Ecology, 102(7), 2021, e03371

Non-additive effects of foundation species determine the response of aquatic ecosystems to nutrient perturbation

Moritz D. Lürig [1,2,3,6,7], Anita Narwani [3], Hannele Penson [3], Bernhard Wehrli [4,5], Piet Spaak [3], and Blake Matthews [2]

[1]*Center for Adaptation to a Changing Environment (ACE), ETH Zürich, Zürich CH-8092 Switzerland*
[2]*Department of Fish Ecology and Evolution, Center for Ecology, Evolution and Biochemistry, Eawag, Swiss Federal Institute of Aquatic Science and Technology, Seestrasse 79, Kastanienbaum 6047 Switzerland*
[3]*Department of Aquatic Ecology, Eawag, Swiss Federal Institute of Aquatic Science and Technolog, Überland Strasse 133, Dübendorf 8600 Switzerland*
[4]*Department of Surface Waters and Management, Center for Ecology, Evolution and Biochemistry, Eawag, Swiss Federal Institute of Aquatic Science and Technology, Seestrasse 79, Kastanienbaum 6047 Switzerland*
[5]*Institute of Biogeochemistry and Pollutant Dynamics, ETH Zürich, Zürich CH-8092 Switzerland*

Citation: Lürig, M. D., A. Narwani, H. Penson, B. Wehrli, P. Spaak, and B. Matthews. 2021. Non-additive effects of foundation species determine the response of aquatic ecosystems to nutrient perturbation. Ecology 102(7):e03371. 10.1002/ecy.3371

Abstract. Eutrophication is a persistent threat to aquatic ecosystems worldwide. Foundation species, namely those that play a central role in the structuring of communities and functioning of ecosystems, are likely important for the resilience of aquatic ecosystems in the face of disturbance. However, little is known about how interactions among such species influence ecosystem responses to nutrient perturbation. Here, using an array ($N = 20$) of outdoor experimental pond ecosystems (15,000 L), we manipulated the presence of two foundation species, the macrophyte *Myriophyllum spicatum* and the mussel *Dreissena polymorpha*, and quantified ecosystem responses to multiple nutrient disturbances, spread over two years. In the first year, we added five nutrient pulses, ramping up from 10 to 50 µg P/L over a 10-week period from mid-July to mid-October, and in the second year, we added a single large pulse of 50 µg P/L in mid-October. We used automated sondes to measure multiple ecosystems properties at high frequency (15-minute intervals), including phytoplankton and dissolved organic matter fluorescence, and to model whole-ecosystem metabolism. Overall, both foundation species strongly affected the ecosystem responses to nutrient perturbation, and, as expected, initially suppressed the increase in phytoplankton abundance following nutrient additions. However, when both species were present, phytoplankton biomass increased substantially relative to other treatment combinations: non-additivity was evident for multiple ecosystem metrics following the nutrient perturbations in both years but was diminished in the intervening months between our perturbations. Overall, these results demonstrate how interactions between foundation species can cause surprisingly strong deviations from the expected responses of aquatic ecosystems to perturbations such as nutrient additions.

Key words: aquatic ecosystems; chlorophyll; eutrophication; foundation species; high-frequency time series; metabolism; non-additive effects; perturbation.

Introduction

Foundation species in an ecosystem can affect how other organisms take up resources, grow, reproduce, and interact with competitors, pathogens, and consumers (Stachowicz 2001, Olff et al. 2009, Kéfi et al. 2012). It is well known that interactions among species can affect the functioning of ecosystems by regulating fluxes of energy and matter, ecosystem productivity and metabolism, and by mediating the response of ecosystems to perturbation (Loreau et al. 2001, Chapin et al. 2011). Species with disproportionate effects on community structure and ecosystem functioning (Angelini et al. 2011, Falkenberg et al. 2012) have been dubbed foundation species (Dayton 1972), in light of their definitive role in creating locally stable conditions for other species. In the face of disturbance, foundation species can individually or interactively affect multiple ecosystem components (Ellison et al. 2005, Darling and Côté 2008), and potentially cause surprising effects on ecosystems (Paine et al. 1998). The interplay between species interactions and external drivers of environmental change makes it particularly challenging to forecast ecosystem responses to multi-faceted biotic and abiotic aspects of

Manuscript received 27 August 2020; revised 15 January 2021; accepted 22 February 2021; final version received 12 April 2021. Corresponding Editor: Shelley E. Arnott.
[7]Department of Biology, Lund University, Lund 22362 Sweden
[6] E-mail: moritz.lurig@biol.lu.se

anthropogenic disturbances (Petchey et al. 2015, Donohue et al. 2016, Spears et al. 2017).

Eutrophication is a threat to aquatic ecosystems worldwide (Smith et al. 1999, Smith 2003), and it is important to characterize whether nutrient pulses lead to gradual or sudden shifts in ecosystem conditions (Scheffer et al. 1993, Smith 2003, Carpenter 2005, van Nes et al. 2007, Hillebrand and Kunze 2020), and to understand the mechanisms underlying these responses (Hillebrand and Kunze 2020). For example, ecosystem responses to nutrient perturbation might be mediated by the interactions among key species and abiotic components of ecosystems (Scheffer et al. 1993, Kéfi et al. 2016). Alternatively, how ecosystems respond and recover from perturbation might depend on a broader community context, such as how ecosystem functioning scales with variation in species composition (Pennekamp et al. 2018, Hillebrand and Kunze 2020). Furthermore, just as multiple stressors can have interactive effects on individual species responses (Darling and Côté 2008, Côté et al. 2016, Jackson et al. 2016), multiple key species (e.g., foundation species) can have interactive effects on entire ecosystems (Stachowicz 2001, Angelini et al. 2011, Falkenberg et al. 2012). As such, non-additive ecosystem responses to synergistic or antagonistic species interactions may impair our ability to predict ecosystem responses to disturbance (Allgeier et al. 2011, Kéfi et al. 2016, Spears et al. 2017, Thompson et al. 2018, Tekin et al. 2020), and to understand ecosystem resistance and resilience (Scheffer et al. 1993, Darling and Côté 2008, Donohue et al. 2016, Jackson et al. 2016).

Both macrophytes and mussels can have important effects on aquatic ecosystems due to their capacity to limit phytoplankton biomass in the face of increasing nutrient loading (Jeppesen et al. 1998, Bierman et al. 2005, Ibelings et al. 2007, Lürig et al. 2020). Macrophytes, which are considered to be important foundation species (Scheffer et al. 2003, Kéfi et al. 2016), can be competitively dominant over phytoplankton at low nutrient loading (Lürig et al. 2020), and may persist at intermediate nutrient loading via a positive feedback between macrophyte growth and water transparency (Carpenter and Lodge 1986, Jeppesen et al. 1998). By comparison, mussels have high grazing rates on phytoplankton, (Johengen et al. 1995, James et al. 1997) and can dramatically increase water clarity in some lake ecosystems (Ibelings et al. 2007). Current theory suggests that both species may facilitate the presence of each other: macrophytes can provide habitat for *Dreissena* mussels to settle on (Ibelings et al. 2007, Karatayev et al. 2014*b*), and mussels can actively decrease local turbidity, thus improving environmental conditions for submerged macrophytes (Ibelings et al. 2007). Such synergies are common in ecological communities (Stachowicz 2001, Angelini et al. 2011, Falkenberg et al. 2012), and a hallmark of foundation species (Ellison 2019). However, there is also potential for antagonistic interactions between macrophytes and mussels that could unfold under nutrient perturbation scenarios. Macrophytes produce polyphenols and fatty acids that inhibit phytoplankton growth (Korner and Nicklisch 2002, Hilt and Gross 2008), potentially limiting food supply for mussels. Mussels, via their grazing pressure, can shift the composition of phytoplankton communities toward species that are potentially less affected by allelochemicals (Vanderploeg et al. 2001, Fishman et al. 2010) or respond more strongly to nutrient perturbation (e.g., cyanobacteria; Smith and Schindler 2009, Lürling et al. 2018).

As foundation species, macrophytes and mussels are also likely to affect other important ecosystem properties, either independently or interactively. For example, if foundations species affect the buildup of dissolved organic matter (DOM) and the overall oxygen metabolism of ecosystems (Scheffer et al. 1993, Kéfi et al. 2016, Lürig et al. 2020), then this could affect how external disturbances propagate through the network of biological and abiotic interactions in aquatic ecosystems (Olff et al. 2009). Pulsed ecosystem disturbances can characteristically affect both the mean and variance of ecosystem conditions (Hillebrand et al. 2020), and previous nutrient addition experiments in aquatic ecosystems have documented such effects (Carpenter et al. 2011, Scheffer et al. 2012, Gsell et al. 2016). However, the data requirements for testing how species interactions affect ecosystem responses to nutrient perturbation are substantial. Ideally, we would want the capacity to make high-resolution ecosystem measurements in well-replicated experiments that are conducted over ecologically relevant time scales for the communities of interest. Automated sondes deployed in each replicate ecosystem of an experiment can provide the appropriate resolution to capture, for example, diurnal changes in phytoplankton biomass concurrently with abiotic changes (e.g., temperature and conductivity) and rates of ecosystem metabolism, such as net primary productivity and respiration (Carpenter et al. 2011, Batt et al. 2013, Nielsen et al. 2013, Lürig et al. 2020). These processes are largely driven by the autotrophic lake community, both benthic (e.g., macrophytes) and pelagic (e.g., phytoplankton) but can also be affected by DOM dynamics associated with the growth and decay of biomass (Catalán et al. 2014). To capture these ecosystem dynamics, the relevant experimental scale might be multiple months to years. Methods have been developed to quantify whole-ecosystem metabolism from high-frequency measurements (Staehr et al. 2010, Lürig et al. 2020), and using such approaches in experimental settings will undoubtedly reveal new insights into the resistance and resilience of aquatic ecosystems (Batt et al. 2013).

