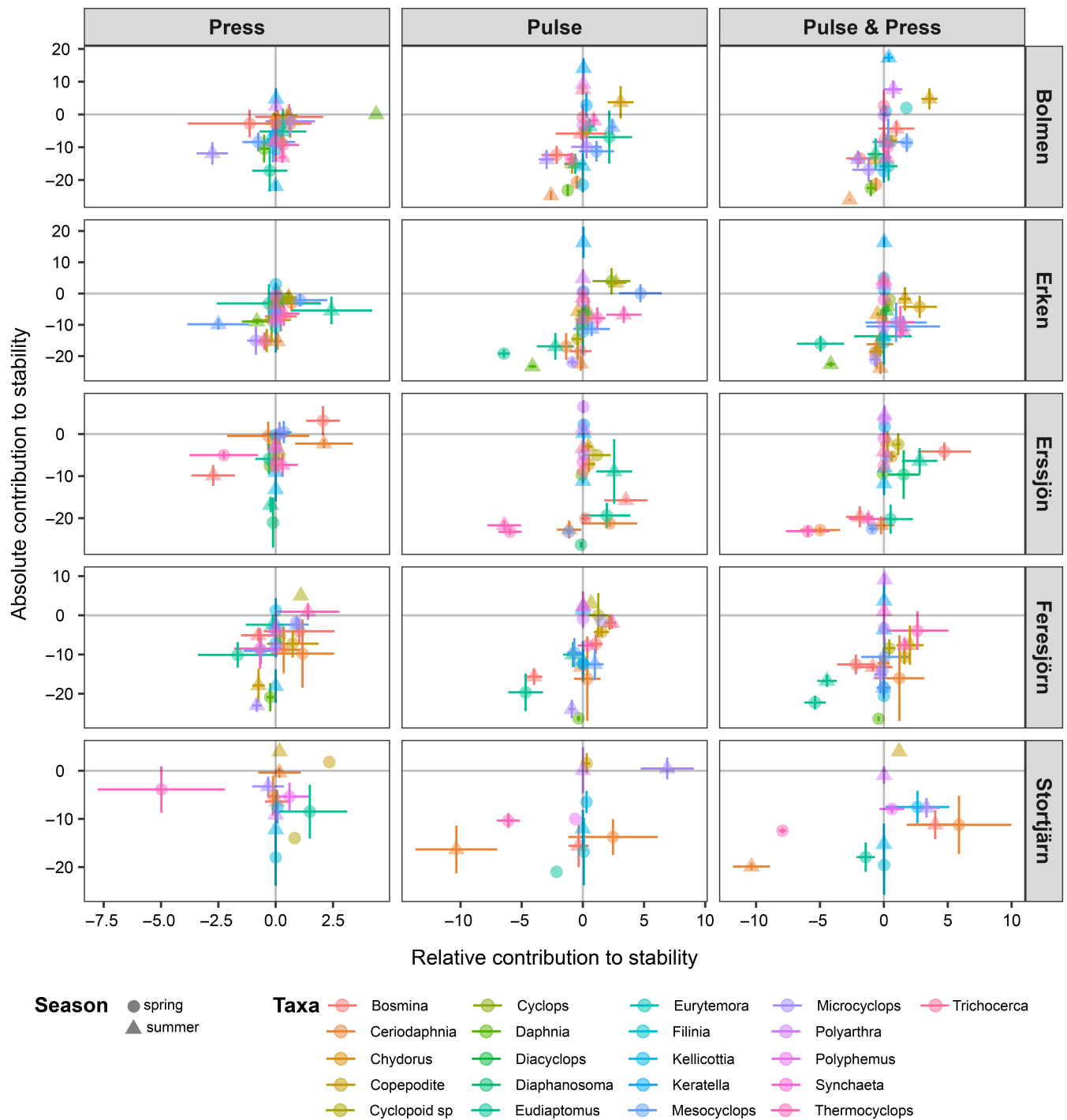
FIGURE 4 Absolute and relative net contributions of zooplankton taxa to functional stability. The experimental treatments comprised a pulse disturbance (fish addition), a press disturbance (shading), and a combination of press and pulse disturbance (fish addition and shading). Each color represents one taxon; the experimental seasons consisted of a summer experiment (closed circles) and a spring experiment (closed triangles). We collapsed values among replicates ($n = 4$); each dot represents mean $\pm$ SE.

