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Functionally reversible impacts of disturbances on lake food webs linked to spatial and seasonal dependencies

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Abstract. Increasing human impact on the environment is causing drastic changes in disturbance regimes and how they prevail over time. Of increasing relevance is to further our understanding on biological responses to pulse disturbances (short duration) and how they interact with other ongoing press disturbances (constantly present). Because the temporal and spatial contexts of single experiments often limit our ability to generalize results across space and time, we conducted a modularized mesocosm experiment replicated in space (five lakes along a latitudinal gradient in Scandinavia) and time (two seasons, spring and summer) to generate general predictions on how the functioning and composition of multitrophic plankton communities (zoo-, phyto- and bacterioplankton) respond to pulse disturbances acting either in isolation or combined with press disturbances. As pulse disturbance, we used short-term changes in fish presence, and as press disturbance, we addressed the ongoing reduction in light availability caused by increased cloudiness and lake browning in many boreal and subarctic lakes. First, our results show that the top-down pulse disturbance had the strongest effects on both functioning and composition of the three trophic levels across sites and seasons, with signs for interactive impacts with the bottom-up press disturbance on phytoplankton communities. Second, community composition responses to disturbances were highly divergent between lakes and seasons: temporal accumulated community turnover of the same trophic level either increased (destabilization) or decreased (stabilization) in response to the disturbances compared to control conditions. Third, we found functional recovery from the pulse disturbances to be frequent at the end of most experiments. In a broader context, these results demonstrate that top-down, pulse disturbances, either alone or with additional constant stress upon primary producers caused by bottom-up disturbances, can induce profound but often functionally reversible changes across multiple trophic levels, which are strongly linked to spatial and temporal context dependencies. Furthermore, the identified dichotomy of disturbance effects on the turnover in community composition demonstrates the potential of disturbances to either stabilize or destabilize biodiversity patterns over time across a wide range of environmental conditions.

Key words: biodiversity; community composition; community turnover; disturbances; ecosystem functioning; global change; lakes; plankton; recovery.

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Introduction

Generating predictions of ecosystem responses to global environmental change is at the heart of the global political and scientific agenda (Millennium Ecosystem Assessment 2005; Intergovernmental Panel on Climate Change 2013; The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services 2019). Such understanding is critical to anticipate the future status of ecosystems and, consequently, to drive adaptive ecosystem management (IPCC 2013; IPBES 2019). However, general predictions are hard to achieve by single-site experiments or observational studies because of the context specificity of responses and/or nonstationary environmental change (De Boeck et al. 2015, Angeler et al. 2020). In order to overcome this limitation, recent years have seen the rise of experimental networks that apply the same treatments to a range of sites, and thus arrive at generalizable statements on the mean and variance of responses to specific forms of environmental change (e.g., Nutrient Network, Borer et al. 2014; Zostera Experimental Network, Duffy et al. 2015). Here, we transfer the idea of modularized experiments from grasslands (Borer et al. 2014) and seagrasses (Duffy et al. 2015) to freshwater plankton communities, testing the interactive effects of pulse and press disturbances on community composition and functioning across three trophic levels.

Pulse disturbances are short-term, but often intense, changes in the environment with either negative or positive consequences on community biomass or abundances (Ives and Carpenter 2007, Donohue et al. 2016). Naturally occurring pulses (e.g., storms, fires, heat waves) are predicted to, and may already have, increased in frequency and intensity because of human intervention in climate and biogeochemical systems (Easterling et al. 2000, IPCC 2013, Seneviratne et al. 2014). Even though pulse perturbations have often relatively short duration, there is increasing evidence that, depending on the disturbance type, they may be strong determinants in driving both short- and long-term community dynamics (Jentsch et al. 2007, Lawson et al. 2015, Stockwell et al. 2020, Urrutia-Cordero et al. 2020). At the same time, gradual and persistent changes in environmental conditions are ongoing (e.g., global mean temperature rising or ocean acidification), which represent "press disturbances" (Donohue et al. 2016; IPBES 2019). The analysis of environmental disturbances and their impact have strongly influenced our understanding of how ecosystems function and communities living in them assemble (Ives and Carpenter 2007, Fraterrigo and Rusak 2008, Keitt 2008, Murphy and Romanuk 2012, Shade et al. 2012). It has also been acknowledged that disturbances rarely occur in isolation and multiple stressor responses need to be analyzed (Folt et al. 1999, Ormerod et al. 2010, Urrutia-Cordero et al. 2017), the more so as the response to an initial disturbance will affect the susceptibility of communities to sequential environmental changes (Vinebrooke et al. 2004, Flöder and Hillebrand 2012). In light of this general understanding, it is surprising how little we know about the interactions between pulse and press disturbances of different nature, and how they affect ecological responses of entire biological communities across multiple trophic levels (Shade et al. 2012, Donohue et al. 2016). With our modularized experiment replicated in space and time, we aim to generate general predictions on how multitrophic communities respond to pulse disturbances with and without additional stress induced by ongoing press disturbances.

The question of interactive effects of pulse and press disturbances and their generalization becomes highly relevant, as the expected community responses may fundamentally differ, especially in terms of their recovery potential. For pulse disturbances, recovery can be expected after the pulse ends as long as the level does not drive the local community extinct or push the system into an alternative regime (Jones et al. 2008, Giling et al. 2016, Güelzow et al. 2017, Hillebrand et al. 2018*a*). A recent meta-analysis (Hillebrand and Kunze 2020) found recovery of functional variables (standing stock, abundance) to be the norm, whereas compositional recovery is often delayed. As such, the recovery of compositional and functional aspects can be coupled (Güelzow et al. 2017, Hillebrand et al. 2018*a*), but functional recovery can also be achieved through compositional turnover (Fernandez et al. 1999). Functional recovery is, however, less likely to occur at the same rate under a press disturbance (Shade et al. 2012). As environmental conditions never ameliorate, functional recovery under ongoing press disturbances depends more than pulse disturbances on the persistence of specific populations (native or new immigrants) that are constitutively resistant or sufficiently plastic to adapt to the disturbance, and which take time to spread within the communities (Bell and Gonzalez 2009, Bell and Gonzalez 2011, Shade et al. 2012). Hence, recovery from pulse disturbances may not be the same when communities are additionally stressed with ongoing press disturbances of different nature.

Here we focus on responses of lake plankton communities because they drive many key ecosystem functions and services delivered by lakes (Millennium Ecosystem Assessment 2005), as well as enable practical testing of fundamental hypotheses in general ecological stability theory because of their high sensitivity to disturbances and short generation times (Adrian et al. 2009, Zhang et al. 2018, Hillebrand et al. 2018*a*). We exposed multitrophic plankton communities (zoo-, phyto- and bacterioplankton) to the same combination of pulse and press disturbances, and repeated this experiment in five lakes located along a latitudinal gradient in Scandinavia during two different seasons (spring and summer). In each of these 10 outdoor mesocosm experiments, we applied a 2×2 factorial design of pulse and press disturbances with four replicates per treatment, resulting in 160

unique experimental units. The setup allowed us to analyze mean responses of both functional (biomass/abundance) and compositional (temporal turnover) aspects of the communities as well as the spatial and temporal variance of these responses.