Here, we performed a pond experiment in which we manipulated, in a factorial design ($N = 16$ ponds; four replicates per treatment combination), the presence and absence of the macrophyte *Myriophyllum spicatum* and the mussel *Dreissena polymorpha*. In the first year of the

study, we progressively increased the input of inorganic nutrients (see *Methods*) to these 16 ponds with a series of five pulses (ranging 10–50 μg P/L over a 10-week period from mid-July to mid-October) and, in the second year, added one large pulse (50 μg P/L in mid-October). We left four additional ponds unperturbed, serving as "oligotrophic controls" (16 + 4 = 20 ponds in total). Over the course of the study, we used automated sondes to quantify high-resolution ecosystem responses of several biotic and abiotic ecosystem parameters. In a previous paper that used the same experimental setup, we found strong interactive effects on the ecosystem in the first year of the nutrient manipulation, based on manual low-frequency sampling, and focused primarily on the phytoplankton community response (Narwani et al. 2019). Here, we characterize whole-ecosystem responses measured at high resolution (15-minute frequency) and over the entire 20-month study, including both time periods where we added nutrients, and the intervening period of about 12 months without nutrient additions. Importantly, the high-resolution measurements allowed us to resolve ecosystem dynamics more finely and to calculate rates of ecosystem metabolism. Furthermore, we could explore how a progressive increase in pulse intensity might affect the capacity of the system to recover between individual pulses and compare this to ecosystem recovery over a prolonged period without direct manipulation. Indeed, variation in the nature of ecosystem disturbance (e.g., frequency and intensity of pulses, duration and timing of disturbance) can have important consequences for ecosystem variability in general (Fraterrigo et al. 2020), and for recovery dynamics in particular (Zelnik et al. 2018). Across the entire study, we found that the strong non-additivity of ecosystem responses to our nutrient manipulations were remarkably similar in both years. These effects were strongest following nutrient additions, and less pronounced in the intervening period. Overall, our results emphasize the importance of understanding how interactions among foundation species can affect ecosystem responses to disturbance.

Materials and Methods

Study design and setup

We conducted a pond experiment ($N = 20$ ponds) on a site next to Eawag Dübendorf in the canton of Zürich, Switzerland (47°24′18.2″ N 8°36′31.7″ E). The outdoor ponds (15,000 L) were made of fiberglass with a smooth surface (Fig. 1D), had a rounded shape with an approximately 4 m diameter and a shallow (0.5 m) and a deep (1.5 m) end. The ponds were initially set up on 6 May 2016 by adding a 5 cm thick layer of gravel (2–4 mm diameter) and filling them with tap water, and inoculating them with a natural phytoplankton population (20 L of lake water collected at 1 m depth and filtered through a 30-μm mesh) that was filtered from Lake Greifensee, a dimictic, mesotrophic lake (Bürgi et al. 2003). We installed multiparameter sondes (EXO2, YSI, Yellow Springs, OH, USA) in each pond, and tracked ecosystem parameters with high-frequency (15-minute intervals) measurements of chlorophyll *a* fluorescence (hereafter chlorophyll) and phycocyanin fluorescence, DOM fluorescence (hereafter fDOM), temperature, and dissolved oxygen. Using these data, along with both light and wind data collected on site, we calculated rates of ecosystem metabolism (gross primary production, net primary production, and respiration). All optical sensors were wiped clean before every measurement with a built-in wiper. Details on sonde calibration and maintenance can be found in the Supplement. Over the first winter period (1 December 2016–28 February 28), we could not monitor ecosystem metabolism due to ice cover in the ponds. To maintain and recalibrate the sensors, we stopped measurement from 1–23 March to (see Supplement for details), and in the fall of 2017 (14 September–3 October 2017). Hence, we consider three phases of the experiment: Phase 1 with the first five nutrient pulses (June–December 2016), Phase 2 without nutrient pulses (March–October 2017), and Phase 3 with the final nutrient pulse (October 2017–February 2018).

To initiate the 20-month experiment (May 2016–February 2018), we manipulated the presence and absence of two foundation species: the macrophyte *M. spicatum* (Fig. 1B*;* hereafter *Myriophyllum*) and the mussel *D. polymorpha* (Fig. 1C*;* hereafter *Dreissena*) in artificial ponds. Both species co-occur within the Greifensee catchment. We used a fully factorial design with either both foundation species absent as a control (C), *Myriophyllum* alone (M), *Dreissena* alone (D) or *Myriophyllum* and *Dreissena* together (MD). Each factorial treatment combination was replicated four times (16 ponds) and received a common nutrient perturbation regime over the entire experiment. In addition, we had four replicate ponds that received neither foundation species nor nutrients over the course of the study (oligotrophic control). The treatments were established on 31 May 2016 by distributing 100 shoots of *Myriophyllum* (19.84 g of dry biomass), each attached with a cable tie to a small rock, within each pond designated to the M and MD treatment. The plants were purchased at a horticulture store, allowing us to standardize the age-distribution of the introduced plants and limit the uncontrolled introduction of organisms associated with the plants into the ponds. Each pond that was designated for the D and MD treatment received 25 adult *Dreissena* (632.7 g of soft tissue dry biomass) that were collected from rocks at 1.5 m depth in Lake Greifensee. Both *Myriophyllum* and *Dreissena* were distributed among the shallow and deep end within each pond. The stocking density roughly matches those observed in nature, at levels where macrophytes are thought to have significant ecosystem effects (~10–15% coverage; approximately 100–150 cm^2 per shoot and approximately 9.2 m^2 benthic surface per pond; Hilt and Gross 2008, McLaughlan and Aldridge 2013, Karatayev et al.

