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Submerged macrophytes affect the temporal variability of aquatic ecosystems

Moritz D. Lürig[1,2,3] (iD) | Rebecca J. Best[2,4] (iD) | Vasilis Dakos[5] (iD) | Blake Matthews[2] (iD)

[1]Department of Aquatic Ecology, Eawag Kastanienbaum, Kastanienbaum, Switzerland

[2]Department of Fish Ecology and Evolution, Eawag Kastanienbaum, Kastanienbaum, Switzerland

[3]Center for Adaptation to a Changing Environment (ACE), Institute of Integrative Biology, ETH Zürich, Zürich, Switzerland

[4]School of Earth and Sustainability, Northern Arizona University, Flagstaff, Arizona, U.S.A.

[5]ISEM, University of Montpellier, CNRS, EPHE, Montpellier, France

Correspondence
Moritz D. Lürig, Department of Aquatic Ecology, Eawag Kastanienbaum, Kastanienbaum, Switzerland.
Email: moritz.luerig@gmail.com

Abstract

1. Submerged macrophytes are important foundation species that can strongly influence the structure and functioning of aquatic ecosystems, but only little is known about the temporal variation and the timescales of these effects (i.e. from hourly, daily, to monthly).

2. Here, we conducted an outdoor experiment in replicated mesocosms (1,000 L) where we manipulated the presence and absence of macrophytes to investigate the temporal variability of their ecosystem effects. We measured several parameters (chlorophyll-*a*, phycocyanin, dissolved organic matter [DOM], and oxygen) with high-resolution sensors (15-min intervals) over several months (94 days from spring to autumn), and modelled metabolic rates of each replicate ecosystem in a Bayesian framework. We also implemented a simple model to explore competitive interactions between phytoplankton and macrophytes as a driver of variability in chlorophyll-*a*.

3. Over the entire experiment, macrophytes had a positive effect on mean DOM concentration, a negative effect on phytoplankton biomass, and either a weak or no effect on mean metabolic rates, DOM composition, and conductivity. We also found that macrophytes increased the variance of dissolved organic carbon composition and metabolic rates, and, occasionally in the observed period, increased the variance of phytoplankton biomass and conductivity. The observation that macrophytes decreased the mean but increased the variance of phytoplankton biomass was consistent with the model that we implemented.

4. Our high-resolution time series embedded within a manipulative experiment reveal how a foundation species can affect ecosystem properties and processes that have characteristically different timescales of response to environmental variation. Specifically, our results show how macrophytes can affect short-term dynamics of algal biomass, while also affecting the seasonal build-up of DOM and the variance of ecosystem metabolism.

KEYWORDS
competition, dissolved organic carbon, mesocosms, metabolism, phytoplankton, variance

1 | INTRODUCTION

Decades of research on submerged macrophytes have documented how aquatic plants can influence a suite of ecosystem properties and processes (Carpenter & Lodge, 1986; Huss & Wehr, 2004; Jeppesen et al., 1997; Reitsema et al., 2018). Acting as foundation species (Dayton, 1972; Ellison et al., 2005), macrophytes create and maintain habitats for other species, affect species interactions, and influence the dynamics of matter and energy in freshwater ecosystems (Carpenter & Lodge, 1986; Jeppesen et al., 1997). Populations of individual macrophyte species, as well as species assemblages, can also influence how aquatic ecosystems respond to environmental change and the propensity of ecosystems to shift between alternative stable states in shallow lakes (a; Faafeng & Mjelde, 1998; Scheffer et al., 1993). Importantly, while the net ecosystem effects of macrophytes in contrasting equilibrium states are well studied, much less is known about how macrophytes affect the temporal dynamics of ecosystem properties and processes over timescales ranging from hours, to days, to months (Iacarella et al., 2018; Madsen & Adams, 1988; Mitchell & Rogers, 1985). High-resolution times series that capture both mean and variance responses of aquatic ecosystems are essential for predicting the effects of environmental change on aquatic ecosystems (Hillebrand et al., 2018; Reitsema et al., 2018) and improving their management in light of increasing disturbance and climate variability (Spears et al., 2017).

The strong and persistent ecosystem effects of macrophyte communities are often linked to their competitive interactions with phytoplankton communities for dissolved nutrients and light (Carpenter & Lodge, 1986; Scheffer et al., 1993). In shallow lakes, the positive feedback between light transmission and macrophyte biomass is an important reason why macrophytes help maintain a clear water state over a wide range of nutrient loading (Blindow et al.,2006; Blindow et al., 1998; Scheffer et al., 1993, 2003). Many types of macrophytes are efficient at taking up nutrients from the water and, if rooted, from the sediment, which can limit phytoplankton growth at low to intermediate nutrient loading (Yamamichi et al., 2018). Furthermore, macrophytes can reduce fish predation pressure on the zooplankton communities that graze on phytoplankton (Jeppesen et al., 1997), and can also produce allelopathic chemicals that inhibit phytoplankton growth (Gross, 2003; Hilt & Gross, 2008; Nakai et al., 2012). While it is known that such mechanisms can contribute to the positive feedbacks that help maintain lakes in a clear water state (Iacarella et al., 2018; Kéfi et al., 2016), surprisingly little is known about the seasonal dynamics of these interactions (Benedetti-Cecchi, 2003; Carpenter, 1988). This is a problematic knowledge gap because the variance of ecosystem properties is increasingly recognised as an important dimension of overall ecosystem resilience (Benedetti-Cecchi, 2003; Cottingham & Carpenter, 1998; Scheffer et al., 2009; Vasseur et al., 2014; Zelnik et al., 2018).

In addition to the effects on phytoplankton dynamics, macrophytes are known to affect the amount and composition of dissolved organic matter (DOM) (Bolan et al., 2011; Kellerman et al., 2015), which is a diverse mixture of low and high molecular weight components of different structure and composition (Bolan et al., 2011; Kellerman et al., 2015). In the clear water state, phototrophic organisms such as macrophytes, phytoplankton and bacteria produce low-weight dissolved organic carbon (DOC) compounds such as carbohydrates that are by-products of photosynthesis (Bolan et al., 2011; Carpenter & Lodge, 1986; Reitsema et al., 2018; Retamal et al., 2007). Macrophytes can both directly produce DOC, and indirectly reduce it by stimulating higher rates of DOC degradation from epiphytic bacteria (Catalán et al., 2014). Given the importance of interactions between macrophytes and different compositions of DOM in aquatic ecosystems (Reitsema et al., 2018) it is important to experimentally test how macrophytes can simultaneously affect the mean and variance of DOM concentration and composition (Catalán et al., 2014; Findlay & Sinsabaugh, 2003; Reitsema et al., 2018), and to consider such effects in models of ecosystem resilience to nutrient perturbation (Kéfi et al., 2016; Spears et al., 2017).

Dissolved organic carbon dynamics driven by competitive interactions between macrophytes and phytoplankton can also alter ecosystem metabolism (Findlay & Sinsabaugh, 2003; Kaenel et al., 2000; Mitchell, 1989; Reitsema et al., 2018). Growth and decay of macrophyte tissue can strongly affect metabolic rates of shallow lakes, depending on plant density, diversity, and lake depth (Żbikowski et al., 2019). In shallow lakes with a given nutrient load, ecosystem productivity is typically higher when macrophytes are dominant over phytoplankton (Brothers et al., 2013; Carpenter & Lodge, 1986; Wetzel, 1964). Macrophytes are known to be efficient photosynthesisers (Kaenel et al., 2000), but also provide additional substrate for the growth of autotrophic periphyton and bacteria (Brothers et al., 2013; Wetzel & Søndergaard, 1998). Additionally, the effects of macrophytes on the dynamics of DOC accumulation and decomposition can affect shifts between net autotrophy and net heterotrophy (Madsen & Adams, 1988; Mitchell & Rogers, 1985; Nielsen et al., 2013). Overall, the potential effects of interactions between macrophytes and phytoplankton on whole ecosystem metabolism are increasingly well documented. However, the ability of macrophytes to resist or moderate perturbations to ecosystem metabolism in the context of global change depends on the relative importance of the described mechanisms and the temporal scale on which they each occur (Zelnik et al., 2018). To our knowledge, only a few studies have investigated the effects of competition for light and nutrients between macrophytes and phytoplankton on dynamics of DOC and metabolism at the temporal resolution necessary to understand how they interact (Benedetti-Cecchi, 2003; Zelnik et al., 2018).