We considered two disturbances of relevance in a global change context as well as of feasibility to be manipulated across lakes, which also differed in the direction of their impact on the food web (either top-down or bottom-up). As pulse disturbance, we opted for a transient presence of a top consumer (planktivorous fish), which induced a selective mortality on parts of the plankton community (on the zooplankton community). Especially small water bodies often experience temporally constrained predation pressure by fish colonization and extinction, and/or from transient migratory patterns (Brönmark et al. 2014). Also, this disturbance has a connection to climate change, as changing temperatures and extreme heat events can boost the predation and reproduction rates of planktivorous fish species, and thereby induce rapid changes in their functional and numerical responses (Hansson et al. 2013, Jeppesen et al. 2014, Urrutia-Cordero et al. 2016). As press disturbance we used a reduction in light availability (hereafter named "shading"), because lakes in boreal and subarctic regions are increasingly experiencing light limitation because of increased precipitation and associated cloud cover from climate change (Weyhenmeyer et al. 2016), or "lake browning" from the discharge of terrestrially derived humic substances (Karlsson et al. 2009, Kritzberg et al. 2019).

We present hypotheses on community functional dynamics (biomass/abundance) in response to both disturbances and their interaction. We also expect changes in the temporal turnover in community composition based on the Jaccard dissimilarity (Magurran and McGill 2011) between the community composition in each time point and the initial community composition.

H1: Fish presence alone has strong short-term effects on plankton communities, but allows for recovery after the pulse disturbance ends. H_{1a}: We expect an immediate decline of zooplankton biomass (direct top-down control) in response to the pulse disturbance and, consequently, increases in phytoplankton biomass and bacterial abundance relieved from top-down control by zooplankton. When fish presence ceases, biomass levels are able to recover to control levels provided there is no resource limitation (Fig. 1B). H_{1b}: We also expect initially a sharp change in composition in the zooplankton community followed by the phytoplankton and bacterial community, which after removal of the fish cease or even revert toward control levels (Fig. 1F).

H2: Shading as press disturbance has long-lasting negative effects on functional and compositional responses. H_{2a}: We expect long-lasting negative effects on functional responses of primary producers, reducing photosynthesis and growth, and thus biomass, which in turn will reduce secondary production and thus both zooplankton biomass and bacterial abundance (Fig. 1C). H_{2b}: We also expect continuously higher community change over time in the press disturbance treatment than the control as light reduction shifts the community to a more shade-tolerant phytoplankton composition, with repercussions on the heterotroph levels (Fig. 1G).

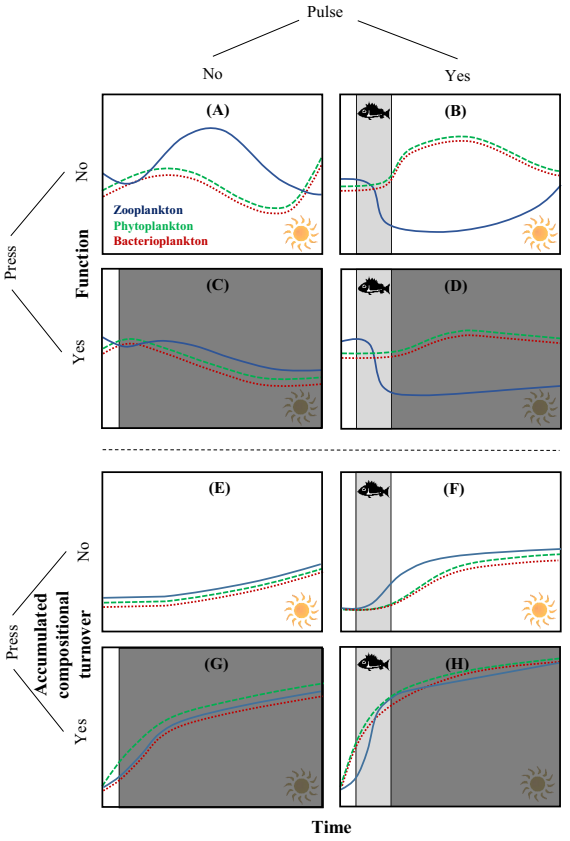

FIG. 1. Expected functional (biomass/abundance; A–D) and compositional changes (accumulated temporal turnover; E–H) over time of the zoo- (blue lines), phyto- (green lines), and bacterioplankton (red lines) communities. Note that the measure of accumulated temporal turnover in community composition was based on the Jaccard dissimilarity between each time point and the initial community composition. Plots with white background: Community dynamics with no pulse and press disturbances (control treatments). Plots with light gray columns and fish: Community dynamics with pulse disturbances. Plots with dark gray background: Community dynamics with press disturbances.

H3: The combined effects of pulse and press disturbances produce qualitatively different functional and compositional dynamics than single disturbances. H_{3a}: For functional responses (Fig. 1D), the initial reduction in zooplankton biomass in response to the fish pulse allows some phytoplankton and bacterial growth, but only to a small extent, because of negative effects of light limitation on primary production. Given the low growth rates, the recovery of zooplankton will be slow or even inhibited, leading to high autotroph to heterotroph

ratios despite light limitation. Interaction between both disturbances are possible, as the positive trophic cascade effect of fish on primary production will be lower in shaded mesocosms (difference between F and FS), whereas the effect of shading might be alleviated if fish presence reduces the grazing pressure on phytoplankton (difference between S and FS). H_{3b}: The combined effects of pulse and press disturbances also lead to higher temporal compositional turnover across the three trophic levels compared to the control. This occurs from the start to the end of the experiment because of the sharp short-term impact by the pulse disturbance and the long-lasting effects of the press disturbance (Fig. 1H).

Methods

Experimental setup

The modularized mesocosm experiment consisted of 10 experiments performed in five different lakes in Sweden during two seasons using the SITES-AquaNet infrastructure[14]. Five experiments (one in each lake) started in June 2017 (for simplicity, hereafter named "Spring" experiments), and the remaining five started in August ("Summer" experiments). The lakes (Feresjön, Bolmen, Erssjön, Erken, and Stortjärn) are located along a latitudinal gradient, and differ considerably in environmental conditions (Appendix S1: Table S1). Each experiment consisted of 16 cylindrical, polyethylene enclosures (diameter = 0.8 m; height = 1.5 m; volume = 700 L; Cipax AB, Sweden) randomized in a Latin square design. The enclosures were submerged in the lake (except the upper 30 cm) and stabilized with ropes to a jetfloat facility established in each lake (Jetfloat International Gmbh, Austria). Each mesocosm was filled with 550 L of unfiltered water from the local lake by using a water pump (Meec tools 735-018, JULA AB, Sweden). The pumps were run at a minimum speed to minimize disruptive effects on the plankton communities living in the water. After filling the mesocosms, the communities were allowed to establish for 3 d before the experimental manipulations were started.