In general, the role of dominance was consistent in our simulations and empirical data, showing clear signs of compensatory dynamics with the exception that simulated communities were close to their carrying capacity. This led to differences in the relationships between species dominance and their contributions, depending on the sensitivity scenario. In simulated communities with one tolerant species (Scenario 2), we observed a negative correlation between dominance and species contributions, which aligns with what we observed in our empirical data.
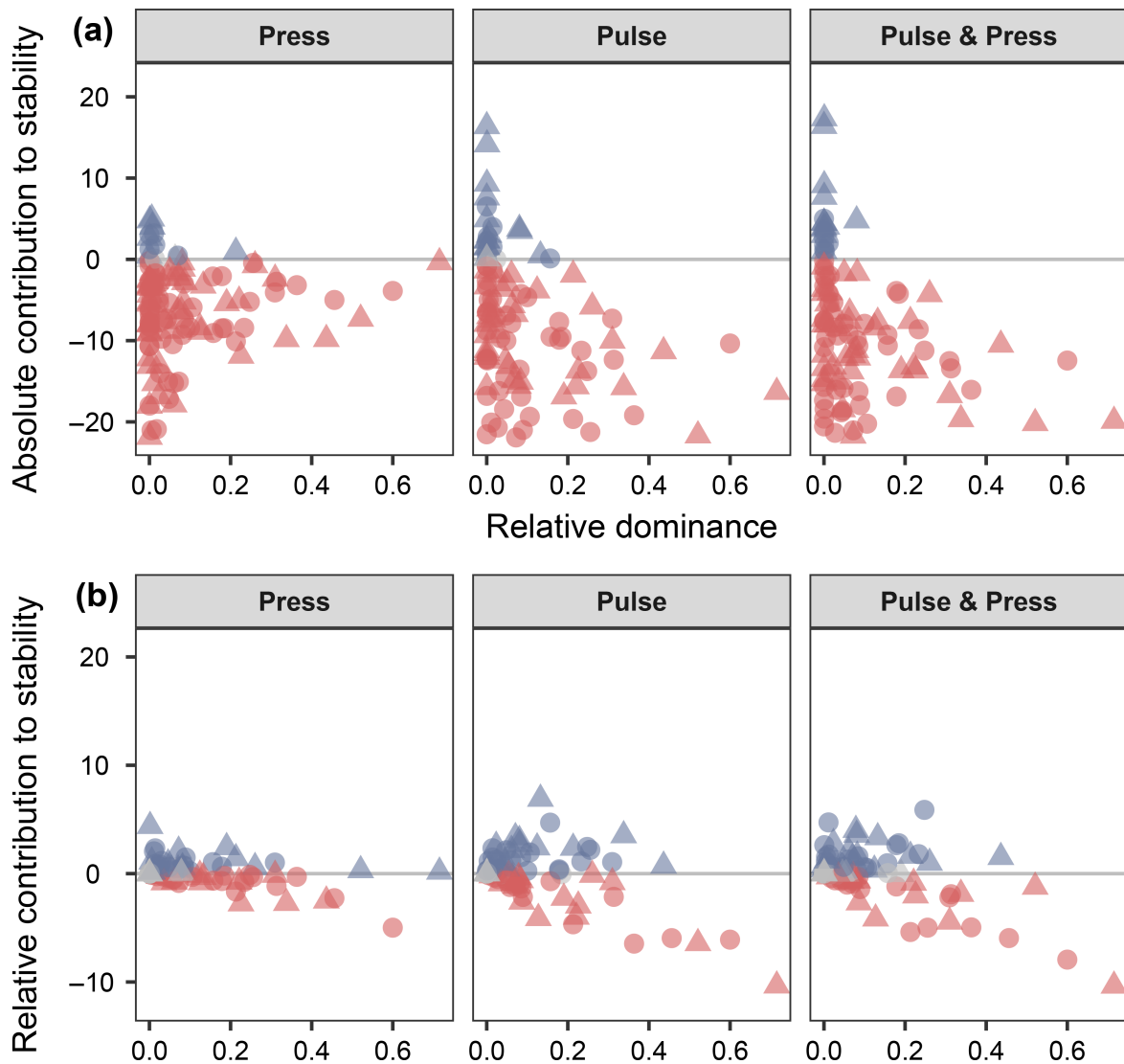
FIGURE 5 Species absolute (a) and relative (b) contributions to stability in our experimental lake communities as a function of their relative dominance in different lakes and experiments. Relative dominance was calculated as species average relative biomass in the control of the respective season and site ($n = 4$), as this enables identification of which species are affected by the treatment and elucidate resulting changes in the community. The experimental seasons consisted of a summer experiment (closed circles) and a spring experiment (closed triangles). We collapsed values among replicates ($n = 4$). Negatively contributing species or species groups are highlighted in red, and positively contributing ones in blue; those with values near 0 are indicated in gray.