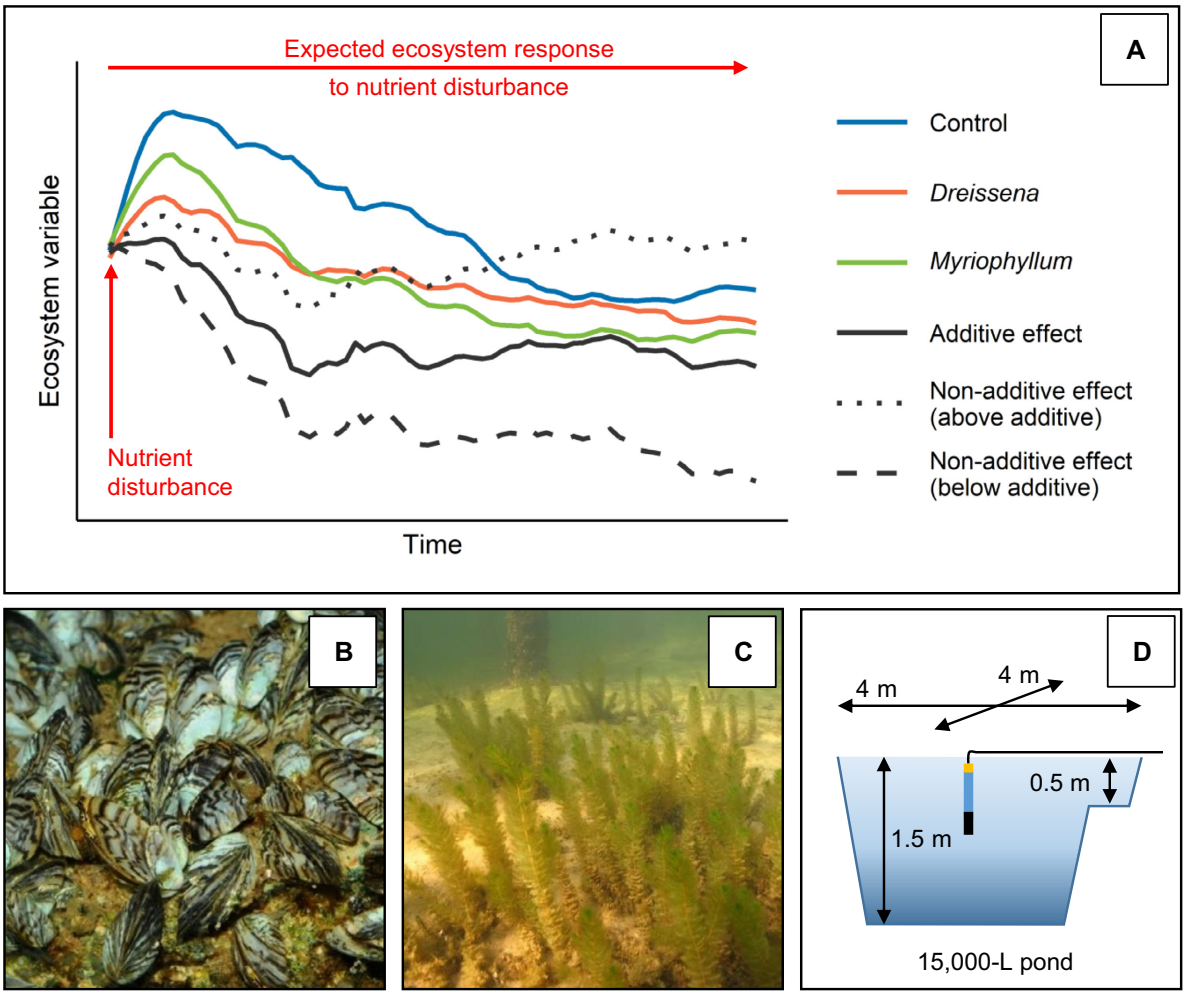

FIG. 1. (A) Schematic depiction of how the absence (control, blue line) and the presence of foundation species (*Dreissena polymorpha*, orange line; *Myriophyllum spicatum*, green line) is hypothesized to affect the ecosystem response ecosystems to a nutrient disturbance. Shown are time series of a generic ecosystem variable (e.g., chlorophyll *a* concentration), which we use to illustrate the expectation for what would be an additive effect on the ecosystem variable (black line, control – (*Myriophyllum* + *Dreissena*)). The recorded time series from ecosystems with both foundation species present can also be non-additive, leading to responses above (dotted lines) or below (dashed line) the additive expectation. (B) *Dreissena polymorpha*, zebra mussel (Photo credit: N. Sloth). (C) *Myriophyllum spicatum*, Eurasian water milfoil (Photo credit: P. Dynowski). (D) Schematic of the experimental ponds: the ponds are approximately 4 m in diameter and have a deep (1.5 m) and a shallow end (0.5 m), where we planted macrophytes and mussels. In the middle of each pond, we placed a multiparameter sonde at 1 m depth to monitor ecosystems dynamics.

2014*a*). We ensured prior to the distribution of plant shoots and mussels that their size distributions were similar across all ponds of the respective treatment. Furthermore, to keep an overall nutrient balance among ponds, we added autoclaved mussels to the M ponds, autoclaved *Myriophyllum* shoots to the D ponds, and both autoclaved mussels and *Myriophyllum* shoots to the C ponds. Given the size of the ecosystems, these additions had no noticeable effects on nutrient concentration and algal biomass. In May 2017, we reestablished our macrophyte treatment after the winter by adding the same amount of either fresh or autoclaved *Myriophyllum* shoots to the respective ponds to maintain the treatment contrasts.

Nutrient disturbances

Over the 20-month experiment, we established a common nutrient addition regime for the 16 ponds that were part of the factorial manipulation of foundation species. As reported in Narwani et al. (2019), there were no differences in nutrient concentrations among the factorial treatment combinations leading up to the first manipulation of nutrients. On 12 August 2016, we began the

nutrient manipulation by progressively increasing additions of P, from 10, 20, 30, 40, to 50 μg/L (in the form of KNO_3 and K_2HPO_4, maintaining a N:P = 32) over eight weeks until 10 October 2016. The target nutrient concentrations are typical for eutrophic lakes (Søndergaard et al. 2003, Welch and Cooke 2005) and are within the nutrient loading range of previous experiments in mesocosms (Iacarella et al. 2018). We chose this increasing intensity of pulses, with 2-week intervals between them (vertical bars in Figs. 2–5), in order to better understand variation in the resistance (amplitude of change) and recovery (degree of or time until returning to pre-disturbance state) of the systems in response to variation in the level of nutrient perturbation. As anticipated, the additions of nutrients temporarily increased the dissolved nutrient concentrations relative to the pre-disturbance levels, and then declined rapidly with increased biomass production (see Fig. 2 in Narwani et al. [2019]). Progressively increasing nutrient additions in the first year allowed us to observe variation in ecosystem recovery, both between pulses and over the entire study duration (20 months in total).

Based on the results from the first round of nutrient additions, we decided to leave the ecosystems unperturbed for 12 months in order to observe whether interactions among foundation species might affect the dynamics of ecosystem recovery in the absence of any nutrient manipulations, but in the presence of typical seasonal variation (including ice cover, storms, rainfall, and heatwaves). Monitoring the ecosystem dynamics over this subsequent year was only practical because we had an automated sonde deployed in each experimental ecosystem. On 10 October 2017, exactly one year after we completed our initial set of five nutrient pulses, we added a final nutrient pulse of 50 μg/L of P (again with an N:P ratio of 32). We used a single pulse in order to test whether the dramatic effects we observed after the final pulse in the first year of nutrient additions would persist after 12 months of ecosystem recovery. Overall, we chose our disturbance scheme for the entire experiment in order to capture variation in the resistance and recovery of the ecosystems, while not overloading them with nutrients and pushing them beyond their capacity to return to more clearwater conditions. We were successful in this respect, because the ecosystems did not exhibit sustained divergence from the oligotrophic control ponds during the recovery period between nutrient additions (Phase 2, Figs. 2–5).

Data analysis

For the time series of ecosystem dynamics, we first performed an outlier analysis by excluding values higher than three times the median absolute deviation of all values in a sliding window (Leys et al. 2013) of one day window size (15-minute interval = 96 data points). In addition to outlier removal, we visually inspected the data and manually removed anomalous periods from the data (<2%; for more details refer to Russo et al. [2020]). After aggregating four measurement points to one per hour (from 96 to 24 data points per day), we calculated mean and coefficient of variation (hereafter CV) of the aggregated data within windows that were sized one week ($7 \times 24 = 168$ data points). We then moved the window across the data set in increments of one data point to calculate mean and CV for the entire data set (sliding window approach). We chose a 7-d window size to have robust estimates of the different metrics that would not be affected by diurnal variability. Moreover, we calculated autocorrelation (hereafter AC, Appendix S1: Fig. S1), which can be used to quantify the characteristics of high-frequency dynamics of disturbed ecosystems (Batt et al. 2013, 2017, Gsell et al. 2016). For example, as ecosystems are disturbed, their properties tend to become more similar to their own past, resulting in an increase in AC (Ives 1995).

Using the data derived from the sliding windows, we tested for differences between treatments using the factorial design manipulating presence and absence of foundation species ($n = 4$ per treatment level; a_D, main effect of *Dreissena*; b_M, main effect of *Myriophyllum*; $C_{(D\times M)}$, interactive effect)

$$y = a_D + b_M + C_{(D\times M)} + \text{error}.$$

We used one linear model with Type III sum of squares per hour (24 models per day) to test for differences between treatments in mean CV and AC of each measured parameter. In each model, the metric (mean, CV, or AC) of the respective ecosystem parameter (chlorophyll, phycocyanin, fDOM, or dissolved oxygen) was the dependent variable. We report P values from linear models for mean and CV directly in Figs. 2 and 3, where points below the time series color coded by treatment indicate a significant difference of the respective treatment from the control. Because there were no systematic differences between treatments for AC, we report results for these metrics in Appendix S1: Fig. S1. For better visual inference, we present data in the figures from the sliding windows aggregated to a single data point per day. In addition, we calculated the predicted additive response of *Myriophyllum* and *Dreissena* for each data point by subtracting the control from the summed single species treatments ((*Dreissena* + *Myriophyllum*) − Control). The interaction between the presence of *Myriophyllum* and *Dreissena* was considered non-additive when the confidence interval of the MD treatment did not overlap with the predicted additive response.