Each experiment lasted 28 d and consisted of four experimental treatments, each replicated four times: (1) A control with no experimental manipulation (abbreviated C). (2) A pulse disturbance in the form of fish presence. Two juvenile crucian carp (*Carassius carassius*; mean length = 5.5 cm) were placed inside of these mesocosms during the first 7 d of the experiment (F), thus representing similar densities as found in natural shallow water bodies (Holopainen and Pitkanen 1985). The individuals were healthy and had neither parasite nor virus infections as revealed by examination at the National Veterinary Institute (SVA, Sweden). Using the same fish species and size class (mean ± SD length: 5.77 ± 0.74) for all lakes offered the advantage to be able to standardize the timing and extent of the disturbance, as well as to end the disturbance completely by removing the fish. (3) A press disturbance in the form of constant shading was applied during the entire experiment by placing a dark polyester mesh on top of the mesocosms reducing the incoming light by about 50% (S). (4) Both disturbances conducted in the same way but combined (FS). The complete experimental design then comprised 160 mesocosms (2 × 2 experimental design with four replicates each, conducted in five lakes and during two seasons). The study was approved by the Uppsala animal ethics committee in permission number 5.8.18-03672/2017.

Sampling and sensor measurements

Each mesocosm in each experiment was sampled six times from Day 1 (just before the experimental treatments were applied) over Days 4, 7 (before the fish were retrieved from the F and FS treatment), 9, 14, and 28. Each sampling comprised an equal number of water samples taken from two mesocosm depths (0–0.5 m and 0.5–1.0 m) with a Ruttner sampler. The water samples were pooled and mixed together in a 15-L bucket, thereby representing an integrated water sample across the entire mesocosm water column. We then collected subsamples to determine the zooplankton biomass and composition, phytoplankton biomass and composition, and bacterial abundance and composition. We also collected subsamples for nutrient analyses as background chemical information in each experiment (see Appendix S1: Table S1 for analytical methods).

Zooplankton samples for both functional and compositional analyses were collected by filtering 5 L of water with a 50-μm nylon mesh. The animals collected on the mesh were then transferred into 100-mL glass bottles and fixed with Lugol's iodine. The zooplankton samples were kept at 4°C until further analyses of community composition (to genus level; counting cladocerans, copepods, and rotifers) on an inverted microscope and biomasses using length–weight regressions (Dumont et al. 1975, Bottrell et al. 1976). Filters (Whatman, GF/C, diameter: 47 mm) with collected phytoplankton biomass after water filtration (50–1,000 mL) were kept frozen at −20°C. The total phytoplankton biomass was derived from chlorophyll-a analyses after extraction with ethanol on a Hitachi U2910 spectrophotometer (method: Swedish Standard SS 028146). To determine the accuracy of chlorophyll-a estimates as a proxy for the total phytoplankton biomass, we collected water samples in 100-mL glass bottles with Lugol's solution at the last sampling of each experiment and obtained the total phytoplankton biovolume based on microscopic counts according to Hillebrand et al. (1999). We then converted the biovolume data into biomass data assuming a density of 1 g/cm^3. Water subsamples (Falcon sterile, 15

[14] (https://www.fieldsites.se)

mL) for bacterial abundance counts were taken and fixed with formaldehyde (4% to the total volume). The samples were later analyzed on a flow cytometer (CytoFLEX V2-B4-R0, Beckman Coulter) according to del Giorgio et al. (1996), with minor modifications by using 1.25 μM of SYTO13 fluorescent nucleic acid stain (Invitrogen, Eugene, Oregon, USA).

To determine phytoplankton and bacterioplankton composition at all sampling days, water samples (50 1,000 mL) were collected on membrane filters (Supor 200, pore size: 0.2 mm) and kept frozen at 80̄C. DNA was later extracted from the filters using the PowerSoil DNA Isolation Kit (MoBio Laboratories Inc., Carlsbad, California, USA). Amplicons of the 16S rRNA and 18S rRNA genes were prepared using a twostep PCR protocol described in detail in a protocol deposited and published at the protocols.io repository.[15] Amplicon paired end sequencing was then performed using Illumina MiSeq v3 sequencing chemistry on the Illumina MiSeq platform at the SciLifeLab SNP&SEQ Technology Platform. Raw sequences have been deposited to the NCBI SRA database with the accession numbers PRJNA544742 (18S rRNA amplicons) and PRJNA531721 (16S rRNA amplicons). Subsequently, sequences for both bacteria and microeukaryotes were analyzed using the DADA2 pipeline and assigned into ASVs at 97% threshold using the SILVA database. A detailed report of the sequence analysis can be found in the supplementary file (Appendix S2).

The photosynthetically active radiation (PAR) was measured at least once in each of the experiments to confirm the effectiveness of the shading manipulations and whether this manipulation indeed reduced the incoming light by about 50% (Appendix S1: Fig. S1). Manual measurements were taken with an Apogee MQ-500 sensor (Apogee Instruments Inc., 721 West 1800 North Logan, UT, USA), mounted on a UV-resistant polyethylene pole placed at the center of each enclosure at a depth of 40 cm (except in Stortjärn at 20 cm).

Data analyses and statistics

We tested for the main and interactive effects of pulse and press disturbances on both functioning (community-level biomass/abundance) and the temporal turnover in community composition based on the Jaccard dissimilarity index (Magurran and McGill 2011). Jaccard is bound between 0 and 1, with 1 being the maximal dissimilarity (complete exchange of taxonomic units) since the start of the experiment. The Jaccard index is based on presence–absence information of taxa, and we refrained from using relative abundances as our phytoplankton compositional data set derived from Illumina 18S gene amplicon sequencing, which can result in biased abundance-based dissimilarity estimates (Gloor et al. 2017, Gong and Marchetti 2019). For consistency with the functional categorization, cyanobacterial ASVs in the 16S data set were extracted and added to the phytoplankton in the 18S data set, such that the bacterioplankton data set is expected to comprise the presence and absence of heterotrophic bacteria primarily. As we were interested in the overall community change over time, we compared the community composition between each time point (Sampling Days 4, 7, 9, 14, and 28) and the initial community composition (Day 1). Specifically, the compositional turnover of any mesocosm at any of the Sampling Days 4, 7, 9, 14, and 28 was calculated based on community composition comparisons (Jaccard dissimilarity) against each of the 16 mesocosms at Day 1. This resulted in a matrix with 16 dissimilarity values for each mesocosm at each sampling day. We then calculated the mean of those 16 dissimilarity values, thus resulting in a final dissimilarity estimate for each mesocosm at each sampling day. To obtain compositional dissimilarity values for all mesocosms at Sampling Day 1, we repeated the process by comparing each mesocosm at Sampling Day 1 against the other remaining 15 mesocosms at Sampling 1, which resulted in a matrix with 15 dissimilarity values for each mesocosm. The mean of those 15 dissimilarity values was then used as final dissimilarity estimate for each mesocosm at the experiment start. These analyses resembled the analyses of distance increase of dissimilarity in spatial and temporal biodiversity analyses (Soininen et al. 2007, Dornelas et al. 2014, Hillebrand et al. 2018*b*).

We were primarily interested in determining the general functional and compositional responses to the treatments over time across all experiments. To this end, we ran linear mixed model analyses (LMMs) for each function (zoo-, phyto-, and bacterioplankton biomass/abundance) and compositional metric (zoo-, phyto-, and bacterioplankton temporal turnover) as response variables, and then included in the model fish presence, shading, time, and their interactions as fixed explanatory variables, and lake, experiment (nested within lake), and mesocosm ID (nested within experiment) as random explanatory variables. Because the variance associated with the random variables (lake and season) was large, we also individually analyzed the treatment effects in each of the experiments for all response variables to check whether the absence of a significant treatment effect was based on the divergent signs of effects in different lakes and seasons, or actually reflected the absence of treatment effects. For this, we ran for each response variable and experiment a LMM with fish presence, shading, time, and their interactions as fixed explanatory variables, and mesocosm ID as random explanatory variable.