Here, we experimentally tested how macrophytes affect the temporal dynamics of oligotrophic aquatic ecosystems in 1,000-L mesocosms over an entire growing season. We manipulated the presence and absence of a macrophyte assemblage consisting of two common species, *Myriophyllum spicatum* and *Chara tomentosa*, and quantified several biotic (two phytoplankton pigments) and abiotic (temperature and conductivity, dissolved oxygen, DOM) properties at high temporal resolution (15 min). We used this data set to test 3 hypotheses. First, we predicted that macrophytes would be able to suppress phytoplankton biomass across seasonal variation in light and temperature. Second, we

predicted that macrophytes would increase overall rates of ecosystem metabolism because they are known to be efficient photosynthesisers. Third, we predicted that macrophytes should impact not only mean ecosystem properties such as phytoplankton biomass, DOM, and metabolism, but also their temporal variance in response to continual changes in resource availability. For this last hypothesis, we also tested whether we could generate observed contrasts in variability using a simple model of competitive interactions between phytoplankton and macrophytes. We compare our findings with previous empirical work and discuss the broad functional spectrum of macrophytes as foundation species in shallow lake ecosystems.

2 | METHODS

2.1 | Experimental design and setup

In an outdoor mesocosm experiment, we manipulated the presence or absence of an assemblage of macrophytes including *M. spicatum* (hereafter *Myriophyllum*), a perennial vascular plant that grows vertically towards the water surface forming a canopy, and *C. tomentosa* (hereafter *Chara*), a green alga that forms tufts of calcium carbonate encrusted stems (typically <30 cm diameter) on the sediment surface. We chose this assemblage because both species are common in Europe and other parts of the world, they commonly occur together in macrophyte assemblages, and their strong influence on lake ecosystems has been previously documented (Berg *et al.*, 1998; Hilt & Gross, 2008; Ibelings et al., 2007; Nakai et al., 2012).

We set up the experiment on a site next to Eawag Kastanienbaum (eight tanks total) with four pairs of 1,000-L mesocosms ($1 \times 1 \times 1$ m), with each pair consisting of a mesocosm with (M+) and without (M−) a macrophyte assemblage (Figure 1). To prepare the mesocosms, we

first established a 2 cm thick layer of limestone gravel from a local quarry (2–4 mm grain size) and a 1 cm thick layer of fine, oligotrophic sediment (Fiskal et al., 2019) that we collected from a vegetation free area of Lake Lucerne (47°00′33.3″N 8°18′33.8″E). Afterwards the mesocosms were filled with water from Lake Lucerne, an oligotrophic, clear water lake (Fiskal et al., 2019), which was pumped up from an inlet at 40 m depth and left in the mesocosms for 2 weeks to allow the sediment to settle and the mesocosm community to assemble. On 25 May 2015, we collected *Myriophyllum* from a clear water stream in Oberriet (47°19′55.5″N 9°34′43.9″E) and kept the plants overnight in additional outdoor mesocosms onsite. The following day we collected *Chara* from a single location in Lake Lucerne (47°00′06.8″N 8°20′02.7″E) and planted both species in the mesocosms. To do so we divided all the macrophyte material manually (on a large and moist plastic sheet) into 18 similar-sized portions based on either an equal number of shoots (i.e. for *Myriophyllum*), or similarly sized tufts (i.e. for *Chara*). We used 10 portions to quantify the initial plant biomass (cleaned of sediment, infauna removed, biomass dried for 48 hr at 45°C) and added 4 portions to the M+ tanks. Given that both plant species were collected from clear water sites and planted in mesocosms filled with oligotrophic water, we assumed that growing conditions were similar for both plant species.

To inoculate the M− mesocosms with macrophyte associated invertebrate and bacterial communities, we submerged the remaining four portions of macrophytes in large mesh enclosures in the middle of the water column for 2 weeks. On 4 July, we added 20 μg/L of P and 144.7 μg/L of N (i.e. Redfield ratio) to every mesocosm to supplement the Lake Lucerne source water with nutrients. Over the course of the experiment, we measured dissolved nutrient concentrations in the mesocosms on four occasions (15 July, 5 August, 8 September, and 20 October; Figure S1). At the end of the experiment (23 October), we quantified total macrophyte biomass in terms of
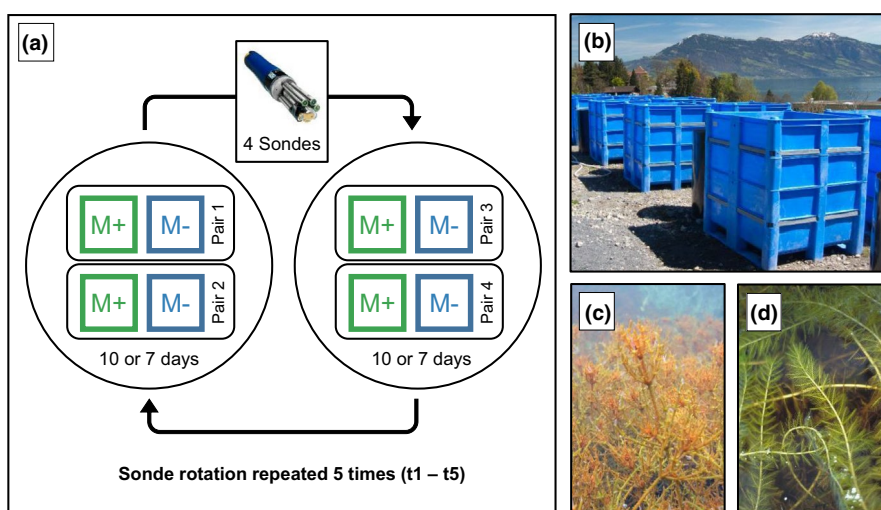

FIGURE 1 (a) Scheme of experimental procedure. Because we were limited to four sondes, we could only measure two tank pairs of macrophyte (M+)/no macrophyte (M−) contrasts. To measure all eight tanks, we followed a rotation scheme in which every tank was measured for 10 consecutive days before the sondes were moved to another tank (for details refer to Methods section). (b) Picture of experimental site showing the set up mesocosms (1,000 L). (c) *Chara tomentosa* (Photo credit: Gustav Johansson). (d) *Myriophyllum spicatum* (Photo credit: Alison Fox)

above-ground dry weight (procedure: see above). This included both the original inoculated species and a filamentous algal species that colonised the sediment surface of all the mesocosms (see Table S1).

2.2 | Ecosystem dynamics measurement using multiparameter sondes

We measured high-frequency ecosystem dynamics in the mesocosms from 18 July to 23 October 2015, using four autonomous multi-parameter instruments (EXO2 modular sensor platform [YSI-WTW], hereafter referred to as sondes). The sondes were placed approximately at the centre of the mesocosm (~0.5 m depth), away from the walls and outside of patches of macrophytes. Additionally, we measured photosynthetically active radiation in 15-min intervals using a quantum sensor (Li-Cor) installed onsite to estimate surface light irradiance. Photosynthetically active radiation and temperature data (Figure S2) were used together with the dissolved oxygen data to calculate metabolic rates (see *Ecosystem metabolism modelling*).

2.2.1 | Sensors

The sondes were equipped with modular sensors that recorded the following ecosystem parameters at 15-min intervals (see Table 1 for details): temperature, chlorophyll-*a*, and phycocyanin (as proxies for phytoplankton biomass), dissolved oxygen, fluorescent DOM (hereafter fDOM) and specific conductivity (hereafter conductivity). The sondes were equipped with an autonomous wiper that cleaned the sensor heads once every hour. All sensors were thoroughly cleaned whenever the sondes were moved to another mesocosm (see *Contrasts and sampling design*).

2.2.2 | Calibration

Prior to the experiment, we performed a 48-hr cross-comparison trial where we installed all the sondes in a single mesocosm, enabling us to correct for differences among sensors and calibrate them against each other. During the cross-comparison trial we also quantified chlorophyll-*a* concentration by analysing water samples with high-performance liquid chromatography (Jasco), and calibrated the optical sensors installed on the sondes in accordance with the manufacturer's manual (YSI-WTW). Hence, we report chlorophyll-*a* as μg/L, Phycocyanin and fDOM as raw fluorescence units. The oxygen sensors were calibrated against water-saturated air.