On the other hand, in simulated communities with one sensitive species (Scenario 3), we found a positive correlation between species contributions and relative dominance, indicating that the dominant species had a competitive advantage. In our empirical data, species contributions declined with increasing relative dominance because dominant species experienced greater biomass loss than rare species in the experiment. This suggests a trade-off between a species' competitive abilities and its capacity to tolerate prevailing environmental conditions, as discussed in detail in Bauer et al. (2021) regarding trait dimensions. For example, zooplankton species are often equipped with various mechanisms to inhibit predation such as morphological and chemical defenses (Diel et al., 2020; Ohman, 1988). Such an investment in tolerance often hampers growth and makes species less dominant when no disturbances prevail.

Indeed, while dominant species were affected severely by the experimental disturbances and experienced substantial declines in biomass, rare species increased in biomass. Subsequently, species that were rare across lakes and seasons contributed positively to functional stability. Such compensatory dynamics likely resulted from negative species interactions, where species were released from competition through the decline of the dominant competitor (Grman et al., 2010). A recent study

demonstrated that species sensitivities to disturbance can change over time, highlighting that rare and fluctuating species may not always be the most susceptible to disturbance (Medeiros et al., 2022). Other studies have found that whether species benefit or suffer from a disturbance depends mainly on their identity, their traits, and how well their traits match the prevailing environmental conditions (Bauer et al., 2021; Lind et al., 2013; Seabloom et al., 2015). Due to their unique trait combinations, rare species thus may play a key role in maintaining stability and ecosystem functioning (Dee et al., 2019; Mouillot et al., 2013; Xiong et al., 2020).

Instead of a trade-off between competitive dominance and resistance to disturbance, the same impression of stability via compensatory dynamics of rare species appears by density-dependent mortality induced by the predator. Generalist consumers, as were introduced in our mesocosm experiment as a pulse disturbance, feed proportionally mainly on the most abundant and largest taxa (Urrutia-Cordero, Langenheder, Striebel, Angeler, et al., 2022; Urrutia-Cordero, Langenheder, Striebel, Eklöv, et al., 2021), which coincide in this study (positive size and dominance correlation; Spearman rank correlation, $R = 0.48$, $p < 0.05$). As such, grazer introduction might promote species coexistence by reducing competition pressure of the competitive dominants on inferior competitors (Gurevitch et al., 2000; Ladouceur et al., 2022). Density-dependent effects of predator additions hence may equally lead to compensatory biomass increase of rare species through competitive release (Gonzalez & Loreau, 2009). In such a case, competitively driven compensatory dynamics by previously rare species contribute to community wide stability, reflecting some of the results in our empirical data. We found regular increases in the absolute and relative contributions of rare species to stability in treatments involving a mortality pulse (Figure 5).