To evaluate overall treatment effects on the particular case of the total phytoplankton biomass estimates derived from microscopic analysis (only available at the last sampling of each experiment), we ran a LMM

[15] dx.doi.org/10.17504/protocols.io.badeia3e

including fish presence, shading, and their interaction as fixed explanatory variables (i.e., without the time factor), and lake and experiment (nested within lake) as random explanatory variables. In addition, we also ran ANOVAs for each experiment, testing for the effects of fish, shading, and their interactions on total phytoplankton biomass.

For each LMM we checked whether the residuals of the models were normally distributed with *q-q* plots. If the distribution of the residuals deviated from normality, the response variable was log- or square-root–transformed. For the LMMs with zooplankton biomass and phytoplankton chlorophyll-a as response variables, we also allowed slopes to vary for the time factor in order to achieve normality assumptions. All analyses were run with the software R-3.4.4.

Results

Zooplankton dynamics

Fish presence had a very strong overall negative effect on the total zooplankton biomass, which diminished over time after fish had been removed (Table 1, significant main effect of fish, and Fish × Time interaction). The total zooplankton biomass was reduced by fish in all experiments, except in Bolmen during summer (Fig. 2; Appendix S1: Table S2, significant main effects of fish). The temporal nature of the pulse disturbance was reflected by the total zooplankton biomass recovering to control conditions in most experiments after the fish had been removed (Fig. 2). In contrast, shading had no significant effect overall (Table 1), reflecting that shading only had slight negative effects on the total zooplankton biomass in two lakes—at Feresjön during the spring (Fig. 2; Appendix S1: Table S2, marginally significant main effects of shading) and Erssjön at the end of the experiment during summer (Fig. 2; Appendix S1: Table S2, significant Shading × Time interaction). We did not find a significant interaction between fish and shading (Table 1; Appendix S1: Table S2).

We found a strong accumulated turnover in zooplankton composition over time (Table 1, significant main effect of time), a temporal trend (i.e., increase in dissimilarity over time from the start of the experiment) influenced by fish presence (Table 1, significant Fish × Time interaction). Fish presence also significantly affected the accumulated compositional turnover in zooplankton communities across experiments (Table 1). Specifically, the general trend was that fish presence increased the accumulated compositional turnover within most of the single experiments, including Feresjön, Erssjön, and Erken during spring, and Erssjön and Storjärn during summer (Fig. 2; Appendix S1: Table S2, significant and marginally significant main effects of fish). However, fish presence reduced the accumulated turnover in community composition by the end of the experiment in Erken during summer and Bolmen during spring (Fig. 2; Appendix S1: Table S2, significant and marginally significant Fish × Time interaction). Shading had neither a significant main effect on zooplankton composition, nor did it change the time course of accumulated compositional turnover (Table 1; Appendix S1: Table S2).

Phytoplankton dynamics

Both fish presence and shading overall increased chlorophyll-a concentrations (Table 1, significant main effects of fish and shading). A marginally significant interaction between fish and shading indicated synergistic positive effects, resulting in highest chlorophyll-a levels in shaded mesocosms with fish presence (Table 1). The positive effect of fish presence on chlorophyll-a was highly consistent across experiments, except in the summer experiment in Stortjärn (Fig. 3; Appendix S1: Table S2, main effects of fish). However, in this case chlorophyll-a levels were close to detection limits (with an average across all enclosures of 0.01 μg/L), and indeed, phytoplankton microscopic analyses in the last sampling day showed a positive effect of fish presence (Appendix S1: Fig. S2) on phytoplankton biomass also in this case. As for the zooplankton biomass, the temporal nature of the pulse disturbance was reflected in phytoplankton communities with chlorophyll-a levels recovering to control conditions in many experiments (Fig. 3). The unexpected positive effects of shading on chlorophyll-a were also widespread and statistically significant in 6 out of 10 experiments (Fig. 3; Appendix S1: Table S2, significant or marginally significant main shading effects).

The composition of phytoplankton increasingly deviated from the initial composition over time (Table 1, significant main effect of time), a highly consistent effect observed in all 10 experiments (Fig. 3; Appendix S1: Table S2). Fish presence had neither a significant main effect on phytoplankton composition nor did it change the time course of accumulated turnover across experiments (Table 1; Appendix S1: Table S2). However, we did find a substantially reduced accumulated turnover with fish during the summer experiment in Bolmen (Fig. 3; Appendix S1: Table S2). Across lakes and seasons, shading decreased the accumulated compositional turnover (Table 1, significant main effect of shading), a consistent pattern specifically reflected in four lakes during the summer experiments (Feresjön, Erssjön, Erken, and Stortjärn). However, we found opposite responses in Erssjön during spring, where shading increased the accumulated compositional turnover (Fig. 3; Appendix S1: Table S2).

Bacterioplankton dynamics

Across lakes and seasons, bacterial abundance significantly changed over time, but none of the manipulations had a significant effect (Table 1, main effect of time). Closer inspection of the temporal dynamics revealed

TABLE 1. Results from linear mixed models evaluating the functional and compositional responses of zoo-, phyto-, and bacterioplankton to the experimental treatments over time across all experiments.

Response	m-R^2	c-R^2	Explanatory	df/df.res	*F* statistic	*P* value
Zooplankton biomass	0.165	0.794	Fish	1/147	172.303	**<0.001**
			Shading	1/147	1.459	0.229
			Time	1/4	0.003	0.96
			Shading × Time	1/147	0.14	0.709
			Fish × Time	1/147	12.679	**<0.001**
			Fish × Shading	1/147	0.633	0.427
			Fish × Shading × Time	1/147	0.852	0.357
Zooplankton composition	0.124	0.616	Fish	1/147	5.19	**0.024**
			Shading	1/147	0.722	0.396
			Time	1/635	243.627	**<0.001**
			Fish × Shading	1/147	0.022	0.881
			Fish × Time	1/635	5.831	**0.016**
			Shading × Time	1/635	0.302	0.582
			Fish × Shading × Time	1/635	0.676	0.411
Phytoplankton chlorophyll-a	0.039	0.958	Fish	1/147	113.203	**<0.001**
			Shading	1/147	27.087	**<0.001**
			Time	1/4	5.499	**(0.080)**
			Fish × Shading	1/147	3.507	**(0.064)**
			Fish × Time	1/143	0.462	0.476
			Shading × Time	1/142	0.058	0.844
			Fish × Shading × Time	1/143	1.703	0.176
Phytoplankton biomass	0.038	0.776	Fish	1/142	17.133	**<0.001**
			Shading	1/142	8.415	**0.004**
			Fish × Shading	1/142	0.648	0.422
Phytoplankton composition	0.452	0.786	Fish	1/145	1.863	0.174
			Shading	1/145	8.253	**0.004**
			Time	1/611	1,607.603	**<0.001**
			Fish × Shading	1/146	0.08	0.777
			Fish × Time	1/613	2.154	0.142
			Shading × Time	1/613	3.058	**(0.080)**
			Fish × Shading × Time	1/613	0.206	0.649
Bacterial abundance	0.025	0.782	Fish	1/147	2.513	0.115
			Shading	1/147	1.376	0.242
			Time	1/636	86.859	**<0.001**
			Fish × Shading	1/147	0.006	0.934
			Fish × Time	1/636	2.13	0.144
			Shading × Time	1/636	0.025	0.872
			Fish × Shading × Time	1/636	0.101	0.75
Bacterial composition	0.243	0.816	Fish	1/144	2.609	0.108
			Shading	1/144	0.037	0.846
			Time	1/600	973.045	**<0.001**
			Fish × Shading	1/144	0.07	0.791
			Fish × Time	1/616	1.993	0.158
			Shading × Time	1/616	0.129	0.719
			Fish × Shading × Time	1/616	0.008	0.927

