

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

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26 **Abstract**

27 Eutrophication is a persistent threat to aquatic ecosystems worldwide. Foundation species,
28 namely those that play a central role in the structuring of communities and functioning of
29 ecosystems, are likely important for the resilience of aquatic ecosystems in the face of
30 disturbance. However, little is known about how interactions among such species influence
31 ecosystem responses to nutrient perturbation. Here, using an array (N=20) of outdoor
32 experimental pond ecosystems (15000 L), we manipulated the presence of two foundation
33 species, the macrophyte *Myriophyllum spicatum* and the mussel *Dreissena polymorpha*, and
34 quantified ecosystem responses to multiple nutrient disturbances, spread over two years. In the
35 first year we added five nutrient pulses, ramping up from 10 to 50µg P/L over a 10-week period
36 from mid-July to mid-October, and in the second year we added a single large pulse of 50µg
37 P/L in mid-October. We used automated sondes to model whole-ecosystem metabolism, and
38 to measure multiple ecosystems properties at high frequency (15min intervals), including
39 phytoplankton and dissolved organic matter fluorescence. Overall, both foundation species
40 strongly affected the ecosystem responses to nutrient perturbation, and, as expected, initially
41 suppressed the increase in phytoplankton abundance following nutrient additions. However,
42 when both species were present, phytoplankton biomass increased substantially relative to
43 other treatment combinations: non-additivity was evident for multiple ecosystem metrics
44 following the nutrient perturbations in both years but was diminished in the intervening months
45 between our perturbations. Overall, these results demonstrate how interactions between
46 foundation species can cause surprisingly strong deviations from the expected responses of
47 aquatic ecosystems to nutrient additions.

48 **Keywords**

49 Eutrophication, aquatic ecosystems, perturbation, non-additive effects, foundation species,
50 high frequency time series, chlorophyll, metabolism

51 **Introduction**

52 Foundation species in an ecosystem can affect how other organisms take up resources, grow,
53 reproduce, and interact with competitors, pathogens, and consumers (Stachowicz 2001, Olff et
54 al. 2009, Kéfi et al. 2012). It is well known that interactions among species can affect the
55 functioning of ecosystems by regulating fluxes of energy and matter, ecosystem productivity
56 and metabolism, and by mediating the response of ecosystems to perturbation (Loreau et al.
57 2001, Harmon et al. 2009, Chapin et al. 2011). Species with disproportionate effects on
58 community structure and ecosystem functioning (Angelini et al. 2011, Falkenberg et al. 2012)
59 have been dubbed foundation species (Dayton 1972), in light of their definitive role in creating
60 locally stable conditions for other species. In the face of disturbance, foundation species can
61 individually or interactively affect multiple ecosystem components (Ellison et al. 2005, Darling
62 and Côté 2008), and potentially cause surprising effects on ecosystems (Paine et al. 1998). The
63 interplay between species interactions and external drivers of environmental change makes it
64 particularly challenging to forecast ecosystem responses to multi-faceted biotic and abiotic
65 aspects of anthropogenic disturbances (Petchey et al. 2015, Donohue et al. 2016, Spears et al.
66 2017).

67 Eutrophication is a threat to aquatic ecosystems worldwide (Smith et al. 1999, Smith
68 2003), and it is important to characterize whether nutrient pulses lead to gradual or sudden
69 shifts in ecosystem conditions (Scheffer et al. 1993, Smith 2003, Carpenter 2005, van Nes et
70 al. 2007, Hillebrand and Kunze 2020), and to understand the mechanisms underlying these
71 responses (Hillebrand and Kunze 2020). For example, ecosystem responses to nutrient

72 perturbation might be mediated by the interactions among key species and abiotic components
73 of ecosystems (Scheffer et al. 1993, Kéfi et al. 2016). Alternatively, how ecosystems respond
74 and recover from perturbation might depend on a broader community context, such as how
75 ecosystem functioning scales with variation in species composition (Pennekamp et al. 2018,
76 Hillebrand and Kunze 2020). Furthermore, just as multiple stressors can have interactive
77 effects on individual species responses (Darling and Côté 2008, Jackson et al. 2016, Côté et al.
78 2016), multiple key species (e.g. foundation species) can have interactive effects on entire
79 ecosystems (Stachowicz 2001, Angelini et al. 2011, Falkenberg et al. 2012). As such, non-
80 additive ecosystem responses to synergistic or antagonistic species interactions may impair our
81 ability to predict ecosystem responses to disturbance (Allgeier et al. 2011, Kéfi et al. 2016,
82 Spears et al. 2017, Thompson et al. 2018, Tekin et al. 2020), and to understand ecosystem
83 resistance and resilience (Scheffer et al. 1993, Darling and Côté 2008, Jackson et al. 2016,
84 Donohue et al. 2016).