While compensatory dynamics were observed in our experiments, others concluded that they are rarely observed in natural systems (Houlahan et al., 2007; Vasseur et al., 2014). While we cannot disentangle this discrepancy in detail, the detection of compensatory dynamics certainly depends on the temporal and spatial scale at which community dynamics are assessed in comparison with the generation time of the organisms (Downing et al., 2008; Shoemaker et al., 2022). Compared with the plant (especially forest) and animal (mainly vertebrates) studies in Houlahan et al. (2007), our experimental systems were large and long-lived with respect to zooplankton body size and generation time. A second aspect may be the comparatively high level of control over the environment in experiments, whereas compensatory dynamics in observational data may be more easily masked by the compensating populations simultaneously responding differently to a suite of abiotic and biotic conditions.

Extension to other disturbances

In summary, we find that in both our simulations (for Scenarios 1 and 2) and our empirical data, species contributions to stability declined with dominance. Across all experimental treatments, compensatory dynamics appear to have played a key role in maintaining stability, as biomass declines in dominant species were followed by biomass increases in rare species. However, while species stabilizing in absolute or relative terms buffer some of the impact, our analyses reveal that the compensation was not perfect; that is, the communities still lost biomass as the reductions of sensitive species were larger than the biomass gains in species that benefited from the disturbance (Appendix S1: Figures S3–S5). Moreover, we found substantial variability in the contributions between lakes, between treatments, and among seasons (Appendix S1: Figures S3 and S4), suggesting that the occurrence of compensatory dynamics is highly context-dependent and varies both spatially and temporally (Downing et al., 2008; Vasseur et al., 2014). In contrast, other studies have reported that compensatory dynamics partially or completely buffered changes in total biomass at long-term sites of rodents and bird communities (Diaz & Ernest, 2024; Ernest et al., 2008), while one study also highlighted the time dependency of compensatory dynamics in fluctuating environments in zooplankton communities (Downing et al., 2008). On the other hand, empirical studies have demonstrated that more dominant and competitive species may increase in biomass after a disturbance by outcompeting less competitive species (Sasaki & Lauenroth, 2011; Violle et al., 2010; Weigelt et al., 2007).

These contrasting results indicate that a comparison of species contributions to stability is limited to within studies. This limitation arises from the impact of community properties such as competition intensity or the community's proximity to its carrying capacity before the disturbance, which affect species' contributions to stability. These constraints contribute to a high level of context specificity in the species contributions. Amending the analyses of experimental data with model simulations will allow specification and exploration of potential species responses, thereby enhancing the understanding of ecological dynamics and outcomes across different scenarios.

We applied this framework to experiments on natural zooplankton communities in field mesocosms, in different geographic locations, and covering two different seasons (spring and summer). Though we quantify species

responses to two common disturbances (alone and in combination), we provide elsewhere examples for the interpretation of the framework for other disturbance scenarios (see Appendix S1: Figure S6), specifically, eutrophication, temperature change, predator loss, and pollution (Chase et al., 2018; Hillebrand & Kunze, 2020). As against the typical disturbances analyzed for this study, eutrophication will in general lead to an increase in community biomass as most species experience a gain in biomass, except for those that suffer due to competitive exclusion (Armstrong & McGehee, 1980; Brauer et al., 2012). In this particular example, species that are gaining biomass would destabilize the community function. By contrast, pollution, predator loss, and warming represent more typical disturbances with negative impacts on the community function and single species (Bestion et al., 2020; Brauer et al., 2012; Donohue et al., 2017; Hébert et al., 2022; Ross et al., 2021; Urrutia-Cordero, Langenheder, Striebel, Eklöv, et al., 2021); therefore, similar patterns to those in our mesocosm experiments will emerge. Overall, emerging patterns of species contributions to stability for other environmental drivers or more complex disturbance scenarios will depend not only on the nature of the introduced disturbances. Instead, these patterns will also be strongly influenced by the dimensions of the disturbances, such as their magnitude, frequency, and intensity (Donohue et al., 2016; Hillebrand et al., 2020). The effects of disturbance regimes are closely linked to the tolerance of species to such disturbances and their ability to recover from them, suggesting that certain disturbance regimes are more prone to altering the (de)stabilizing role of species within ecosystems. Insights into how the different disturbance dimensions affect species contributions to stability can help identify which disturbance regimes are more likely to disrupt ecosystem dynamics.