Notes: For each response variable (except phytoplankton biomass derived from microscopy analysis), the linear mixed models (LMMs) included fish presence, shading, time, and their interactions as fixed explanatory variables, and lake, experiment (nested within lake) and mesocosm ID (nested within experiment) as random explanatory variables. For phytoplankton biomass derived from microscopy analysis, the LMMs included fish presence, shading, and their interaction as fixed explanatory variables (i.e., without the time factor), and lake and experiment (nested within lake) as random explanatory variables. The degree of variation explained by the fixed effects is indicated by the m-R^2, whereas c-R^2 stands for the total variation explained including both fixed and random effects. F is fish presence; S is shading; FS is fish predation presence and shading combined; T is time. Boldface *P* values and boldface *P* values in brackets denote significant effects of the explanatory variables at $\alpha = 0.05$ and $\alpha = 0.1$, respectively.

that bacterial abundances increased over time in some experiments, but decreased in others, especially during the second half of the experiment (Fig. 4; Appendix S1: Table S2, main effect of time). Initial fish presence increased bacterial abundance in Stortjärn during both seasons (Fig. 4; Appendix S1: Table S2, significant main

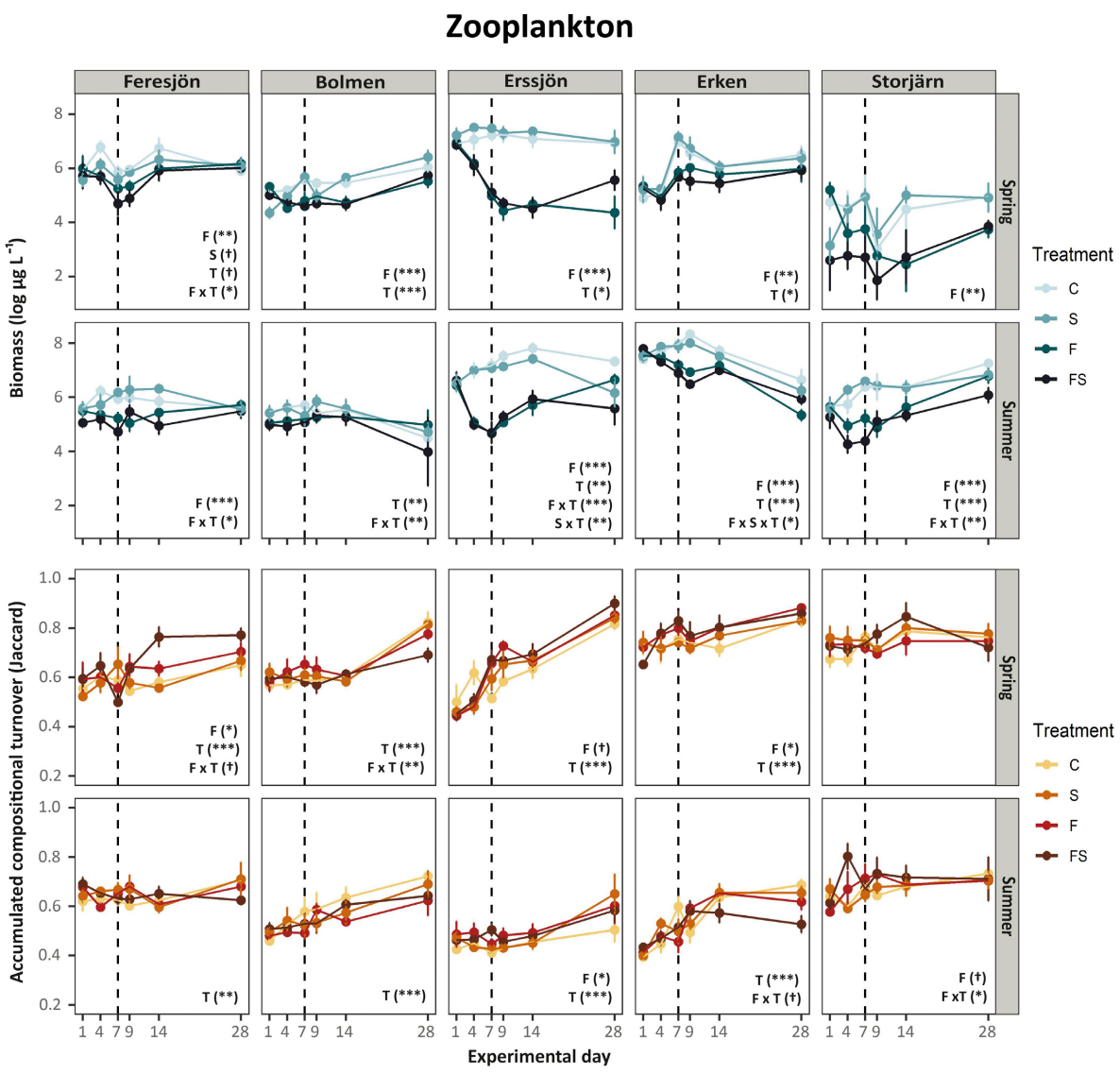

FIG. 2. Functional and compositional dynamics over time of the zooplankton communities in all experiments. Columns indicate lake names and rows seasons for where and when the experiment was conducted, respectively. Upper two rows of panels: Values represent the total zooplankton biomass (means ± SE) over time in each experimental treatment. Bottom two rows of panels: Values represent the accumulated compositional turnover (means ± SE) in each experimental treatment based on the dissimilarity between each time point and the initial community composition (Jaccard index). Significant treatment and interaction effects from linear mixed model analyses are shown for each experiment: C is control; F is fish presence; S is shading; FS is fish predation presence and shading combined (Appendix S1: Table S2). †$P < 0.1$, *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$. The dashed vertical line indicates the time point when the fish were removed from the F and FS treatments.

effects of fish) and reduced the temporal decline of bacterial abundance in Erssjön during summer (Fig. 4; Appendix S1: Table S2, significant Fish × Time interaction). Fish presence only had slightly negative effects on bacterial abundances in Bolmen during summer (Fig. 4; Appendix S1: Table S2, significant main effects of fish). Across lakes and seasons, shading had no significant main effect on bacterial abundance (Table 1). As such, we only found a significant negative effect of shading on bacterial abundance in Stortjärn during summer (Fig. 4; Appendix S1: Table S2, main effect of shading).