85 Both macrophytes and mussels can have important effects on aquatic ecosystems due
86 to their capacity to limit phytoplankton biomass in the face of increasing nutrient loading
87 (Jeppesen et al. 1998, Bierman et al. 2005, Ibelings et al. 2007, Lürig et al. 2020). Macrophytes,
88 which are considered to be important foundation species (Scheffer et al. 2003, Kéfi et al. 2016),
89 can be competitively dominant over phytoplankton at low nutrient loading (Lürig et al. 2020),
90 and may persist at intermediate nutrient loading via a positive feedback between macrophyte
91 growth and water transparency (Carpenter and Lodge 1986, Jeppesen et al. 1998). By
92 comparison, mussels have high grazing rates on phytoplankton, (Johengen et al. 1995, James
93 et al. 1997) and can dramatically increase water clarity in some lake ecosystems (Ibelings et al.
94 2007). Current theory suggests that both species may facilitate the presence of each other:
95 macrophytes can provide habitat for *Dreissena* mussels to settle on (Ibelings et al. 2007,
96 Karatayev et al. 2014b), 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, Lüring 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 foundation 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, Nielsen et al. 2013, Batt 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; 4 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 to 50µg P/L over a 10-week period from mid-July to mid-October), and in the second year added one large pulse (50µg 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, 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 (15min 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 000L) were made of fiberglass with a smooth surface (Fig. 1D), had a rounded shape with an approximately four-meter diameter and a shallow (0.5 m) and a deep (1.5 m) end. The ponds were initially set up on May 6th 2016 by adding a five 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 1m 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, Xylem) in each pond, and tracked ecosystem parameters with high frequency (15 min 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 productivity, net primary productivity, and respiration; see below). 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 (December 1st 2016 - February 28th 2017), we could not monitor ecosystem metabolism due to ice cover in the ponds. To maintain and recalibrate the sensors, we stopped measurement from March 1st to 23rd (see supplement for details), and in the fall of 2017 (September 14th - October 3rd 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 - Feb 2018), we manipulated the presence and absence of two foundation species: the macrophyte *Myriophyllum spicatum* (Fig. 1B; hereafter *Myriophyllum*) and the mussel *Dreissena 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 May 31st, 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 1.5m 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; approx. 100-150 cm⁻² per shoot and approx. 9.2 m² benthic surface per pond) (Hilt and Gross 2008, McLaughlan and Aldridge 2013, Karatayev et al. 2014a). 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 re-established 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 August 12th, 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 KNO₃ and K₂HPO₄, maintaining a N:P = 32) over eight weeks until October 10th, 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 two-week intervals between them

(vertical bars in Fig. 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 October 10th, 2017, exactly one year after we completed our initial set of five nutrient pulses, we added a final nutrient pulse of 50 $\mu\text{g/L}$ 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, Fig. 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 min interval = 96 data points). In addition to outlier removal, we visually inspected the data and manually removed anomalous periods from the data (less than 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 ($7 * 24 = 168$ data points). We then moved the window across the dataset in increments of one data-point to calculate mean and CV for the entire dataset (sliding window approach). We chose a seven-day window size to have robust estimates of the different metrics that would not be affected by diurnal variability. Moreover, we calculated autocorrelation (hereafter AC, 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):

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

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 Fig. 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 Supplementary 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 productivity, 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 as surface light levels (collected on site with a light meter [LI-1500 and LI-190R, LI-COR Biosciences GmbH]) and wind speed at 10 m from a nearby (200m) weather station operated by Meteo Swiss (Dübendorf, Giessen, 47°24'10" 08°36'49"). 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 1:00 and 5:00 for the night. Visual inspection of the data indicated that piston velocities defining gas exchange were rather constant during these times and potential non-linear 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 seven days. 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 Fig. 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 150-200%) 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 (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, Fig. S1), but we did not identify treatment specific differences in AC. Similarly, there were no consistent treatment specific differences in GEV or Skewness in any of the ecosystem parameters (Fig. S2 and Fig. S3).

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 towards 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 times significant) both prior to nutrient additions and in the recovery phase between nutrients additions (Phase 2), but they re-emerged 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

368 expected, as *Myriophyllum* is known to be a producer of a wide range of organic substances
369 (Lürig et al. 2020), including allelopathic chemicals that can be either actively released by the
370 plant or dissolve into the water column upon its death (Catalán et al. 2014, Reitsema et al.
371 2018).

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

386 The observed non-additive dynamics of chlorophyll fluorescence in the presence of
387 both *Myriophyllum* and *Dreissena* coincided with a dramatic shift towards cyanobacteria in the
388 first year (Fig. 2, Narwani et al. 2019). Indeed, in an analysis of phytoplankton species
389 composition of the ponds in year 1, Narwani et al. (2019) found that the small cyanobacterium
390 *Synechococcus* was only dominant when both *Myriophyllum* and *Dreissena* were both present.
391 In a laboratory experiment, Narwani et al. (2019) tested how a factorial manipulation of
392 *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 manipulation, the dynamics of ecosystem metabolism show 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 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 towards 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.

Acknowledgements

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.S. (310030L_166628), B.W (206021_157750), and B.M. (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.

Data availability

We made all raw data and code leading to the presented results available through an Open Science Foundation data repository (Lürig 2021).

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684 **Figure legends**

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

698 Figure 2 - Effect of foundation species on the mean of ecosystem parameters in Phase 1, Phase
699 2 and Phase 3 (left, middle, and right panel, respectively). The lines indicate the respective
700 average of all four ponds per treatment per hour (mean \pm SE), the gray shading indicates the
701 disturbance phases, and the colored bars underneath the time series indicate whether a treatment
702 was significantly different from the control (one linear model per hour: (orange=*Dreissena*
703 main effect [D treatment], green=*Myriophyllum* main effect [M treatment], purple=interactive
704 effect [MD treatment])). The data stem from a seven day long sliding window (168 data points).
705 The black line indicates the predicted additive response based on the sum of the separate
706 macrophyte or mussels treatment with the control subtracted (e.g. (Macrophyte *Chl* +
707 *Dreissena Chl*) - Control *Chl* = predicted additive response).

Figure 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 \pm 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 seven day long sliding window (168 data points).

Figure 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 all four ponds per treatment per hour (mean \pm 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.

Figure 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 the respective average of all four ponds per treatment per hour (mean \pm 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 seven day long sliding window (168 data points).