2.2.3 | Contrasts and sampling design

At the beginning of the experiment, all four sondes were randomly assigned to two pairs of M+ and M− tanks. Because we only had four sondes available, the four sondes were taken out of these tanks after 10 days, thoroughly cleaned, and then introduced to the two remaining pairs, where they were left for another 10-day period (Figure 1). Over the entire study, we repeated this two-part cycle five times, yielding five distinct periods in which all tanks were sampled (Figures 2–4: t1–t5). In the third sampling period (t3) we reduced the length of the measurement period to 7 days per set of tanks due to battery issues with the Sondes. Between all transfers, we thoroughly cleaned the sondes by hosing down the sondes and sensor bodies with a power washer before reinstalling them. We included the distinct periods (t1–t5) resulting from the rotation scheme and each individual tank as a random effect in all statistical models (see *Statistical Analysis*).

## 2.3 | Ecosystem metabolism estimation

We used the temperature and oxygen measurements (mg/L) from the sondes and the photosynthetically active radiation measurements from the light sensor to model whole ecosystem metabolic rates of each mesocosm (for an overview of the abiotic conditions see Figure S2). We used the *streamMetabolizer* package (Appling et al., 2018) in the programming language R (R Core Team 2017), which applies inverse modelling to estimate daily rates of ecosystem gross primary productivity (GPP), ecosystem respiration (ER), and gas exchange (K600) as g oxygen m^{-2} day^{-1}.

TABLE 1 Parameters measured in high frequency using autonomous sondes

Parameter	Unit	Sensor type	Calibration
Chlorophyll A	mg/L	Optical, fluorescence	HPLC, cross
Phycocyanin	Raw fluorescence	Optical, fluorescence	Cross
fDOM	Raw fluorescence	Optical, fluorescence*	Cross
Dissolved oxygen	% saturation**	Optical, luminescence	Saturated air, cross
Conductivity (specific)	μS × cm^{-1}	4-electrode cell	Conductivity standard
Temperature	°C	Thermistor	Cross

Note: Prior to the experiment, we performed a cross-comparison trial with all four sondes, after which we corrected all sensors for relative differences among them (i.e. Cross = cross calibration = calibrated against each other). Chlorophyll-a sensors were additionally calibrated with samples taken during this trial that were analysed for their chlorophyll-*a* content with high-performance liquid chromatography (HPLC). Oxygen sensors were calibrated against water-saturated air. (*fluorescent dissolved organic matter [fDOM] sensors measure emission at 365 ± 5 and excitation at 480 ± 40 nm. **For metabolism modelling, concentration [mg O$_2$/L] output was used).

FIGURE 2 Sliding window results from high frequency measurements of chlorophyll-*a* and phycocyanin over time (days 2–9 in each of five consecutive sampling periods). Lines show mean $\pm$ *SE* ($n = 8$ tanks), asterisks indicate significant differences ($p \leq 0.05$), and dots indicate marginal significance ($p \leq 0.1$). One generalised additive model was used per period, including tank and the pair it was in (see Figure 1) as random effects. Here the sliding window time series of the mean from both blocks are shown pooled for better illustration. Because the sliding window had a width of 1 day, only aggregate days 2–9 for each measurement are shown. CV, coefficient of variation
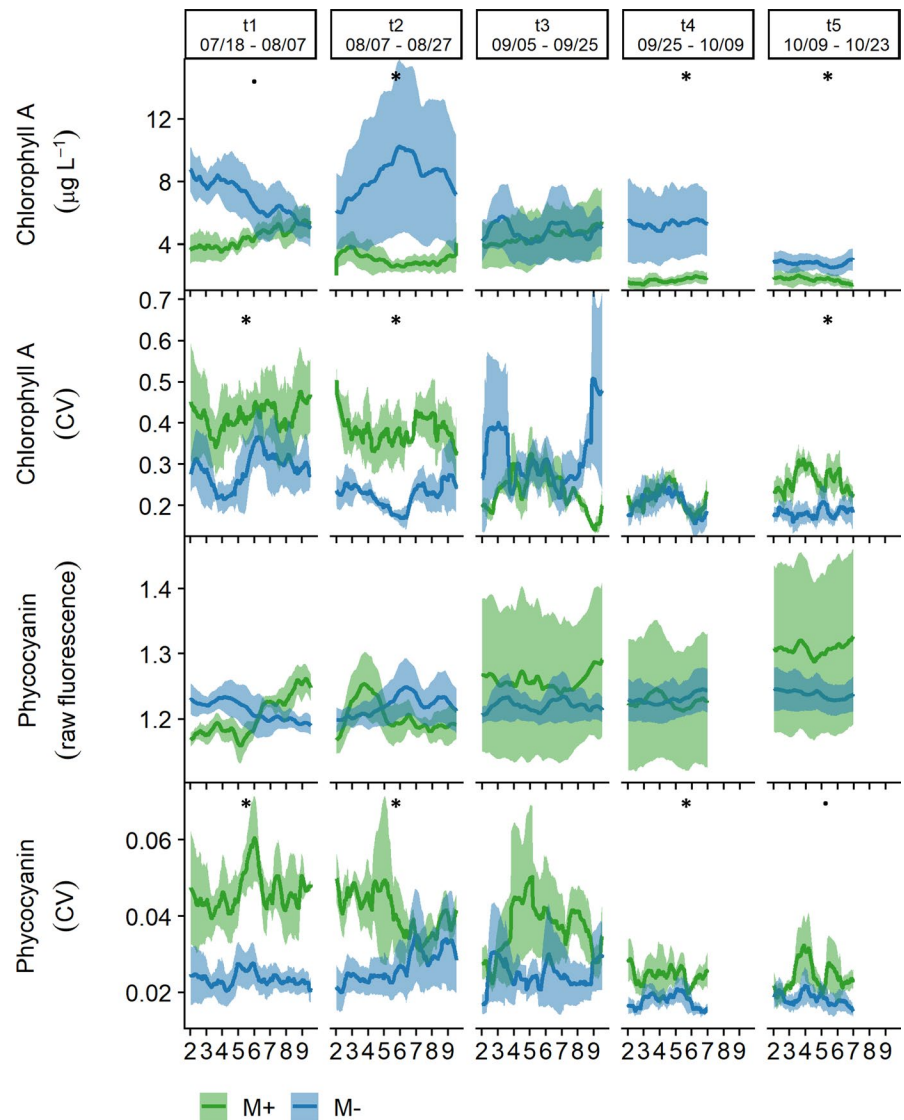
For every modelled rate we calculated the ratio of GPP and ER. Prior to modelling we smoothed all input data with a 12-hr moving average window to facilitate model convergence (A. Appling, personal communication) and for more conservative estimates. Occasionally the model converged towards positive daily respiration rates (eight out of 312 estimates) and negative daily productivity rates (two out of 312 estimates), which we omitted. We used a Bayes-type model with pooled K600 for gas-exchange and lognormal priors (K = 0–1). Because the dissolved oxygen time series reflects oxygen produced and consumed by all organisms in the whole ecosystem, we assumed the model reflects the net effects of any biomass changes throughout the experiment, for example, due to plant or epiphytic growth, or biomass decay.