Bacterial community composition showed accumulating temporal turnover (Table 1, main time effect). Across lakes and seasons, fish presence did not affect bacterial accumulated compositional turnover (Table 1), which was a result of fish presence either increasing or decreasing the accumulated compositional turnover depending on single-experiment outcomes. Fish presence increased accumulated compositional turnover in Storjärn during spring, and Erken during summer (Fig. 4; Appendix S1: Table S2, significant main fish effects), whereas it reduced the accumulated

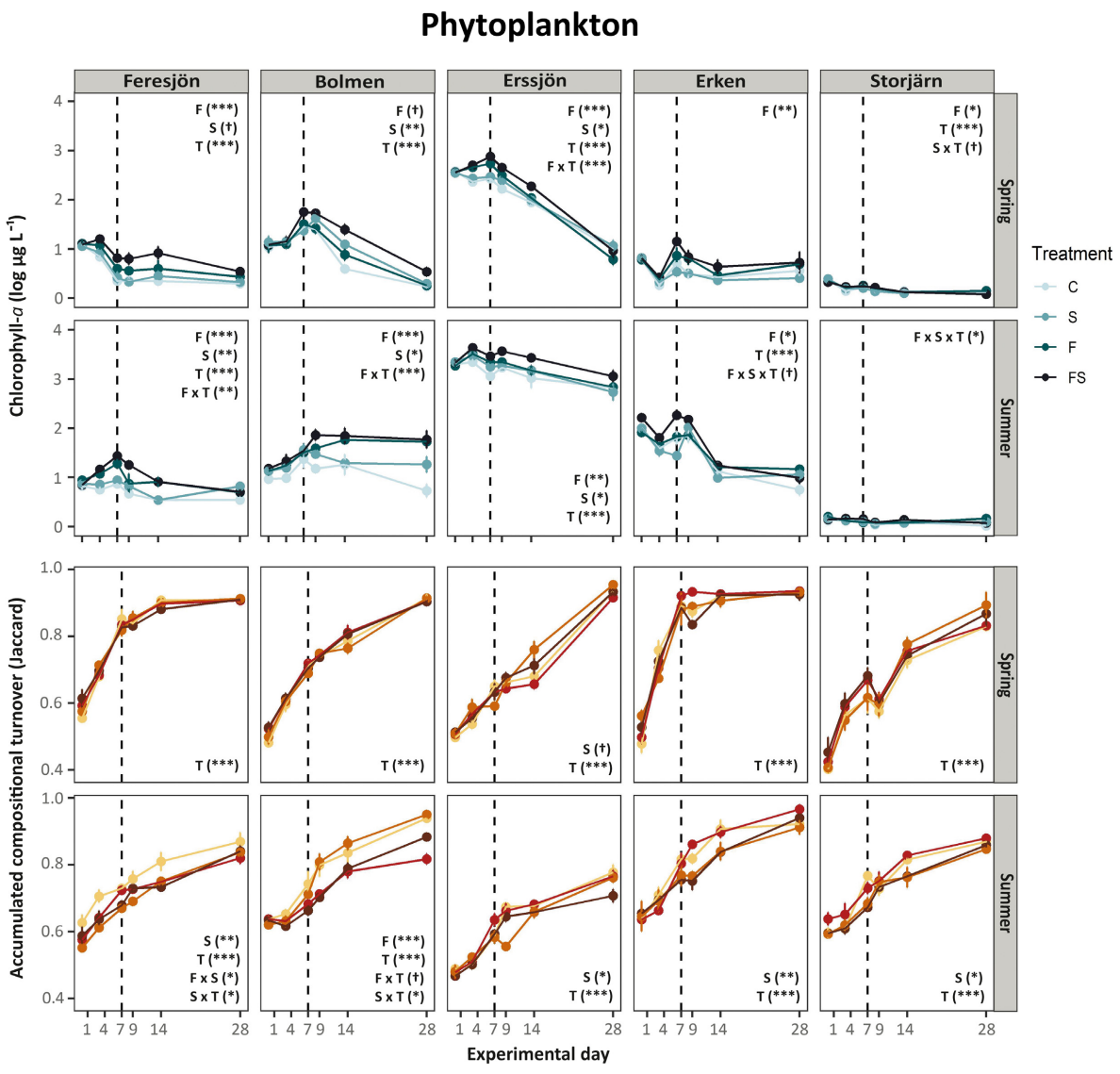

FIG. 3. Functional and compositional dynamics over time of the phytoplankton communities in all experiments. Columns indicate lake names and rows seasons for where and when the experiment was conducted, respectively. Upper two rows of panels: Values represent the total phytoplankton biomass (means ± SE) over time in each experimental treatment. Bottom two rows of panels: Values represent the accumulated compositional turnover (means ± SE) in each experimental treatment based on the dissimilarity between each time point and the initial community composition (Jaccard index). Significant treatment and interaction effects from linear mixed model analyses are shown for each experiment: C is control; F is fish presence; S is shading; FS is fish predation presence and shading combined (Appendix S1: Table S2). †$P < 0.1$, *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$. The dashed vertical lines indicates the time point when the fish were removed from the F and FS treatments.

compositional turnover in Feresjön during spring and by the end of the experiments in Bolmen and Erssjön during summer (Fig. 4; Appendix S1: Table S2, significant and marginally significant Fish × Time interaction). Shading had no overarching effect on bacterial accumulated compositional turnover (Table 1), as it only reduced it in Feresjön and Stortjärn during summer at different times in the experiments (Fig. 4; Appendix S1: Table S2, Shading × Time interactions).

DISCUSSION

As climate warming proceeds and extreme heat events become more common, functional and numerical responses in planktivorous fish assemblages are to be expected (Jeppesen et al. 2014), with repercussions in the form of pulse perturbations for lower trophic levels through, for example, increased short-term variability in fish densities and predation pressure (Ersoy et al. 2019).