Ecosystem metabolism

We calculated gross primary productivity, net ecosystem production, and respiration (hereafter GPP, NEP, and R, respectively) of each pond using the equations in Staehr et al. (2010), which uses time series of dissolved oxygen and temperature collected by the sondes, as well

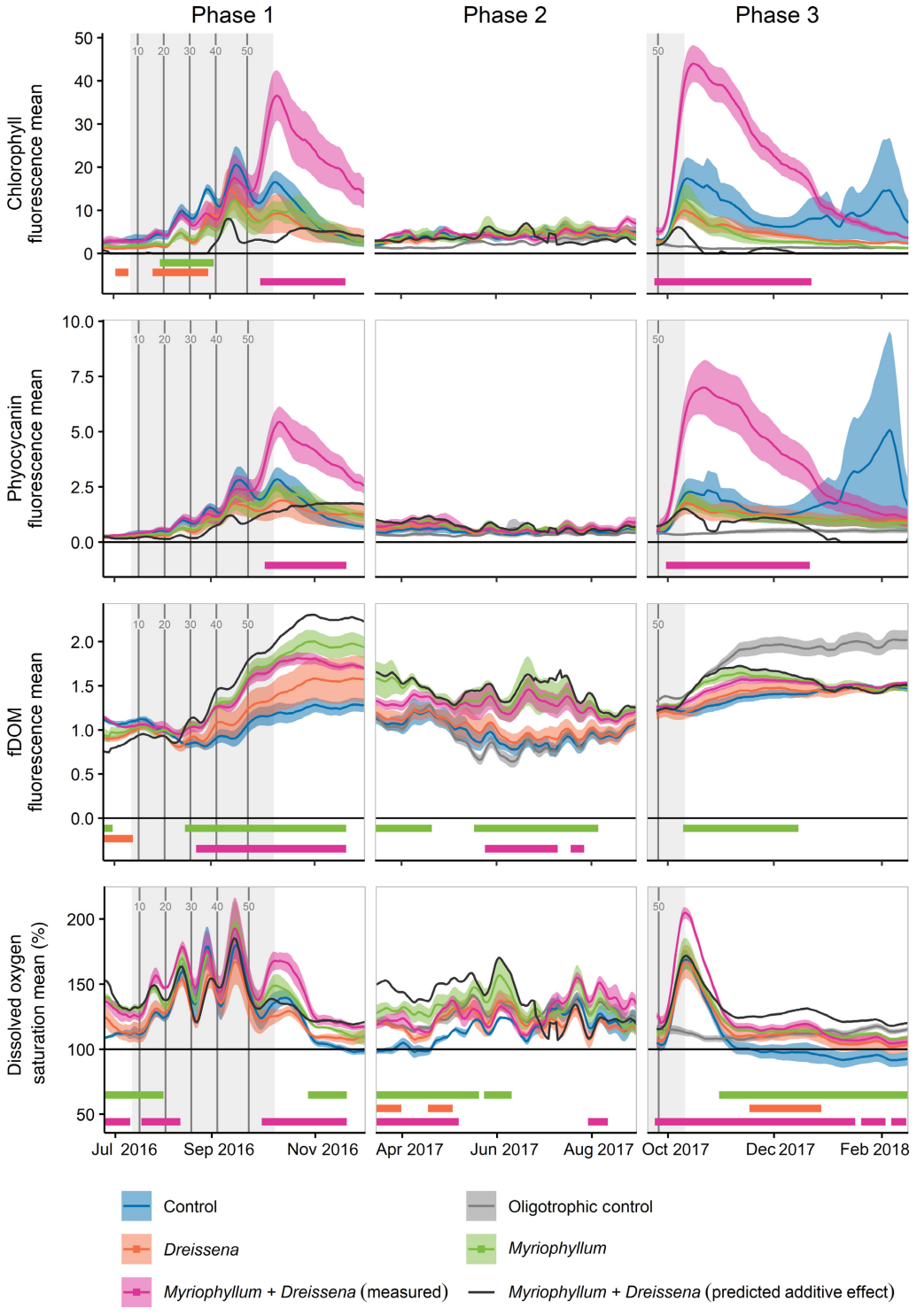

FIG. 2. Effect of foundation species on the mean of ecosystem parameters in Phase 1, Phase 2, and Phase 3 (left, middle, and right panel, respectively). The lines indicate the respective average of all four ponds per treatment per hour (mean ± SE), the gray shading indicates the disturbance phases, and the colored bars underneath the time series indicate whether a treatment was significantly different from the control (one linear model per hour: orange, *Dreissena* main effect [D treatment]; green, *Myriophyllum* main effect [M treatment]; purple, interactive effect [MD treatment]). The data stem from a 7-d long sliding window (168 data points). The black line indicates the predicted additive response based on the sum of the separate macrophyte or mussels treatment with the control subtracted (e.g., (macrophyte chlorphyll + *Dreissena* chlorophyll) − control chlorophyll = predicted additive response; chlorophyll is chlorophyll *a*). DOM fluorescence is abbreviated fDOM.

as surface light levels (collected on site with a light meter [LI-1500 and LI-190R, LI-COR Biosciences GmbH, Lincoln, NE, USA]) and wind speed at 10 m from a nearby (200 m) weather station operated by Meteo Swiss (Dübendorf, Giessen, 47°24'10″ N, 08°36'49″ E). Because the ponds were oversaturated with respect to dissolved oxygen, we determined average rates of change in dissolved oxygen from a linear regression to hourly averages in the time intervals between 13:00 and 17:00 for the day and 01:00 and 05:00 for the night. Visual inspection of the data indicated that piston velocities defining gas exchange were rather constant during these times and potential nonlinear effects caused by the formation and dissolution of gas bubbles in the oversaturated waters were small (Staehr et al. 2010). Using the metabolism data we calculated the mean and CV of all three metabolism parameters by applying a sliding window with the size of 7 d. We then tested for differences between treatments with single species (M and D, main effect) and multiple species (MD, interactive effect) and control (C) using one linear model per day. We report the results from the linear models directly in Figs. 4 and 5 as color coded points that indicate significant differences in metabolic rates of M, D, or MD from C. Furthermore, we calculated the predicted additive effect in the same fashion as for the other ecosystem parameters.

Results

Effects of foundation species on mean ecosystem parameters

Myriophyllum and *Dreissena* affected a wide range of ecosystem parameters. During the first nutrient addition, ponds with *Myriophyllum* or *Dreissena* alone had lower chlorophyll fluorescence than the C ponds, consistent with their anticipated negative effects on the phytoplankton community (Fig. 2). However, following both disturbances, the co-occurrence of these species had strong positive effects on algae abundance (i.e., non-additive and in the opposite direction). Furthermore, after the first set of nutrient additions, and throughout the remainder of the experiment, the presence of *Myriophyllum* increased the concentration of DOM in the ecosystems, independent of *Dreissena* presence (i.e., in both M and MD treatments). The presence of *Myriophyllum* and *Dreissena*, either alone or in combination, positively affected dissolved oxygen saturation throughout most of the experiment, except during the perturbation periods where nutrient addition dramatically increased DO saturation (between 150% and 200%) in all treatments.

Effects of foundation species on variance of ecosystem parameters

We found only weak effects of *Myriophyllum* and *Dreissena* presence on the CV (Fig. 3) and AC (Appendix S1: Fig. S1) of ecosystem parameters. In all ponds receiving nutrients, we found strong increases in CV immediately after the nutrient additions. Prior to the first nutrient additions, the ponds with either *Myriophyllum* or *Dreissena* alone were less variable in chlorophyll fluorescence (Fig. 3). After the second nutrient pulse, the ponds with both species had significantly higher variance in chlorophyll and phycocyanin fluorescence than when species were either alone or absent. There were almost no effects of foundation species on the variance of DOM fluorescence (Fig. 3). There were some indications that *Myriophyllum* affected the CV of dissolved oxygen saturation, but these effects were weak and varied in their sign over time. As expected, each nutrient addition led to a temporary increase in AC across all treatment contrasts and parameters (visible as spikes in the time series, Appendix S1: Fig. S1), but we did not identify treatment specific differences in AC.

Ecosystem metabolism

GPP and NEP, as well as *R* were strongly affected by nutrient perturbation and seasonal dynamics, and more weakly affected by the treatment combinations of foundation species (Fig. 4). Each nutrient addition led to correlated increases of GPP, NEP, and *R*, which reverted within days after the maximum was reached. During each of these peaks, there were only small differences among treatments across all metabolism metrics. During spring 2017, at the beginning of the second phase, all ponds containing *Myriophyllum* or *Dreissena* had lower NEP and higher *R* than ecosystems without foundation species. We found a similar pattern toward the end of the experiment, after the second nutrient addition in Phase 3, where both GPP and NEP were lower and *R* higher when foundation species were present. Overall, there were only weak effects on variance patterns of ecosystem metabolism (Fig. 5): there was a tendency for MD ponds to have higher CV of GPP and NEP than ponds without any foundation species, especially in Phase 3. Interestingly, the CV of GPP and NEP increased during the nutrient perturbations, but not R, whose CV appeared to increase only after the last pulse had been added.