2.4 | Dissolved organic carbon sampling

For each pair of tanks within each measurement period (i.e. every 10 or 7 days: Table S2), we took a water sample for the analysis of DOC concentration and absorbance properties (Figure S3). Water samples were filtered through 47-mm ashed GF/Fs (6 hr at 450°C), acidified with HCl 2 M and preserved at 4°C in the dark until analysis via high temperature catalytic oxidation (TOC-VCS, Shimadzu), with a detection limit of 0.5 mg/L ($\pm$0.5). Specific ultraviolet absorbances (SUVA) were measured on the same samples from scans (1-nm intervals) on a Shimadzu UV1700 spectrophotometer, using 1-cm quartz cuvettes. We selected absorbance at 254 nm ($SUVA_{254}$) as a proxy of aromaticity and reactivity of DOC (Weishaar et al., 2003). Furthermore, we measured $SUVA_{350}$, which is an indicator for how much UVA radiation is absorbed in the water (Fischer et al., 2015). We normalised the SUVA measurements by dividing the sample absorbances by the total DOC concentration (Hansen et al., 2016). Finally, we calculated spectral slope ratio (SSR) as the ratio of linear regressions of the log-transformed spectra of 275–295 nm and 350–400 nm (Hansen et al., 2016; Helms et al., 2008). Spectral slope ratio is a common proxy for DOC molecular weight, to which it should be inversely related. We were unable to analyse two DOC timepoints over the course of the experiment (2 and 17 October) due to technical problems with the TOC analyser.
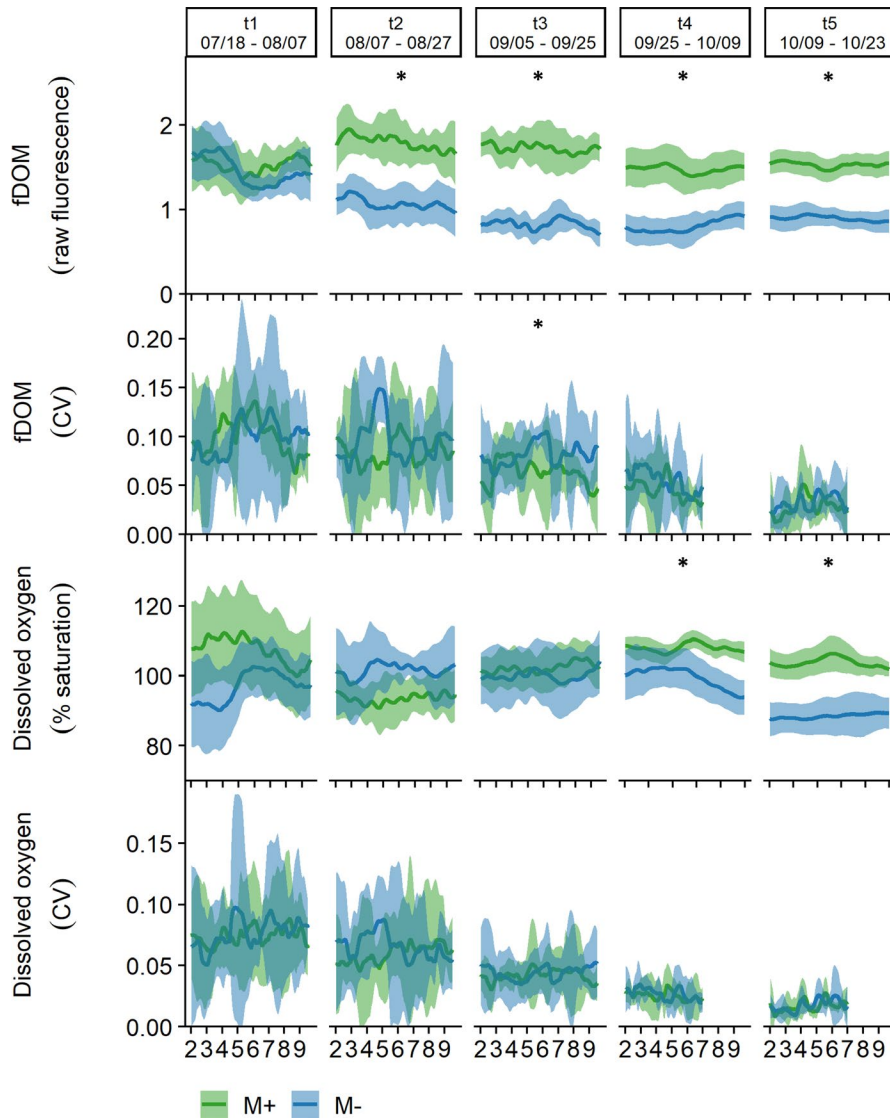
FIGURE 3 Sliding window results from high frequency measurements of fluorescent dissolved organic matter (fDOM) and dissolved oxygen over time (days 2–9 in each of five consecutive sampling periods). Lines show mean ± *SE* (*n* = 8 tanks), asterisks indicate significant differences (*p* ≤ 0.05). One generalised additive model was used per period, including tank and the pair it was in (see Figure 1) as random effects. Here the sliding window time series of the mean from both blocks are shown pooled for better illustration. Because the sliding window had a width of 1 day, only aggregate days 2–9 for each measurement are shown. CV, coefficient of variation

2.5 | A model for competition between macrophytes and phytoplankton

We used an existing model for competition between macrophytes and phytoplankton (Scheffer & Carpenter, 2003) to explore how mesocosm phytoplankton dynamics might differ in the presence and absence of macrophytes. This model assumes standard features of macrophyte–phytoplankton interactions and implicitly accounts for competition for light and nutrients (Figure 5). In the model, growth of macrophytes M and of phytoplankton P is determined by a gain and a loss term following:

$$\frac{dP}{dt} = r_P \frac{n}{n + h_P} \frac{1}{1 + \alpha_P P} P - l_P P + \sigma \varepsilon_P(t) \tag{1a}$$

$$\frac{dM}{dt} = r_M \frac{1}{1 + \alpha_M M + bP} M - l_M M + \sigma \varepsilon_M(t) \tag{1b}$$

Phytoplankton grows with a maximum growth rate r_P that is limited by nutrients n in a saturating function with half-saturation constant hp. Limitation of phytoplankton growth by macrophytes comes through nutrient availability given by Equation 2:

$$n = \frac{Ntot}{1 + q_M M + q_P P} \tag{2}$$

where *Ntot* is the total amount of nitrogen in the system and nutrients decrease in a nonlinear way depending on the biomass of macrophytes and phytoplankton. Parameters q_M and q_P determine the strength of the response in decreasing nutrients per biomass increase in macrophytes and phytoplankton, respectively. Phytoplankton growth is also limited by light due to self-shading scaled by α_P where $1/\alpha_P$ is the biomass of phytoplankton that makes the maximum growth rate equal to half, whereas loss is determined by loss rate l_p. Macrophyte maximum growth rate r_M is limited only due to competition for light (in contrast to phytoplankton which is

FIGURE 4 Ecosystem gross primary productivity (GPP), ecosystem respiration (ER), and GPP:ER ratio, calculated from high frequency measurements of dissolved oxygen concentration (g m^{-2} day^{-1}), temperature, light, and air pressure. Shown are mean $\pm$ SE ($n = 8$ tanks), asterisks indicate significant differences ($p < 0.05$), dots indicate marginal significance ($p < 0.1$). One generalised additive model was used per period, including both consecutive blocks as random variables. Here the time series of metabolic rates from both blocks are shown pooled for better illustration. The modelling procedure requires full days to be included, but because of the model parameterisation to start each day 1 hr before sunrise, the last day is incomplete and thus cannot be modelled. Hence, only aggregate days 1–8 are shown
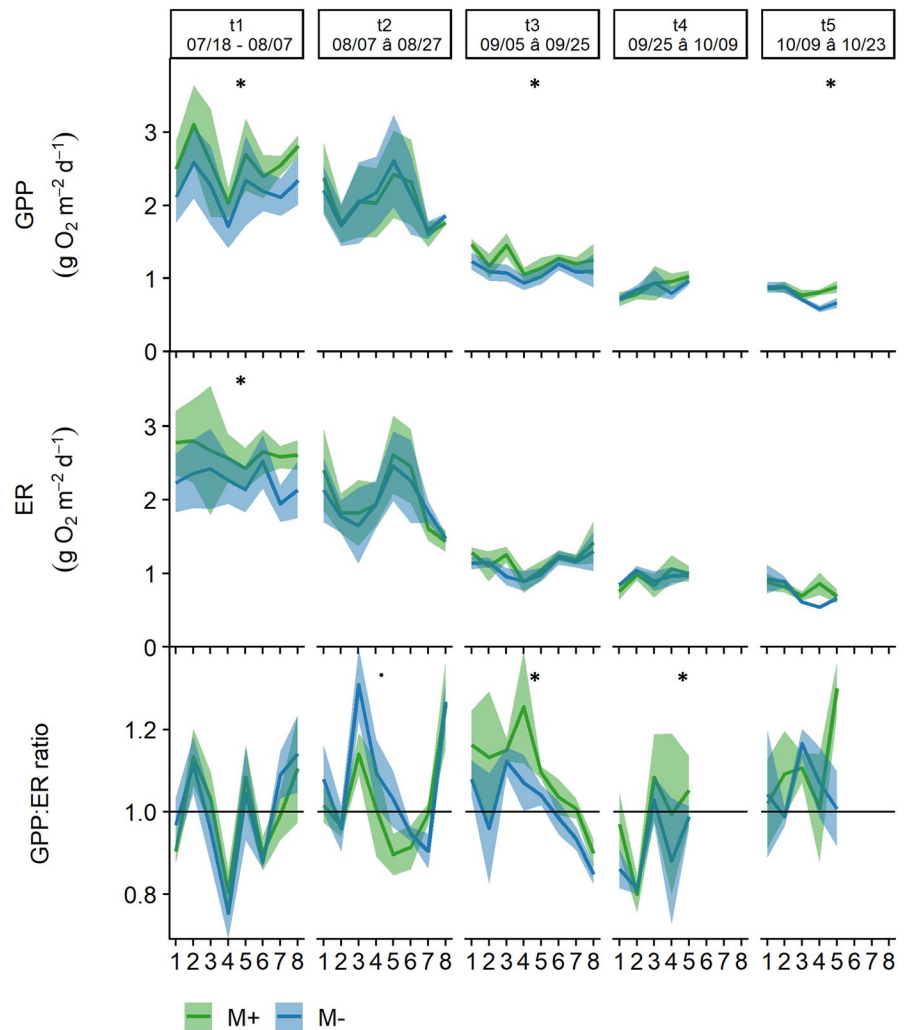
also limited by nutrients). In that case, light limitation is driven by self-shading through parameter a_M and due to shading by phytoplankton by parameter b. Loss is determined by loss rate l_M. In this simplified model formulation, we ignore some potentially important interactions for which we had no empirical data, including nutrient uptake by macrophytes from the sediment, and interactions between macrophytes and periphyton biomass over time.