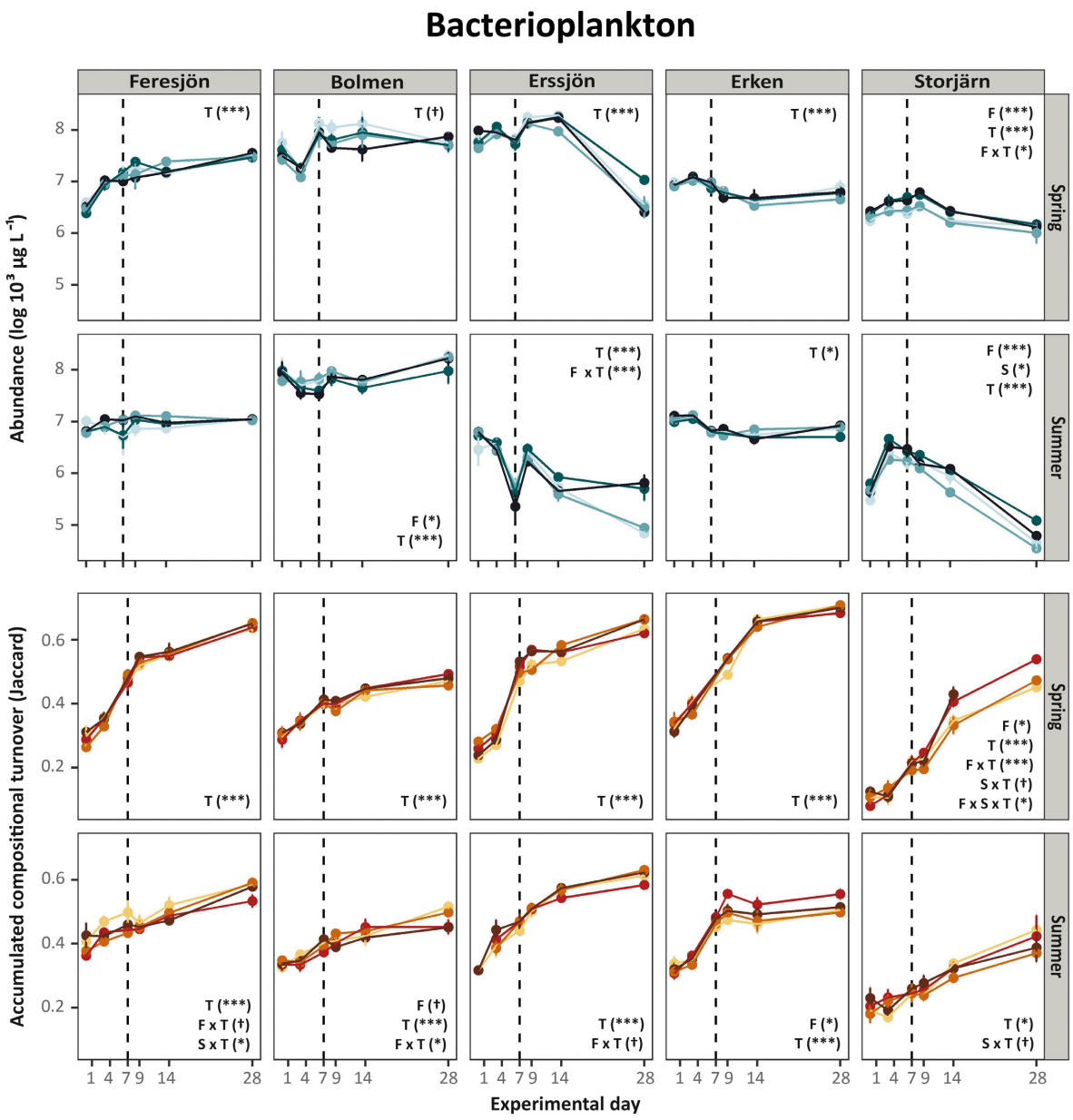

FIG. 4. Functional and compositional dynamics over time of the bacterioplankton communities in all experiments. Columns indicate lake names and rows seasons for where and when the experiment was conducted, respectively. Upper two rows of panels: Values represent the total bacterioplankton biomass (means ± SE) over time in each experimental treatment. Bottom two rows of panels: Values represent the accumulated compositional turnover (means ± SE) in each experimental treatment based on the dissimilarity between each time point and the initial community composition (Jaccard index). Significant treatment and interaction effects from linear mixed model analyses are shown for each experiment: C is control; F is fish presence; S is shading; FS is fish predation presence and shading combined (Appendix S1: Table S2). †$P < 0.1$, *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$. The dashed vertical lines indicate the time point when the fish were removed from the F and FS treatments.

Of critical importance is to improve our understanding of how plankton communities may react and recover from such pulses with and without ongoing press disturbances in the form of reduced light availability. Projected increases in precipitation and associated cloud cover from climate change or lake browning are predicted to impair primary production in many boreal and subarctic lakes further (Karlsson et al. 2009, Weyhenmeyer et al. 2016, Kritzberg et al. 2019), thus potentially altering responses to top-down pulse disturbances. Our modularized experiment across space and time offers a broad view of the mean and variance in the response of plankton communities to these disturbances, but also provides novel insights to further our understanding of how

communities may react to other pulse and press disturbances. First, most of the variation in the functional and compositional dynamics of communities was driven by the spatial and temporal specificity associated with each experiment. These spatial and temporal influences on community functional and compositional dynamics were reflected by the large variation explained by the random structure of the models evaluating overall treatment effects across all experiments (Table 1). Despite this, we found strong effects on the three trophic levels with the top-down pulse disturbance, with signs for interactive impacts with the shading press disturbance on primary producers (phytoplankton communities). Second, if the functioning of a trophic level was vulnerable to any disturbance (i.e., displayed a nonneutral response) it would almost always show the same direction in the response, either consistently positive or negative regardless of the site and season. Conversely, the accumulated compositional turnover within each trophic level either increased or decreased in response to the disturbances depending on the site and season. And third, we found that functional recovery from the pulse disturbance occurred by the end of most experiments for at least one or more trophic levels. No previous experimental study has provided insights into this spatial and temporal extent on responses of three trophic levels to pulse top-down disturbances in systems with and without additional stress induced by press bottom-up disturbances. This is especially important for microbial communities, which have received little attention in the past because of methodological constraints to characterize their composition (but see Wasserman et al. 2015, Sullam et al. 2017).

Fish presence as pulse disturbance had strong short-term effects on zooplankton and phytoplankton biomasses across all sites and seasons (partially corroborating H_{1a}). The inverse patterns observed in most single experiments between zooplankton biomass (decrease) and phytoplankton biomass (increase) levels are in accordance with trophic cascade theory, whereby high zooplankton mortalities from fish predation weaken top-down control on phytoplankton and, consequently, increase their biomass levels (Carpenter et al. 1985, Carpenter and Kitchell 1993). In addition, we observed significant changes in total phosphorus concentrations in some experiments (e.g., Appendix S1: Table S2, Fig. S6), indicating potential positive effects of fish on primary production via nutrient recycling (Schindler et al. 1993, Vanni 2002, Stuparyk et al. 2019).

Importantly, we noted a dilution of the effect from fish presence on both community function and composition across trophic levels. In addition to the observed strong effects on zooplankton and phytoplankton biomasses, the overall effects of fish presence were also reflected in strong changes in the accumulated turnover of the zooplankton community composition across all experiments (partially corroborating H_{1b}). However, we did not observe such strong patterns for the accumulated compositional turnover of phytoplankton and bacterial communities. In addition, we did not find overall effects of fish presence on bacterial abundances (partially rejecting H_{1a}). The absence of overall effects of fish presence on bacterial abundances was because only the experiments at the most humic lakes (Erssjön and Stortjärn) showed increased bacterial abundances in response to fish presence, whereas one single experiment (Bolmen during summer) showed a slight decrease in bacterial abundances. Overall, these findings revealed that the top-down effects of fish presence at lower trophic levels (especially bacteria) can go in different directions: (1) our findings confirm results from previous single experimental studies showing that bacterial abundances tend to increase in response to fish presence because of reduced top-down control by large-bodied zooplankters (Riemann 1985, Christoffersen et al. 1993, Jurgens 1994, Sullam et al. 2017), as well as more recent findings revealing shifts in their community structure (Sullam et al. 2017). (2) Conversely, our results also show that bacterial abundance responses to fish presence can be neutral or negative. Studies have shown that decreased zooplankton grazing can increase abundances of bacterivorous protozoa (Tranvik and Hansson 1997, Bertilsson et al. 2003). Increased top-down control by bacterivorous protozoa on bacterial communities could then be a likely mechanism behind the observed neutral or opposite patterns in different single experiments. These results highlight that local environmental conditions are likely to play a considerable role in constraining the effects of top-down disturbances at lower trophic levels, thus diminishing their overall impact on multiple communities. Although the analyses of this study are centered on the overall mean and variance in response to the disturbances across lakes and seasons, future studies should explicitly address mechanisms that can be behind the observed response variability as influenced by multiple potential local abiotic and biotic factors.