Discussion

The pulsed nutrient perturbations caused strong ecosystem responses, some of which were dependent on the presence of foundation species and their co-occurrence. In the first year of nutrient pulses, both *Myriophyllum* and mussels independently suppressed algal biomass relative to ponds without these foundation species (control [C] ponds). However, when both species were in the ponds, the same nutrient additions led to a stark increase in algal biomass: evidence for a strong non-additive effect of both foundation species on these pond ecosystems. Such effects were less evident (albeit at

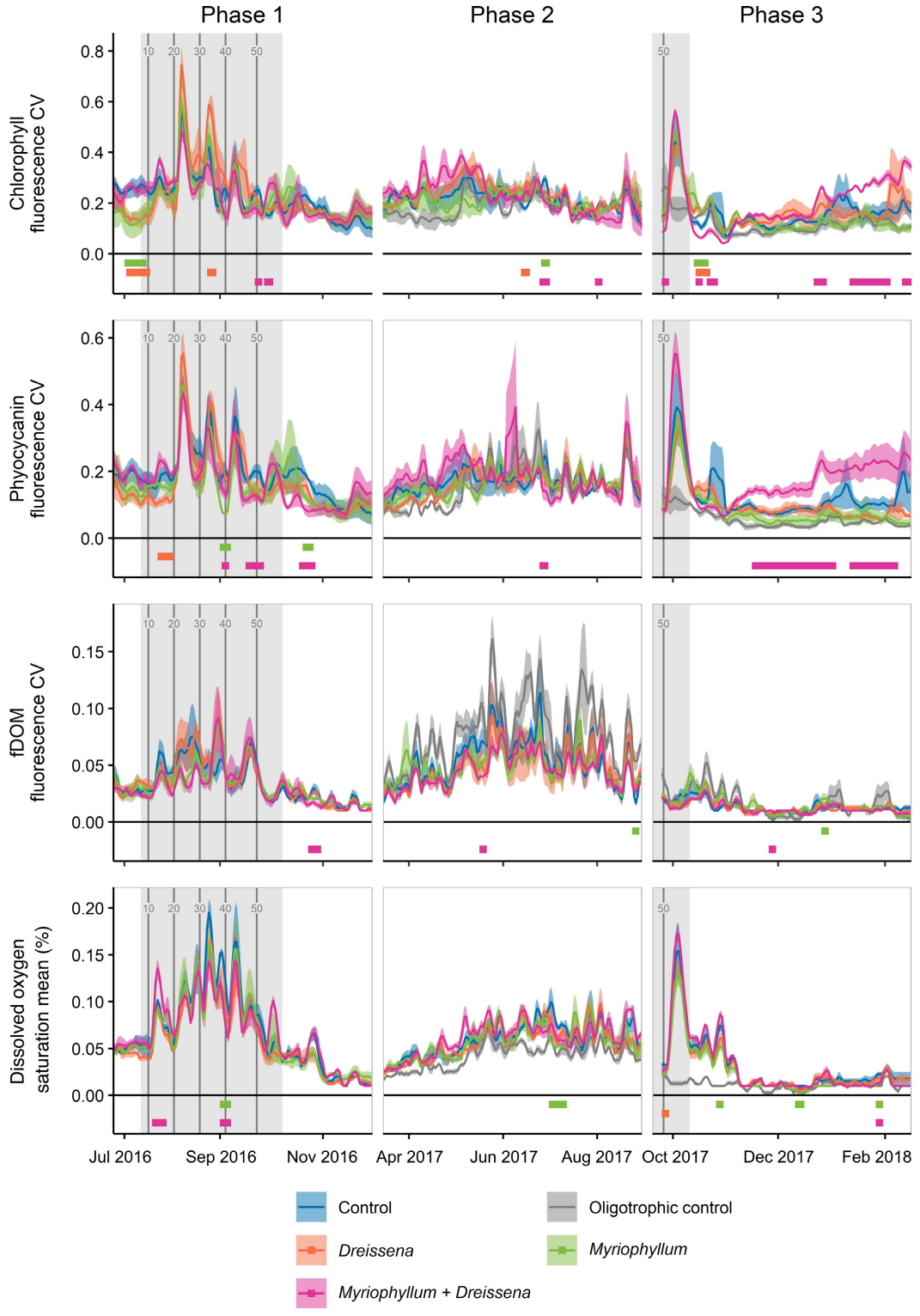

FIG. 3. Effect of foundation species on variance (coefficient of variation, CV) of ecosystem parameters in Phase 1, Phase 2, and Phase 3 (left, middle, and right panel, respectively). The lines indicate the respective average of all four ponds per treatment per hour (mean ± SE), the gray shading indicates the disturbance phases, and the colored bars underneath the time series indicate whether a treatment was significantly different from the control (one linear model per hour: orange, *Dreissena* main effect [D treatment]; green, *Myriophyllum* main effect [M treatment]; purple, interactive effect [MD treatment]). The data stem from a 7-d long sliding window (168 data points).

times significant) both prior to nutrient additions and in the recovery phase between nutrients additions (Phase 2), but they reemerged following a nutrient pulse near the end of the study.

The suppression of phytoplankton responses to increased nutrient loading by either macrophytes or mussels alone is consistent with a large body of previous theoretical and empirical work (van Nes et al. 2007, Iacarella et al. 2018, Yamamichi et al. 2018, Lürig et al. 2020). For example, macrophytes can outcompete phytoplankton under certain nutrient loading and light conditions (Iacarella et al. 2018, Lürig et al. 2020), and produce allelopathic substances that inhibit phytoplankton growth (Nakai et al. 2001, 2012, Korner and Nicklisch 2002, Hilt and Gross 2008). However, these mechanisms are typically insufficient to suppress phytoplankton when nutrient loading is high and light transparency is sufficiently low (Scheffer et al. 1993, van Nes et al. 2007, Kéfi et al. 2016, Yamamichi et al. 2018). In our experiment, macrophytes died back over the course of the first year and were at a low abundance during the first set of nutrient additions. However, *Myriophyllum* is known to have strong effects even at extremely low densities (Hilt and Gross 2008), so it is possible that even with greatly reduced coverage (initially 10–15% of the benthic surface) macrophyte effects were still detectable. Moreover, the observed differences between treatments with and without *Myriophyllum* could be explained by their prior effects (e.g., on the plankton community or water parameters) on the ecosystems throughout the summer and early fall. Despite the collapse of macrophytes by the end of the first year, their presence and production over the summer likely affected the dynamics of dissolved organic matter (Fig. 2): fDOM increased more rapidly and to higher levels in both M and MD treatments than in ponds without *Myriophyllum* (C and D). This was expected, as *Myriophyllum* is known to be a producer of a wide range of organic substances (Lürig et al. 2020), including allelopathic chemicals that can be either actively released by the plant or dissolve into the water column upon its death (Catalán et al. 2014, Reitsema et al. 2018).

The sole presence of *Dreissena* also led to a significant suppression of phytoplankton biomass relative to control ponds (C) in both years following nutrient additions. *Dreissena* can remove large quantities of algae and suspended materials from the water column, thereby maintaining greater water transparency in response to nutrient loading (Gulati et al. 2008, McLaughlan and Aldridge 2013). It has been shown that population growth of mussels can be very high in eutrophic lakes (Karatayev et al. 2014*a*, Strayer et al. 2019), if sufficient amounts of hard substrate are available (Ibelings et al. 2007, Fishman et al. 2010). In such cases, *Dreissena* can not only affect water clarity and nutrient cycling, but also shift the composition of the phytoplankton community toward a higher proportion of cyanobacteria (Vanderploeg et al. 2001, Bierman et al. 2005, Fishman et al. 2010). *Dreissena* can also selectively reject particles as "pseudofeces," which will release less palatable particles like cyanobacteria back to the environment (Vanderploeg et al. 2001). If this loosely consolidated substrate contains viable cyanobacteria, these cells can be resuspended in the water column while other phytoplankton species are filtered from the water column and consumed by the mussel.

The observed non-additive dynamics of chlorophyll fluorescence in the presence of both *Myriophyllum* and *Dreissena* coincided with a dramatic shift toward cyanobacteria in the first year (Fig. 2; Narwani et al. 2019). Indeed, in an analysis of phytoplankton species composition of the ponds in year 1, Narwani et al. (2019) found that the small cyanobacterium *Synechococcus* was only dominant when both *Myriophyllum* and *Dreissena* were both present. In a laboratory experiment, Narwani et al. (2019) tested how a factorial manipulation of *Dreissena* grazing and a water solution from *Myriophyllum* incubations ("*Myriophyllum*-tea"), affected the relative concentration of two species of microalgae (*Lagerheimia* sp. and *Synechococcus* sp.): two species present in the ponds prior to the first nutrient additions. In this laboratory experiment, *Synechococcus* increased in abundance relative to the green algae *Lagerheimia* when both *Dreissena* and *Myriophyllum*-tea were present together (Narwani et al. 2019). In our ponds, we suspect that the combination of allelochemicals and direct grazing by *Dreissena* had differential effects on *Synechococcus* and *Lagerheimia,* such that *Synechococcus* gained a competitive advantage and increased its dominance in the MD pond communities over the first summer of the experiment. Subsequently, the nutrient additions caused the greatest biomass production in those pond communities dominated by *Synechococcus.*

In our 20-month pond study, ecosystem metabolism varied seasonally, responded strongly to nutrient manipulations in the early fall, and was influenced by our manipulations of foundation species. Being an outdoor experiment, all ponds experienced the same seasonal forcing. All metabolic rates increased over the spring until the middle of June, and then decreased until the final nutrient addition at the beginning of Phase 3 in October. Overall, the effects of seasonality on phytoplankton concentration were small compared to the effects of our nutrient manipulations. In the first year, for example, our progressive increase in the nutrient pulse magnitude led to progressively stronger increases in algal biomass over a period with decreasing daylight. Furthermore, after both nutrient manipulations, the dynamics of ecosystem metabolism showed evidence of significant non-additivity caused by the manipulation of the foundation species (Fig. 4, Phase 1 and 3), whereas the differences among treatments in the intervening phase without disturbance (Fig. 4, Phase 2) were more subtle. In the MD treatment, for example, the CV of GPP was often significantly higher than the other treatments during Phase 2, when we would otherwise expect