We used model parameters such that both macrophytes and phytoplankton were equivalent in the rates of growth ($r_P = r_M = 0.5$), mortality ($l_P = l_M = 0.05$), and self-shading ($\alpha_P = \alpha_M = 0.01$). Instead, we modelled asymmetry between macrophytes and phytoplankton in terms of light and nutrient limitation. Phytoplankton growth was limited by nutrients ($h_P = 0.2$), through macrophytes having a stronger impact on retaining the available nutrients in the water column ($Ntot$; $q_M = 0.075$ and $q_P = 0.005$). Macrophytes became light limited by phytoplankton due to shading ($b = 0.02$). We set $Ntot = 3.2$. This is a total nutrient level value for which the model can give rise to two alternative states, one state with both macrophytes and phytoplankton present (M+) and an alternative with phytoplankton but no macrophytes (M–). These two states resemble our experimental setup.

We simulated model dynamics at these two contrasting states in the presence of environmental stochasticity $\varepsilon P(t)$, $\varepsilon M(t)$ (iid and different for macrophytes and phytoplankton) with strength σ (= 0.5). We produced 200 simulated sets of 1,000 timepoints in length for each of the two states using the same sequence of stochastic realisations for both states. In that way, differences in the recorded standard deviation and coefficient of variation were independent of the stochasticity and only due to the stability of the two states. The model was implemented in MATLAB R2016b (Mathworks) using Grind v2 (https://www.sparcs-center.org/resources/dynamical-modelling-tools.html). Equilibria and eigenvalues were estimated numerically, stochastic equations were solved with Euler–Murayama integration using a 0.01 step.

2.6 | Statistical analysis

2.6.1 | Data treatment

Prior to the statistical analysis we removed incomplete days at the beginning and end of each measurement period (five time series:
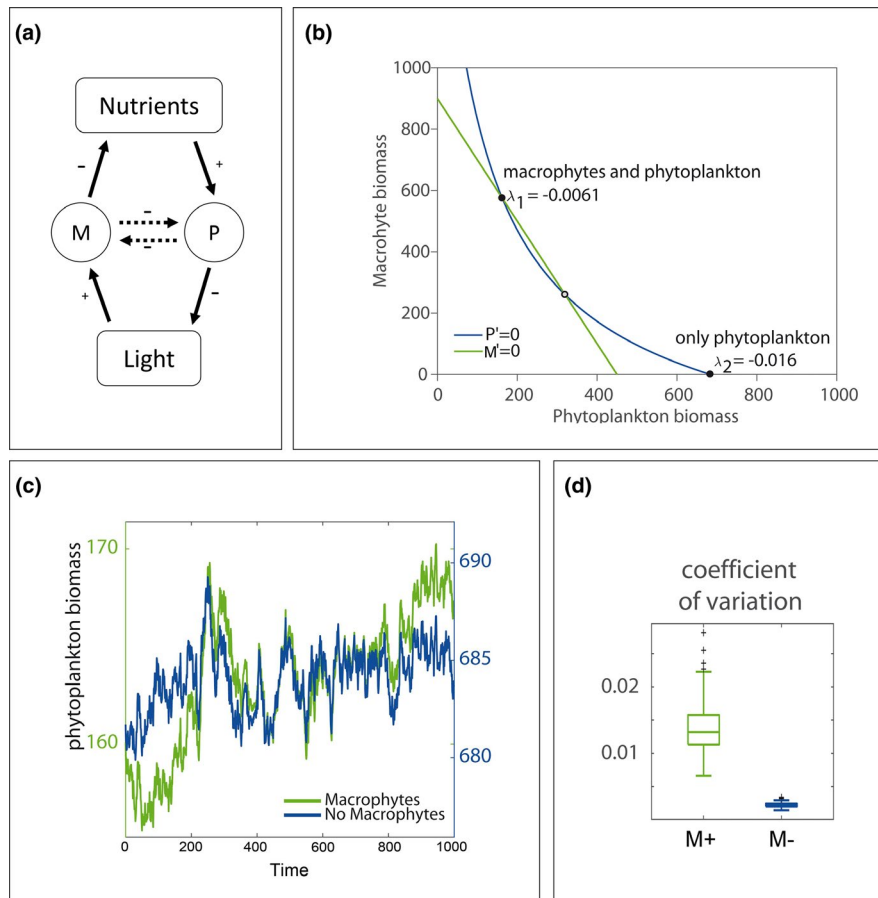
FIGURE 5 A simple model of competition for light and nutrients between macrophytes and phytoplankton (for details see Supplement). (a) Schematic of interactions between macrophytes (M) and phytoplankton (P). Macrophytes consume nutrients, which has a negative indirect effect on phytoplankton. If phytoplankton biomass becomes too high, it reduces light levels such that there is a negative indirect effect on macrophytes. Thus, macrophytes are more strongly limited by light, and phytoplankton by nutrients. (b) Zero-growth curves of macrophytes (green line) and phytoplankton (blue line). Black points mark the two alternative stable equilibria of either a macrophyte-and-phytoplankton state or an only-phytoplankton state. Although these two states exist for the same level of nutrients in the water, their stability (measured as the dominant eigenvalue λ) differs: the only-phytoplankton is more stable than the macrophyte-and-phytoplankton state. (c) Simulated time series of phytoplankton biomass in the presence (green) and in the absence (blue—note second y-axis) of macrophytes for the same level of nutrients in the water. (d) Coefficient of variation of phytoplankton biomass estimated from 200 simulated sets

t1–t5). After this, each of the five time series had 864 data points (15-min interval = 96 data points per day = 9 days) for t1–3 and 576 data points (= 6 days) for t4 and t5. In a second step, we identified residuals of the detrended data that were outside 2.5 times the interquartile range as outliers and removed them from the data set. Finally, we used sliding windows with a size of 96 timepoints (= 1 day) to calculate time series of mean and coefficient of variation (CV), resulting in 768 data points for t1–t3 and 480 data points for t4–t5 (8 and 5 days, respectively).

2.6.2 | Ecosystem dynamics

We analysed time series of chlorophyll-*a*, phycocyanin, dissolved oxygen, and fDOM separately for each of the five measurement periods to account for any variation due to the sonde-switching. To test for effects of macrophytes on the mean and variance of each

parameter we implemented a series of generalised additive models (GAMs) using the R-package *mgcv* (Wood, 2004): one model per parameter (chlorophyll-*a*, phycocyanin, fDOM, oxygen concentration, conductivity) per measurement period (t1–t5) per metric (mean or CV), resulting in a total of 50 separate GAMs. Each model used data from all eight tanks to test for differences in the mean or CV, with the presence or absence of macrophytes as the independent variable and tank and pair (see Figure 1) as random effects. All GAMs included a term that accounted for first order autocorrelation and used penalised thin plate regression splines with automatic knot selection.