Extension to observational data

In this study, we discuss the application and interpretation of our species contribution framework to experimental studies. This framework can be applied to observational data of community time series only if (1) species-specific values of post-disturbance dynamics are reported and (2) a baseline of an undisturbed state is available. Specifically, species contributions could then be calculated from species-specific responses (i.e., biomass and proportion) in the disturbed community and in the pre-disturbance community. Different overall patterns may emerge depending on the choice of response variables (biomass vs. abundance) (Diaz & Ernest, 2024; Ernest et al., 2008; Houlahan et al., 2007) and the spatial and temporal scale (Shoemaker et al., 2022; Vasseur et al., 2014).

Recommendations for future research

Drawing from our results, we see a critical need for the following types of studies: (1) manipulative experiments building up the level of complexity from monocultures to polycultures by combining single species into communities; such a bottom-up approach will allow disentangling of whether a species contributes because of unique traits (sampling effects) or because it has different traits compared with the rest of the community (complementarity effects); (2) manipulative experiments on multiple trophic levels, which allow testing the effect of trophic interactions on species contributions to stability using network analysis; (3) cross-system–cross-organism analyses to determine the importance of species trait distributions for community stability in different realms (e.g., marine and terrestrial); and (4) multi-factorial manipulation of disturbance dimensions to improve our understanding of how systems respond to disturbances and which disturbance types are likely to cause shifts in species contributions. Ultimately, these studies will allow quantification of the extent to which stability arises from species identity or is an emergent property of the community.

CONCLUSIONS

Our approach underscores the view that species that are presently rare nonetheless carry much of a system's ability to respond to changing conditions (Dee et al., 2019; Xiong et al., 2020). Specifically, we found that rare species contribute to stability by compensating for the biomass loss of dominant, vulnerable species. However, rare species may also contribute based on their unique trait combinations (Dee et al., 2019; Mouillot et al., 2013; Xiong et al., 2020), as asynchronously fluctuating species responses will enhance stability even in communities without species interactions (Hautier et al., 2014; Loreau & de Mazancourt, 2013). Overall, our findings reinforce recent calls for the need to protect more species than are presumed critical given the enhanced value of biodiversity for maintaining stability and functioning for ecosystems under global change (Dee et al., 2017, 2019; White et al., 2020).

AUTHOR CONTRIBUTIONS
Charlotte Kunze, Helmut Hillebrand, and Ian Donohue conceived the study and planned the analyses. Egle Kelpsiene, Maren Striebel, Pablo Urrutia-Cordero, and Silke Langenheder collected the empirical data that led to Figures 4 and 5. Charlotte Kunze and Dominik Bahlburg conducted the model simulations that led to

Figures 2 and 3. Charlotte Kunze wrote the first draft of the paper and conducted the initial analyses with substantial input from Helmut Hillebrand and Ian Donohue. Dominik Bahlburg, Egle Kelpsiene, Maren Striebel, Pablo Urrutia-Cordero, and Silke Langenheder extensively revised the manuscript before the first round of submission.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT
All empirical and simulated data (Kunze et al., 2024a) are available on Zenodo at https://doi.org/10.5281/zenodo.11046700. Lake-specific data subsets (Langenheder et al., 2020) are also published on the SITES portal at https://doi.org/10.23700/3724-2Q62. Code (Kunze et al., 2024b) is available on Zenodo at https://doi.org/10.5281/zenodo.11242330.

ORCID
Charlotte Kunze https://orcid.org/0000-0002-1130-7417
Dominik Bahlburg https://orcid.org/0000-0003-0210-0649
Pablo Urrutia-Cordero https://orcid.org/0000-0001-9560-8374
Maren Striebel https://orcid.org/0000-0003-2061-2154
Egle Kelpsiene https://orcid.org/0000-0002-7952-5760
Silke Langenheder https://orcid.org/0000-0002-5245-9935
Ian Donohue https://orcid.org/0000-0002-4698-6448
Helmut Hillebrand https://orcid.org/0000-0001-7449-1613

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SUPPORTING INFORMATION

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