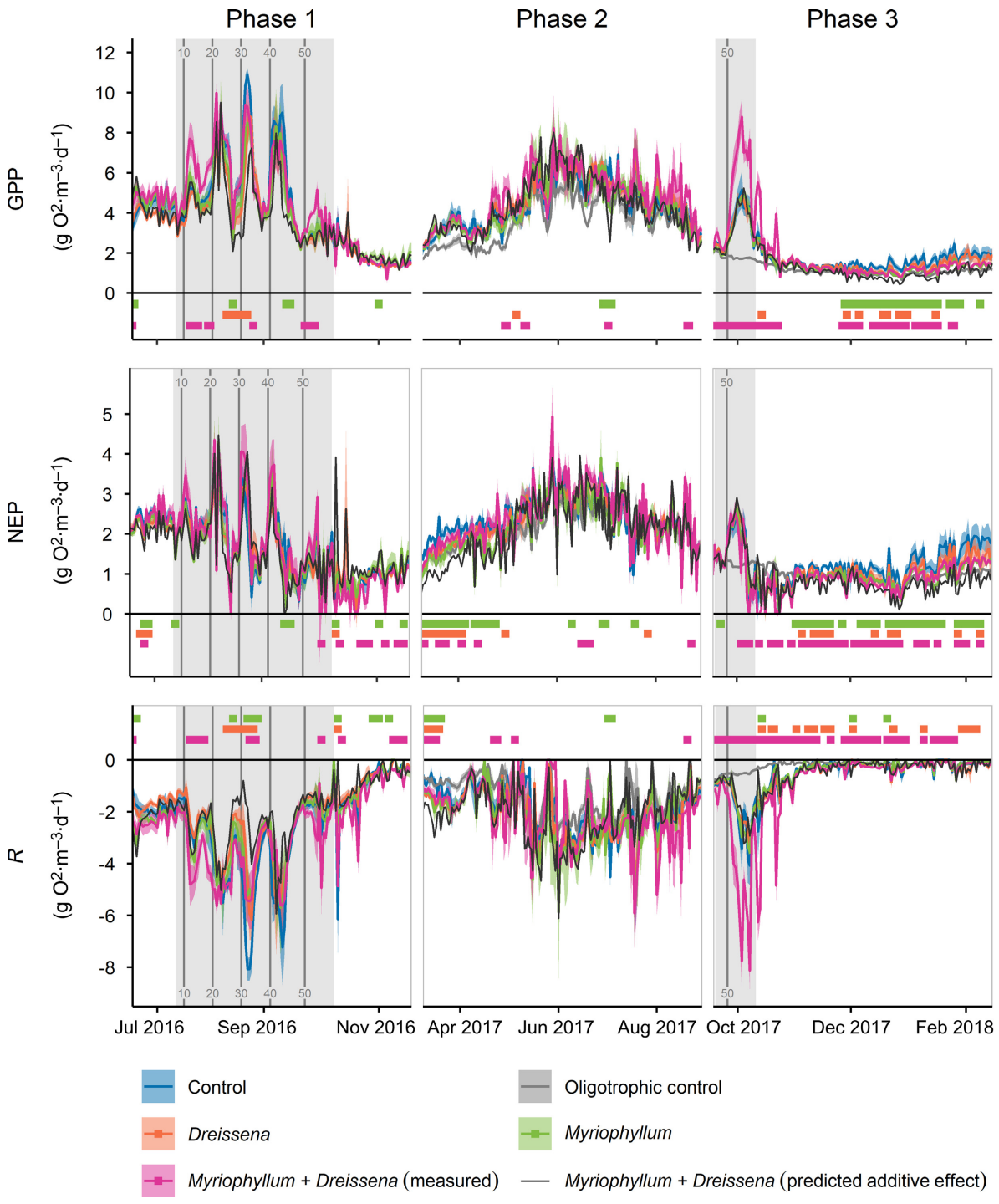

FIG. 4. Effect of foundation species on mean metabolic rates of the ecosystems in Phase 1, Phase 2, and Phase 3 (left, middle, and right panel, respectively). The lines indicate the respective average of gross primary production (GPP), net ecosystem production (NEP), and respiration (*R*) in all four ponds per treatment per hour (mean ± SE). The gray shading indicates the disturbance phases, and the colored bars underneath the time series indicate whether a treatment was significantly different from the control (one linear model per hour: (orange, *Dreissena* main effect [D treatment]; green, *Myriophyllum* main effect [M treatment]; purple, interactive effect [MD treatment]). All rates were calculated using Odum's diel oxygen technique (Staehr et al. 2010). The black line indicates the predicted additive response based on the sum of the separate macrophyte or mussels treatment with the control subtracted.

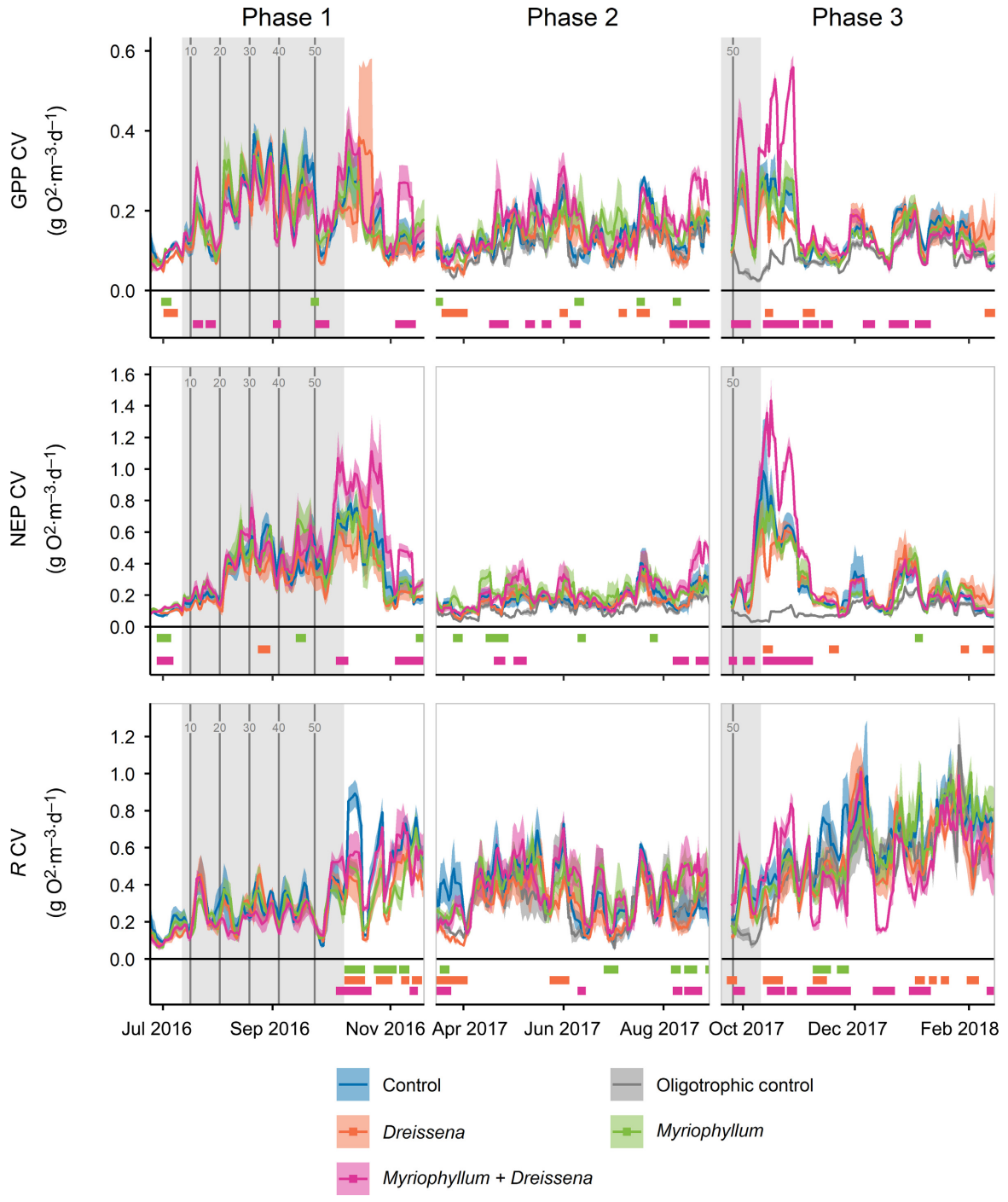

FIG. 5. Effect of foundation species on variance (coefficient of variation, CV) of ecosystem metabolism in Phase 1, Phase 2, and Phase 3 (left, middle, and right panel, respectively). The lines indicate respective average CV of gross primary production (GPP), net ecosystem production (NEP), and respiration (*R*) in all four ponds per treatment per hour (mean ± SE). The gray shading indicates the disturbance phases, and the colored bars underneath the time series indicate whether a treatment was significantly different from the control (one linear model per hour: orange, *Dreissena* main effect [D treatment]; green, *Myriophyllum* main effect [M treatment]; purple, interactive effect [MD treatment]). The data stem from a 7-d long sliding window (168 data points).

seasonal events (e.g., ice cover, storms, rainfall, or heatwaves) to dominate the dynamics. In the weeks following the final nutrient addition, all ecosystems containing foundation species (D, M, and MD) showed significantly lower GPP and NEP, but higher *R* than the control ponds (C). One possible explanation is that chlorophyll concentration in the C ponds continued to increase, while DOM concentration in all other ponds remained stable (Fig. 2), culminating in a divergence in ecosystem metabolism toward the end of the experiment (Fig. 4).