In addition to the GAMs we also calculated pairwise log response ratios (LRRs) for macrophyte presence in all five periods for the high frequency measurements. To do so we divided vectors of mean and CV (coming either from the sliding window for the water parameters or from the daily estimates of metabolism) for M+ by the corresponding vector of M− for each given pair of tanks. We then

FIGURE 6 Average log response ratios (LRRs) for macrophyte presence on mean and coefficient of variation (CV) of all ecosystem parameters measured in this experiment. Effect sizes were calculated differently for each data type: high frequency (●), metabolism (▲), or dissolved organic carbon (DOC) point measurements (■)—for details refer to the methods section. Each point shows the average (mean $\pm$ SE) macrophyte LRR across all tank pairs ($n = 4$, Figure 1) and in all measurement periods (t1-t5, except for the DOC point measurements, where all 10 measurements were used to calculate LRR for mean and CV). ER, ecosystem respiration; GPP, gross primary productivity; SSR, spectral slope ratio; SUVA, specific ultraviolet absorbance.
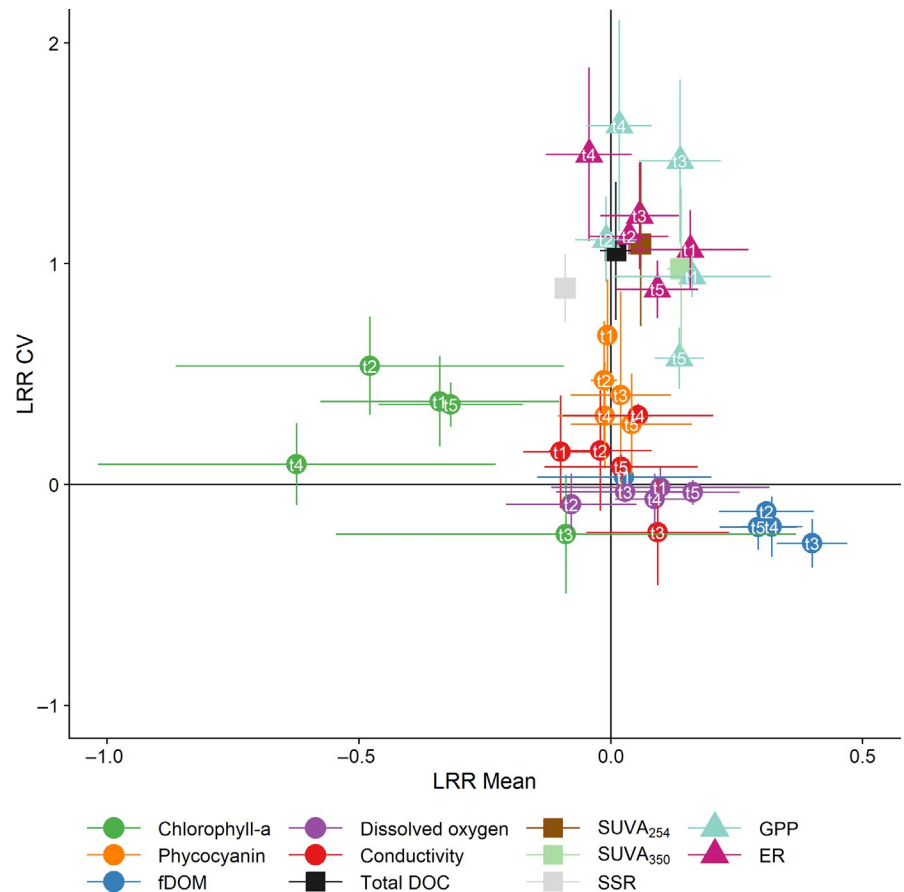
calculated the natural logarithm for these ratios for each measurement period and for each tank (for a summary of all response ratios see Figure 6).

2.6.3 | Ecosystem metabolism

To test for statistical differences in metabolic rates, we used the output from the ecosystem metabolism models, which were 8 or 5 consecutive days for t1–t3, and t4–t5, respectively (streamMetabolizer does not provide estimates for the final day in a time series). In a similar fashion as for the ecosystem dynamics, each model used data from all eight tanks within a measurement period to test for differences in GPP, ER, or GPP:ER, using macrophyte presence as the independent variable and pair and tank as random effects. We calculated LRRs in the same way as described for the high frequency ecosystem dynamics. We used paired t-tests to test for differences in metabolism CV for each measurement period.

2.6.4 | Dissolved organic carbon

We used paired t-tests to test for differences in mean and CV of total DOC concentration, SUVA$_{254}$ and SUVA$_{350}$, and SSR between mesocosms with and without macrophytes. For each date (10 dates in

total, see Table S2) we performed separate tests for all four metrics ($n = 8$ tanks). We performed t-tests with the *stats* R-package (R Core Team 2017) and calculated pairwise LRRs for all DOC metrics (for a summary of all response ratios see Figure 6).

3 | RESULTS

3.1 | Macrophyte biomass and nutrients

The overall biomass of the macrophyte community changed over the course of the experiment, decreasing in the M+ treatment and increasing slightly in the M− treatment. At the end of the experiment substantially less *Chara* biomass was present in the M+ mesocosms than at the beginning (from 165.1 ± 21.65 to 5.08 ± 7.6 g dry weight per mesocosm, mean $\pm$ SD; Table S1), whereas *Myriophyllum* biomass increased 3-fold from 2.84 ± 0.54 g to 8.45 ± 1.6 g dry weight. In the M− treatment there was no *Myriophyllum*, but *Chara* biomass increased slightly due to growth from the sediment (from 0 to 0.27 ± 0.54 g dry weight per mesocosm, mean $\pm$ SD). In both treatments, filamentous algae grew over the course of the experiment to a final biomass of 8.33 ± 10.54 g dry weight (M+) and 3.21 ± 5.46 g dry weight per mesocosm (M−), mean $\pm$ SD, respectively. Throughout the experiment we observed no differences in concentrations of phosphate or nitrogen between mesocosms with and without macrophytes (Figure S1). The nutrients we supplied on

TABLE 2 Statistical results of generalised additive models testing time series of water parameters and metabolic rates

Parameter	Metric	t1 t-Value	t1 p-Value	t1 R²	t2 t-Value	t2 p-Value	t2 R²	t3 t-Value	t3 p-Value	t3 R²	t4 t-Value	t4 p-Value	t4 R²	t5 t-Value	t5 p-Value	t5 R²
Chlorophyll-a	Mean	1.724	0.085	0.81	2.696	0.007	0.95	0.355	0.722	0.86	3.14	0.001	0.92	3.6	<0.001	0.93
	CV	-2.04	0.041	0.78	-3.31	0.001	0.8	1.578	0.115	0.55	-0.39	0.698	0.66	-2.8	0.005	0.73
Phycocyanin	Mean	0.311	0.756	0.75	0.637	0.524	0.75	-0.45	0.656	0.87	0.006	0.995	0.88	-0.73	0.467	0.88
	CV	-4.85	<0.001	0.67	-2.09	0.037	0.56	-1.35	0.176	0.62	-2.11	0.035	0.54	-1.89	0.059	0.7
fDOM	Mean	-0.3	0.762	0.64	-4.92	<0.001	0.89	-9.62	<0.001	0.96	-6.69	<0.001	0.98	-6.55	<0.001	0.97
	CV	-0.05	0.958	0.51	1.119	0.263	0.36	4.036	<0.001	0.43	0.746	0.456	0.63	0.431	0.666	0.49
Dissolved oxygen	Mean	-0.88	0.38	0.76	1.163	0.245	0.78	-0.35	0.726	0.82	-2.01	0.044	0.86	-3.27	0.001	0.89
	CV	0.244	0.808	0.62	1.186	0.236	0.56	0.949	0.343	0.32	0.566	0.571	0.36	0.312	0.755	0.4
Conductivity	Mean	2.064	0.039	0.97	0.112	0.911	0.94	-1.17	0.244	0.91	-0.53	0.594	0.88	-0.02	0.985	0.88
	CV	-0.28	0.781	0.34	-0.97	0.334	0.36	1.664	0.096	0.37	-0.99	0.323	0.46	-0.06	0.95	0.58
Temperature	Mean	-0.08	0.934	0.45	0.386	0.699	0.73	-0.37	0.711	0.65	0.657	0.511	0.78	-0.11	0.91	0.9
	CV	-0.23	0.816	0.32	-0.25	0.801	0.45	0.914	0.361	0.26	0.193	0.847	0.42	0.886	0.376	0.43
GPP	Mean	-3.65	<0.001	0.71	-1.17	0.249	0.46	-2.15	0.036	0.17	1.381	0.176	0.05	-3.4	0.002	0.41
ER	Mean	-3.47	0.001	0.33	0.121	0.905	0.55	-0.37	0.36	0.46	-0.42	0.681	0.24	-0.35	0.34	0.23
GPP:ER	Mean	0.16	0.874	0.03	1.816	0.074	0.01	-4.81	<0.001	0.09	-3.39	0.002	0.3	-0.65	0.52	0.12