In summary, multiple lines of evidence suggest that non-additive interactions between *Myriophyllum* and *Dreissena* strongly affected ecosystem dynamics in ponds experiencing progressive nutrient perturbations. Such effects were particularly evident in the phytoplankton response: the presence of both *Myriophyllum* and *Dreissena* led to strongly positive effects on algae biomass relative to control ponds, rather than an expected negative effect based on their individual effects. This demonstrates how interactions between two foundation species can have surprising, non-additive effects of aquatic ecosystem responses to nutrient additions. In our particular case, we think this is mediated by a shift in the dominance of the phytoplankton community toward species that respond more strongly to nutrient additions (e.g., cyanobacteria). Ecological synergies following ecosystem perturbation are a known phenomenon, but the underlying mechanisms are poorly understood (Suttle et al. 2007, Darling and Côté 2008, Thompson et al. 2018). In our experiment, the ecosystems converged to very similar conditions in the intervening period between nutrient disturbance periods (Phase 2). Nevertheless, the capacity to differentially respond to nutrient perturbation persisted, and a subsequent perturbation of the ecosystems a year later (at the beginning of Phase 3) led to a qualitatively similar effect as the initial response in Phase 1. While high-frequency ecosystem monitoring has enormous potential to improve our ability to anticipate ecosystem response, in our experiment the monitoring our pond ecosystems in the intervening period between disturbances did not provide obvious clues about how they would respond to subsequent nutrient pulse. Overall, our results illustrate that, for a given disturbance regime, the effects of species interactions on ecosystems can be substantial in their magnitude, surprising in their direction, and persist over time between disturbances.

Acknowledgments

We thank J. Jokela, F. Pomati, and F. Altermatt for discussions regarding experimental design, and J. Jokela, M. Hoyer, M. Reyes, S. Käser, and G. Siegrist for help in setting up the experiment. We also thank D. Steiner for laboratory analyses of chlorophyll for the sensor calibrations. Furthermore, we would like to thank C. Ebi for installing the sonde-grid on site at Dübendorf. This work was supported by a Strategic grant from Eawag, and project grants from the Swiss National Science Foundation to P. Spaak (310030L_166628), B. Wehrli (206021_157750), and B. Matthews (31003A_175614). M. D. Lürig was funded by the Center for Adaptation to a Changing Environment (ACE) at ETH Zürich, and by the Aquatic Ecology Department at Eawag.

Literature Cited

Allgeier, J. E., A. D. Rosemond, and C. A. Layman. 2011. The frequency and magnitude of non-additive responses to multiple nutrient enrichment. Journal of Applied Ecology 48:96–101.

Angelini, C., A. H. Altieri, B. R. Silliman, and M. D. Bertness. 2011. Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. BioScience 61:782–789.

Batt, R. D., S. R. Carpenter, J. J. Cole, M. L. Pace, and R. A. Johnson. 2013. Changes in ecosystem resilience detected in automated measures of ecosystem metabolism during a whole-lake manipulation. Proceedings of the National Academy of Sciences USA 110:17398–17403.

Batt, R. D., S. R. Carpenter, and A. R. Ives. 2017. Extreme events in lake ecosystem time series. Limnology and Oceanography 2:63–69.

Bierman, V. J., J. Kaur, J. V. Depinto, T. J. Feist, and D. W. Dilks. 2005. Modeling the role of zebra mussels in the proliferation of blue-green algae in Saginaw Bay, Lake Huron. Journal of Great Lakes Research 31:32–55.

Bürgi, H. R., H. Bührer, and B. Keller. 2003. Long-term changes in functional properties and biodiversity of plankton in Lake Greifensee (Switzerland) in response to phosphorus reduction. Aquatic Ecosystem Health & Management 6:147–158.

Carpenter, S. R. 2005. Eutrophication of aquatic ecosystems: bistability and soil phosphorus. Proceedings of the National Academy of Sciences USA 102:10002–10005.

Carpenter, S. R., et al. 2011. Early warnings of regime shifts: a whole-ecosystem experiment. Science 332:1079–1082.

Carpenter, S. R., and D. M. Lodge. 1986. Effects of submersed macrophytes on ecosystem processes. Aquatic botany 26:341–370.

Catalán, N., B. Obrador, and J. L. Pretus. 2014. Ecosystem processes drive dissolved organic matter quality in a highly dynamic water body. Hydrobiologia 728:111–124.

Chapin, F. S., P. A. Matson, and P. M. Vitousek. 2011. Species Effects on Ecosystem Processes. Pages 321–336 *in* F. S. Chapin, P. A. Matson, and P. M. Vitousek, editors. Principles of terrestrial ecosystem ecology. Springer, New York, New York, New York, USA.

Côté, I. M., E. S. Darling, and C. J. Brown. 2016. Interactions among ecosystem stressors and their importance in conservation. Proceedings of the Royal Society B 283:20152592.

Darling, E. S., and I. M. Côté. 2008. Quantifying the evidence for ecological synergies. Ecology Letters 11:1278–1286.

Dayton, P. K. 1972. Toward an understanding of community resilience and the potential effects of enrichments to the benthos at McMurdo Sound, Antarctica. Pages 81–96 *in* Proceedings of the colloquium on conservation problems in Antarctica. Allen Press, Lawrence, Kansas, USA.

Donohue, I., et al. 2016. Navigating the complexity of ecological stability. Ecology Letters 19:1172–1185.

Ellison, A. M., et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. Frontiers in Ecology and the Environment 3:479–486.

Ellison, A. M. 2019. Foundation species, non-trophic interactions, and the value of being common. iScience 13:254–268

Falkenberg, L. J., B. D. Russell, and S. D. Connell. 2012. Stability of strong species interactions resist the synergistic effects

of local and global pollution in kelp forests. PLoS ONE 7: e33841.

Fishman, D. B., S. A. Adlerstein, H. A. Vanderploeg, G. L. Fahnenstiel, and D. Scavia. 2010. Phytoplankton community composition of Saginaw Bay, Lake Huron, during the zebra mussel (*Dreissena polymorpha*) invasion: a multivariate analysis. Journal of Great Lakes Research 36:9–19.

Fraterrigo, J. M., A. B. Langille, and J. A. Rusak. 2020. Stochastic disturbance regimes alter patterns of ecosystem variability and recovery. PLoS ONE 15:e0229927.

Gsell, A. S., et al. 2016. Evaluating early-warning indicators of critical transitions in natural aquatic ecosystems. Proceedings of the National Academy of Sciences USA 113:E8089–E8095.

Gulati, R. D., L. M. Dionisio Pires, and E. Van Donk. 2008. Lake restoration studies: failures, bottlenecks and prospects of new ecotechnological measures. Limnologica 38:233–247.

Hillebrand, H., I. Donohue, W. S. Harpole, D. Hodapp, M. Kucera, A. M. Lewandowska, J. Merder, J. M. Montoya, and J. A. Freund. 2020. Thresholds for ecological responses to global change do not emerge from empirical data. Nature Ecology & Evolution 4:1502–1509.

Hillebrand, H., and C. Kunze. 2020. Meta-analysis on pulse disturbances reveals differences in functional and compositional recovery across ecosystems. Ecology Letters 23:575–585.

Hilt, S., and E. M. Gross. 2008. Can allelopathically active submerged macrophytes stabilise clear-water states in shallow lakes? Basic and Applied Ecology 9:422–432.

Iacarella, J. C., J. L. Barrow, A. Giani, B. E. Beisner, and I. Gregory-Eaves. 2018. Shifts in algal dominance in freshwater experimental ponds across differing levels of macrophytes and nutrients. Ecosphere 9:e02086.

Ibelings, B. W., R. Portielje, E. H. R. R. Lammens, R. Noordhuis, M. S. van den Berg, W. Joosse, and M. L. Meijer. 2007. Resilience of alternative stable states during the recovery of shallow lakes from eutrophication: Lake Veluwe as a case study. Ecosystems 10:4–16.

Ives, A. R. 1995. Measuring resilience in stochastic systems. Ecological Monographs 65:217–233.

Jackson, M. C., C. J. G. Loewen, R. D. Vinebrooke, and C. T. Chimimba. 2016. Net effects of multiple stressors in freshwater ecosystems: a meta-analysis. Global Change Biology 22:180–189.

James, W. F., J. W. Barko, and H. L. Eakin. 1997. Nutrient regeneration by the zebra mussel (*Dreissena polymorpha*). Journal of Freshwater Ecology 12:209–216.