Note: Results are from individual models (one model per parameter and measurement period). For mean and coefficient of variation (CV) of water parameters, N per model is 768 for t1–t3 and 480 for t4 and t5. For metabolic rates, N per model is 8 23 for t1–t3 and 5 for t4 and t5. Trends (p < 0.1) indicated by bold font; significant results (p < 0.05) indicated by underlined bold font. t-value = model estimate/ model estimate SD, R² = R squared of model fit. ER, ecosystem respiration; fDOM, fluorescent dissolved organic matter; GPP, gross primary productivity

4 July were almost completely consumed by 18 July and were consistently low (<2 μg P/L, <50 μg N/L) over the entire experiment. However, concentrations of both nutrients tended to increase towards the end of the experiment, probably due to decomposition of plant material (e.g. Chara, Table S1).

3.2 | Ecosystem dynamics

As expected, solar radiation and water temperature decreased strongly over the course of the experiment from 18 July to 20 October (Figure S2). Several parameters differed between M+ and M− tanks over the course of the experiment, with the magnitude of the difference depending on period (Figure 2 and Figure 6; for p-values see Table 2). As expected, mean phytoplankton biomass was significantly higher without macrophytes (M−) in three of the five periods (t2, t4, and t5; Table 2), and, unexpectedly, the CV of phytoplankton biomass was higher in the tanks with macrophytes (M+) in three periods (t1, t2, and t5; Figure 3). By comparison, mean phycocyanin was not significantly different between M+ and M− (Figure 2), but the CV of phycocyanin was significantly higher in the M+ treatment during three periods (Figure 3; t1, t2, t4). In tanks with macrophytes (M+), fDOM was higher in four periods (GAM, t2–t5), and the CV was significantly lower in one period (GAM, t3). The mean concentration of dissolved oxygen was significantly higher in M+, but only towards the end of the experiment (t4 and t5; Figure 3). In these two periods when irradiance was decreasing (Figure S2), the tanks lacking macrophytes (M−) became undersaturated with dissolved oxygen indicating net heterotrophy. During the entire experiment, there were no differences between M+ and M− in the CV of dissolved oxygen. Effect sizes of macrophyte presence on mean and variance of all parameters measured in high frequency are summarised in Figure 6.

3.3 | Ecosystem metabolism

We found weak and seasonally variable differences in mean ecosystem metabolism between mesocosms with and without macrophytes (Figure 4). In three measurement periods mesocosms with macrophytes had significantly higher gross primary productivity (t1, t3, and t5). During t1, mesocosms with macrophytes also had higher respiration (GAM, main effect of macrophytes, $p = 0.001$). In t2 there was a tendency for higher GPP:ER ratio in mesocosms without macrophytes (GAM, main effect of macrophytes, $p = 0.074$), but in t3 and t4 we found the opposite pattern with significantly higher GPP:ER ratio in the presence of macrophytes (GAM, main effect of macrophytes, $p < 0.001$ and $p = 0.002$, respectively. Overall, GPP and ER decreased significantly over the course of the experiment, probably due to seasonal dynamics (decreasing temperature and light, Figure S2) but the GPP:ER ratio remained around 1. Across all measurement periods, both productivity and respiration increased with chlorophyll-a biomass (slope in Figure S4). However, for a given chlorophyll-a concentration, both metabolic rates were higher in the presence of macrophytes than in their absence (intercept in Figure S4). Moreover, we found higher variance of metabolic rates when macrophytes were present (all t-tests of metabolism CV significantly different - Figure 6).

3.4 | Dissolved organic carbon

Total DOC concentration was not significantly different between M+ and M− mesocosms (Table S2, Figure S3). However, there were clear effects of macrophytes on chromophoric (impacting light transparency) DOC components: $SUVA_{254}$ and $SUVA_{350}$ were often higher in the presence of macrophytes (Table S2, Figure S3), indicating that less UV light was able to penetrate in these ecosystems. Spectral slope ratio diverged among treatments early in the experiment and remained higher in the −M treatment for most of the season (Figure S3), potentially indicating dissolved substances of lower molecular weight in the absence of macrophytes (e.g. sugars or amino acids). We also found higher variance in all metrics of DOC composition in the presence of macrophytes (Figure 6).

3.5 | Simulated interactions between macrophytes and phytoplankton

Our simulation model produced results parallel to those observed in the mesocosms. Under identical nutrient levels, phytoplankton biomass was on average lower in the presence of macrophytes, but also varied more strongly around the mean (i.e. lower mean and higher CV under M−). This was also reflected in the stability regimes measured as the dominant eigenvalue λ, which was higher in the absence and lower in the presence of macrophytes (Figure 5, panel B). These results emerged solely from differences in the relative effects of macrophytes versus phytoplankton on nutrient versus light limitation and illustrate that differential competition for these resources can impact both mean and variance in phytoplankton biomass.

4 | DISCUSSION

Over the course of the mesocosm experiment, macrophytes affected a wide range of ecosystem parameters. Most notably, from those measured at high frequency, chlorophyll-a fluorescence (i.e. phytoplankton biomass) was significantly lower in the presence of macrophytes. Our high-resolution measurements also revealed some unexpected variance patterns of phytoplankton and DOC components in the presence of macrophytes. While the former may be explained by resource competition between macrophytes and phytoplankton, as indicated by our competition simulation, the mechanisms behind elevated DOC variability are currently speculative. Below we discuss the implications of our joint findings from the high-resolution time series and the simulation model, as well as the outcomes of the ecosystem metabolism models. Overall, our findings indicate that some macrophyte effects on ecosystem parameters are of more limited duration (e.g. phytoplankton was decreased

only temporarily and most strongly in t2), whereas others remain stable across the season (e.g. fDOM was consistently higher from t2 onwards).

As expected from existing theoretical and experimental work, and confirming our first hypothesis, we observed higher phytoplankton biomass in the absence of macrophytes (Blindow et al., 2006; Blindow et al., 1998; Scheffer et al., 1993). This is in agreement with a large body of previous work that documents the outcome of competition between macrophytes and phytoplankton for dissolved nutrients and light (Faafeng & Mjelde, 1998; Nes et al., 2007; Sand-Jensen & Borum, 1991; Scheffer et al., 1993). The ability of macrophytes to keep phytoplankton biomass low is also known to be important in maintaining a clear water state in response to nutrient additions (Ibelings et al., 2007; Scheffer et al., 1993). However, a finding we did not expect based on existing theory was the higher variability of phytoplankton biomass in the presence of macrophytes, a phenomenon that has not been previously reported. One mechanism for higher variability of phytoplankton biomass could be that the ongoing photosynthesis, growth, and decay of macrophytes increases the short-term variability of nutrient and carbon availability, and that phytoplankton respond more rapidly to these changes in nutrient concentrations than macrophytes themselves (Eichel et al., 2014; Mitchell, 1989; Setaro & Melack, 1984). Importantly, however, the much larger reservoir of macrophytes biomass can repeatedly suppress these rapid increases in phytoplankton growth. Rooted macrophytes build up biomass over time and can also store nutrients (Faafeng & Mjelde, 1998; Søndergaard & Moss, 1998; Yamamichi et al., 2018), and thus probably prevented a high mean level of phytoplankton biomass and repeatedly suppressed multiple bouts of phytoplankton growth.

We implemented a model to explore how competitive interactions between macrophytes and phytoplankton might affect the mean versus the variance of phytoplankton biomass. Specifically, we modelled competitive interactions such that macrophytes limit nutrient availability and phytoplankton limit light availability (Scheffer & Carpenter, 2003). This model reproduced the same contrast in phytoplankton biomass that we observed in the mesocosms: lower mean phytoplankton biomass but higher variance (CV) in the presence of macrophytes. Thus, the model predicted that a phytoplankton-dominated state would be more stable than a macrophyte-dominated state under the same nutrient loading condition. At first sight, this result might appear counterintuitive as a macrophyte-dominated state is expected to be more stable to the unfavourable phytoplankton-dominated state. The biological explanation may be that when macrophytes and phytoplankton are competing for nutrients (and light), variation arising from the depletion of these resources is larger than with just one consumer (i.e. only phytoplankton in M−). However, whether variability is always expected to be higher in a macrophyte dominated than in a phytoplankton-dominated state, or under what conditions, would require more empirical work to validate. The model shows that this is the case considering only one aspect of macrophyte–phytoplankton interactions (i.e. competition),

which qualitatively matched with the high-resolution algal biomass data we collected. However, macrophytes can affect other compartments of the ecosystem (e.g. sediment, epiphytes, DOC) that are not considered in our model. Macrophytes can produce allelochemicals such as polyphenols and fatty acids (Nakai et al., 2012) that inhibit phytoplankton production (Hilt & Gross, 2008; Nakai et al., 2012), can modify the light environments via the production of DOC Catalán et al. (2014); Reitsema et al. (2018), which could potentially influence the variance of phytoplankton biomass. This may be especially the case for *Myriophyllum*, which is known to produce large amounts of allelochemicals (Hilt & Gross, 2008; Nakai et al., 2012) and also was the dominant plant in the mesocosms with macrophytes. Nevertheless, our study does illustrate that high resolution monitoring of ecosystem conditions (Mandal et al., 2019), might provide new insights into the underlying mechanisms whereby macrophytes (or other foundation species) can affect ecosystem dynamics in general, and the relationships between mean and variance of ecosystem responses in particular.

In line with macrophytes being efficient primary producers in shallow lakes (Kaenel et al., 2000), we confirmed our second hypothesis that mesocosm ecosystems with macrophytes had higher metabolic rates than those without macrophytes. Differences in productivity were most pronounced in July, where mesocosms with macrophytes were significantly more productive than macrophyte free mesocosms (t1). However, this difference disappeared during the phytoplankton bloom in the second measurement period (t2). This suggests that at intermediate concentrations, phytoplankton can increase productivity of aquatic ecosystems and match rates of primary production of macrophytes. For any given chlorophyll-*a* biomass we measured, metabolic rates were higher when macrophytes were also present. This indicates that even at relatively low density, macrophytes (*Myriophyllum*, *Chara*, and filamentous algae) can produce a significant metabolic signal. Higher productivity of ecosystems with macrophytes was also reflected in GPP:ER ratio, which is on average slightly higher for those mesocosms in t3 and t4 (5 September–9 October). During t2 (7–27 August), there was a tendency for higher GPP:ER in mesocosms without macrophytes, probably due to very high phytoplankton biomass. Towards the second half of the experiment, the growth of filamentous algae may have also contributed to higher rates of whole ecosystem productivity in M+ tanks, where filamentous algae biomass was higher (8.33 ± 10.54 g dry weight, mean ± *SD*) than in the M− tanks (3.21 ± 5.46 g dry weight, mean ± *SD*). Overall, these findings suggest that macrophytes, regardless of their growth form, might make shallow lake ecosystems more productive across the seasonal succession of ecosystem metabolism (Blindow et al., 2006; Blindow et al., 1998; Brothers et al., 2013; Madsen & Adams, 1988). These dynamics require additional investigation, especially in the context of successive phytoplankton blooms and their effects on the macrophyte community, but also in the context of rising temperatures and eutrophication.

Another important axis by which macrophytes affected the experimental ecosystems is their effects on the concentration and

composition of dissolved organic matter. From the beginning of t2 (8 August) to the end of the experiment, fDOM measurements in mesocosms with macrophytes were nearly twice as high as in mesocosms without macrophytes. Higher mean, but also lower variance of DOM was expected, because especially *Myriophyllum*, which was the dominant plant in the M+ mesocosms, is known to produce allelochemicals to inhibit algae growth that are broken down only slowly (Hilt & Gross, 2008; Nakai et al., 2012). However, total DOC concentrations were similar in both treatments, suggesting that not all components of the DOM pool are affected the same way by macrophytes (Catalán et al., 2014; Reitsema et al., 2018). Moreover, measurements from the scanning spectrophotometer showed consistently lower SSRs, indicating the presence of DOC compounds with higher molecular weight. The build-up and decay of macrophyte detritus could explain the low SSR ratios at similar total DOC levels, particularly since much of the initial *Chara* biomass contributed to decomposition rather than taking root, and/or grew but then decayed over the course of the experiment. However, *Myriophyllum* biomass also increased substantially, and could have added high MW compounds into the mesocosms. It is also possible that production rates of DOC were similar in M+ and M– treatments (as the total DOC was similar), but that material originating from macrophytes has a higher MW, and is more difficult to break down by bacteria (Bolan et al., 2011; Reitsema et al., 2018). Overall, changes in DOC composition and variance might reflect differences in the balance of production and decomposition rates of different photosynthetic compounds, such as low MW sugars that are a byproduct of recent photosynthetic activity (Bolan et al., 2011; Carpenter & Lodge, 1986; Reitsema et al., 2018). However, more work needs to be done to understand the specific mechanisms behind such patterns, e.g. biomass production and decomposition or the production of secondary metabolites.

Using a common macrophyte assemblage, our experiment shows that communities of submerged plants can affect the mean and variance of a wide range of biotic and abiotic ecosystem properties and processes over a relatively short amount of time (Figure 6). Some of the effects we found on mean values, such as macrophytes decreasing phytoplankton biomass and increasing fDOM are not particularly surprising nor are they novel. However, the elevated variability of both phytoplankton pigments in the presence of macrophytes was unexpected, and potentially linked to competitive interactions. Across all our ecosystem metrics, we found that changes in CV covaried negatively with changes in the mean, or that CV increased despite no effect on the mean. Such results, show the importance of considering the variance of ecological dynamics, which is increasingly recognised as an important aspect of ecosystem dynamics (Benedetti-Cecchi, 2003; Carpenter, 1988) and is used in a wide array of applications, e.g. ecological forecasting (Petchey et al., 2015; Pennekamp et al., 2019), early warning signals for critical transitions (Carpenter et al., 2011; Scheffer et al., 2009), and ecological modelling (Bartell et al., 1988; Cottingham & Carpenter, 1998). Furthermore, our high frequency measurements can begin to reveal and quantify characteristic differences in timescales of ecosystem change, such as the high variability in phytoplankton communities

versus the relative stability of DOM and oxygen concentration throughout the season. Future experiments targeting shallow lake ecosystems should also encompass measurements in high resolution, e.g. to detect the potential outcome of interactions among different trophic levels (e.g. between macrophytes, zooplankton, and fish) or quantify the response to perturbations (e.g. nutrients or temperature). Our study highlights how complex and temporally variable interactions around foundation species can be and underscores the need for further research that investigates biotic and abiotic components of these networks of interactions in detail.

CONFLICT OF INTEREST
The authors declare no conflict of interests.

AUTHOR CONTRIBUTIONS
M.D.L., B.M., and R.J.B. designed the study. M.D.L. and R.J.B. implemented and maintained the experiment and collected the data. M.D.L., V.D., and B.M. analysed the data. V.D. implemented the simulation model. All authors made substantial contributions to the manuscript.

DATA AVAILABILITY STATEMENT
A copy of the (cross) calibrated data is accessible at the Dryad open-access repository: https://doi.org/10.5061/dryad.18931zcvt (Lürig et al., 2020), together with instructions on how to reproduce all shown results.

ORCID
Moritz D. Lürig https://orcid.org/0000-0002-8175-6234
Rebecca J. Best https://orcid.org/0000-0003-2103-064X
Vasilis Dakos https://orcid.org/0000-0001-8862-718X
Blake Matthews https://orcid.org/0000-0001-9089-704X

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.