Jeppesen, E., M. Sondergaard, M. Sondergaard, and K. Christoffersen. 1998. Pages 115–133 *in* L. M. M. Caldwell, G. Heldmaier, O. L. Lange, E.-D. Schulze, and U. Sommer, editors. The structuring role of submerged macrophytes in lakes. Springer, New York, New York, USA.

Johengen, T. H., T. F. Nalepa, G. L. Fahnenstiel, and G. Goudy. 1995. Nutrient changes in Saginaw Bay, Lake Huron, after the establishment of the zebra mussel (*Dreissena polymorpha*). Journal of Great Lakes Research 21:449–464.

Karatayev, A. Y., L. E. Burlakova, C. Pennuto, J. Ciborowski, V. A. Karatayev, P. Juette, and M. Clapsadl. 2014*a*. Twenty five years of changes in *Dreissena* spp. populations in Lake Erie. Journal of Great Lakes Research 40:550–559.

Karatayev, V. A., A. Y. Karatayev, L. E. Burlakova, and L. G. Rudstam. 2014*b*. Eutrophication and *Dreissena* invasion as drivers of biodiversity: a century of change in the mollusc community of Oneida Lake. PLoS ONE 9:e101388.

Kéfi, S., et al. 2012. More than a meal... integrating non-feeding interactions into food webs. Ecology Letters 15:291–300.

Kéfi, S., M. Holmgren, and M. Scheffer. 2016. When can positive interactions cause alternative stable states in ecosystems? Functional Ecology 30:88–97.

Korner, S., and A. Nicklisch. 2002. Allelopathic growth inhibition of selected phytoplankton species by submerged macrophytes. Journal of Phycology 38:862–871.

Leys, C., C. Ley, O. Klein, P. Bernard, and L. Licata. 2013. Detecting outliers: do not use standard deviation around the mean, use absolute deviation around the median. Journal of Experimental Social Psychology 49:764–766.

Loreau, M., et al. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804–808.

Lürig, M. 2021. Data from: non-additive effects of foundation species determine the response of aquatic ecosystems to nutrient perturbation. Open Science Framework. https://doi.org/10.17605/OSF.IO/X6V9H

Lürig, M. D., R. J. Best, V. Dakos, and B. Matthews. 2020. Submerged macrophytes affect the temporal variability of aquatic ecosystems. Freshwater Biology 66:421–435.

Lürling, M., M. M. E. Mello, F. van Oosterhout, L. de Senerpont Domis, and M. M. Marinho. 2018. Response of natural cyanobacteria and algae assemblages to a nutrient pulse and elevated temperature. Frontiers in Microbiology 9:1851.

McLaughlan, C., and D. C. Aldridge. 2013. Cultivation of zebra mussels (*Dreissena polymorp*ha) within their invaded range to improve water quality in reservoirs. Water Research 47: 4357–4369.

Nakai, S., Y. Inoue, and M. Hosomi. 2001. Algal growth inhibition effects and inducement modes by plant-producing phenols. Water Research 35:1855–1859.

Nakai, S., G. Zou, T. Okuda, W. Nishijima, M. Hosomi, and M. Okada. 2012. Polyphenols and fatty acids responsible for anti-cyanobacterial allelopathic effects of submerged macrophyte *Myriophyllum spicatum*. Water Science and Technology: A Journal of the International Association on Water Pollution Research 66:993–999.

Narwani, A., M. Reyes, A. L. Pereira, H. Penson, S. R. Dennis, S. Derrer, P. Spaak, and B. Matthews. 2019. Interactive effects of foundation species on ecosystem functioning and stability in response to disturbance. Proceedings of the Royal Society B 286:20191857.

Nielsen, A., L. Liboriussen, D. Trolle, F. Landkildehus, M. Søndergaard, T. L. Lauridsen, M. Søndergaard, S. E. Larsen, and E. Jeppesen. 2013. Daily net ecosystem production in lakes predicted from midday dissolved oxygen saturation: analysis of a five-year high frequency dataset from 24 mesocosms with contrasting trophic states and temperatures: predicting lake net ecosystem production. Limnology and Oceanography, Methods/ASLO 11:202–212.

Olff, H., D. Alonso, M. P. Berg, B. K. Eriksson, M. Loreau, T. Piersma, and N. Rooney. 2009. Parallel ecological networks in ecosystems. Philosophical Transactions of the Royal Society B 364:1755–1779.

Paine, R. T., M. J. Tegner, and E. A. Johnson. 1998. Compounded perturbations yield ecological surprises. Ecosystems 1:535–545.

Pennekamp, F., et al. 2018. Biodiversity increases and decreases ecosystem stability. Nature 563:109–112.

Petchey, O. L., et al. 2015. The ecological forecast horizon, and examples of its uses and determinants. Ecology Letters 18:597–611.

Reitsema, R. E., P. Meire, and J. Schoelynck. 2018. The future of freshwater macrophytes in a changing world: dissolved organic carbon quantity and quality and its interactions with macrophytes. Frontiers in Plant Science 9:629.

Russo, S., M. Lürig, W. Hao, B. Matthews, and K. Villez. 2020. Active learning for anomaly detection in environmental data. Environmental Modelling & Software 134:104869.

Scheffer, M., et al. 2012. Anticipating critical transitions. Science 338:344–348.

Scheffer, M., S. H. Hosper, M. L. Meijer, B. Moss, and E. Jeppesen. 1993. Alternative equilibria in shallow lakes. Trends in Ecology & Evolution 8:275–279.

Scheffer, M., S. Szabo, A. Gragnani, E. H. Van Nes, S. Rinaldi, N. Kautsky, J. Norberg, R. M. M. Roijackers, and R. J. M. Franken. 2003. Floating plant dominance as a stable state. Proceedings of the National Academy of Sciences USA 100:4040–4045.

Smith, V. H. 2003. Eutrophication of freshwater and coastal marine ecosystems: a global problem. Environmental Science and Pollution Research International 10:126–139.

Smith, V. H., and D. W. Schindler. 2009. Eutrophication science: where do we go from here? Trends in Ecology & Evolution 24:201–207.

Smith, V. H., G. D. Tilman, and J. C. Nekola. 1999. Eutrophication: impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. Environmental Pollution 100:179–196.

Søndergaard, M., J. P. Jensen, and E. Jeppesen. 2003. Role of sediment and internal loading of phosphorus in shallow lakes. Hydrobiologia 506:135–145.

Spears, B. M., et al. 2017. Ecological resilience in lakes and the conjunction fallacy. Nature Ecology & Evolution 1:1616–1624.

Stachowicz, J. J. 2001. Mutualism, facilitation, and the structure of ecological communities. BioScience 51:235–246.

Staehr, P. A., D. Bade, M. C. Van de Bogert, G. R. Koch, C. Williamson, P. Hanson, J. J. Cole, and T. Kratz. 2010. Lake metabolism and the diel oxygen technique: state of the science: guideline for lake metabolism studies. Limnology and Oceanography, Methods/ASLO 8:628–644.

Strayer, D. L., et al. 2019. Long-term population dynamics of dreissenid mussels (*Dreissena polymorpha* and *D. rostriformis*): a cross-system analysis. Ecosphere 10:e02701.

Suttle, K. B., M. A. Thomsen, and M. E. Power. 2007. Species interactions reverse grassland responses to changing climate. Science 315:640–642.

Tekin, E., E. S. Diamant, M. Cruz-Loya, V. Enriquez, N. Singh, V. M. Savage, and P. J. Yeh. 2020. Using a newly introduced framework to measure ecological stressor interactions. Ecology Letters 23:1391–1403.

Thompson, P. L., M. M. MacLennan, and R. D. Vinebrooke. 2018. Species interactions cause non-additive effects of multiple environmental stressors on communities. Ecosphere 9: e02518.

van Nes, E. H., W. J. Rip, and M. Scheffer. 2007. A theory for cyclic shifts between alternative states in shallow lakes. Ecosystems 10:17–27.

Vanderploeg, H. A., J. R. Liebig, W. W. Carmichael, M. A. Agy, T. H. Johengen, G. L. Fahnenstiel, and T. F. Nalepa. 2001. Zebra mussel (*Dreissena polymorpha*) selective filtration promoted toxic Microcystis blooms in Saginaw Bay (Lake Huron) and Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 58:1208–1221.

Welch, E. B., and G. D. Cooke. 2005. Internal phosphorus loading in shallow lakes: importance and control. Lake and Reservoir Management 21:209–217.

Yamamichi, M., T. Kazama, K. Tokita, I. Katano, H. Doi, T. Yoshida, N. G. Hairston, and J. Urabe. 2018. A shady phytoplankton paradox: when phytoplankton increases under low light. Proceedings of the Royal Society B 285:20181067.

Zelnik, Y. R., J.-F. Arnoldi, and M. Loreau. 2018. The impact of spatial and temporal dimensions of disturbances on ecosystem stability. Frontiers in Ecology and Evolution 6:224.

Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3371/suppinfo

Open Research

Data and code (Lürig 2021) are available from the Open Science Foundation data repository: https://doi.org/10.17605/OSF.IO/X6V9H.