Shading alone significantly altered the functionality (biomass measured as chlorophyll-a) and composition of phytoplankton across experiments. As a result, we found near-significant interactive effects between fish presence and shading across experiments on chlorophyll-a concentrations, with higher chlorophyll-a concentrations in shaded mesocosms with fish than without fish. However, the effects of shading on phytoplankton communities and its interactive effects with fish presence did not propagate enough to extend to other trophic levels (partially refuting $H_{2a,b}$ and $H_{3a,b}$). Zooplankton and bacterial communities were mostly unaffected by the shading treatment, and there were only clear changes in the time course of bacterial accumulated compositional turnover in two single experiments (Feresjön and Stortjärn during spring and summer, respectively), thus also resulting in the absence of interactive effects with fish presence.

Our shading manipulations mimicked potential shading effects of increased precipitation and associated cloud cover from climate change (Weyhenmeyer et al.

2016). In addition, the shading level (50% reduction in light availability; Appendix S1: Fig. S1) falls within the range of observed lake browning effects in the light climate of many boreal and subarctic lakes (Weyhenmeyer et al. 2016), where light limitation is the primary repercussion for food web structure and functioning because of the very high background concentration of dissolved organic matter (Karlsson et al. 2009, Kritzberg et al. 2019). Such reduction in light availability (halving the amount of incoming light) has previously been shown to affect both lake primary producers and consumers (Striebel et al. 2008, Ptacnik et al. 2016). So why did shading not have such profound impacts across trophic levels? A plausible reason for this is that the negative effects of shading on phytoplankton biomass were present but slow, and did not cascade across trophic levels within the time frame of our experiments. This notion is strengthened by microscopic analyses of the phytoplankton, which revealed significant negative effects of shading on phytoplankton biomasses across experiments at the last sampling days (partially accepting H_{2a}) (Table 1; Appendix S1: Fig. S2), suggesting that shading may suppress phytoplankton growth and biomass in the longer run. We also observed overall significant effects of shading on the temporal turnover of phytoplankton composition (partially corroborating H_{2b}). However, negative short-term effects of shading on phytoplankton biomass production were unlikely.

Our analyses revealed that chlorophyll-a concentrations were not reduced by shading in any of the experiments. Instead, we found a significant positive effect of shading on chlorophyll-a concentrations across experiments, which was likely the result of an adaptive response of phytoplankton to decreased light input. This adaptive response of phytoplankton was reflected in shaded mesocosms producing more chlorophyll-a per phytoplankton biomass unit than in the controls (Appendix S1: Fig. S3). Chlorophyll-a concentrations in the shaded mesocosms approached control levels at the last sampling days in many single experiments, indicating an erosion of this adaptive response over time, possibly because of their inability to maintain energetically costly demands for chlorophyll-a upregulation (Murphy and Cowles 1997). Therefore, the energy expenditure to capture more light in this well-known adaptation of phytoplankton (Brown and Richardson 1968, Perry et al. 1981) possibly enabled them to buffer the negative effects of the press disturbance on their growth in the short term, and thus constrained cascading effects across other trophic levels. In addition, in some systems the dissolved fractions of N and P were low or absent, indications that these nutrients could also be limiting phytoplankton growth (Appendix S1: Fig. S4 and S5). Nutrient limitation from other resources might then be an additional reason why shading had limited impact on phytoplankton biomass; that is, other resources were already setting the upper limits for phytoplankton biomass production, a hypothesis that also merits further investigation in future studies along with the potential influence of other multiple potential abiotic and biotic factors.

Importantly, we observed almost consistent directionality of functional responses within each trophic level across all experiments; that is, if the functionality of a community was affected by a particular disturbance, it would almost always show the same direction of response (either an increase or decrease) regardless of the site and season. The only exception was found for bacterial abundances in Bolmen during summer, which showed a minor decrease in response to fish predation presence during a few samplings, and therefore slightly deviated from the general positive response trend in bacterial communities. The strong consistent directionality of functional responses in zooplankton and phytoplankton communities may not appear surprising in line with basic principles of trophic cascades driven by either bottom-up or top-down forces. For example, the presence of planktivores has generally negative effects on zooplankton biomasses via direct predation pressure (Carpenter et al. 1985, Carpenter and Kitchell 1993), provided that positive effects via increased nutrient cycling on zooplankton production are weaker (Schindler et al. 1993, Vanni 2002, Stuparyk et al. 2019). However, disturbances in the form of pulses can also often reverse these patterns after the disturbance ends (Hillebrand et al. 2018*a*). This reversal of patterns may occur when the pulse disturbance leads to community changes such that new dominant taxa drive a different functionality at the community level (e.g., higher biomass production for zooplankton, in this case; Hillebrand et al. 2018*b*). Despite this recognition, we did not find strong signs for this phenomenon in any of the experiments.

Remarkably, we observed rather the opposite for the temporal turnover in community composition. We had hypothesized that both disturbances would lead to greater accumulated temporal turnover in community composition for all trophic levels as compared to control conditions (H_{1b}, H_{2b}, and H_{3b}), which is the result of the combined effects of greater rates of both taxa gains and losses (Hillebrand et al. 2010, Berga et al. 2012, 2017). In contrast, we found that either pulse or press disturbances did not only lead to greater accumulated compositional turnover of communities than the controls in single experiments (e.g., fish effects in Erken during spring for zooplankton), but sometimes also reduced compositional turnover depending on the site and season (e.g., fish effects in Erken during summer for zooplankton). Altogether, these findings indicate that disturbances may not only destabilize community composition over time, but often act in the opposite direction by stabilizing it. Although the actual causes behind these complex results need to be elucidated in further studies, it is important to stress that some natural or anthropogenic disturbances can influence and reduce colonization rates through, for example, priority effects (Fukami 2015). Generalist consumers can also prevent the most competitive prey species from becoming

dominant over time by proportionately feeding mainly on the most abundant taxa, which then avoids the complete displacement or extinction of inferior competitors (Terborgh 2015, Yvon-Durocher et al. 2015). These could be plausible mechanisms that could increase compositional stability over time.

Finally, we found in most single experiments functional recovery after the pulse ended to be the norm (regardless of the concomitant effects of the press disturbance), with the exception for bacterial abundances due to often-lagged responses to the disturbances. These results are in accordance with a recent meta-analysis across marine, terrestrial, and freshwater realms that found that functional recovery occurs more often than previously known (Hillebrand and Kunze 2020). In contrast, we found many cases where differences in the accumulated compositional temporal turnover between pulse-treated and control mesocosms were maintained or increased even more after the pulse ended for zooplankton (e.g., Feresjon, Bolmen, Erssjön, and Erken during spring, or Erssjön and Erken during summer) and phytoplankton communities (e.g., Feresjon and Bolmen during summer). These results therefore show that changes in community composition in response to pulse disturbances can deviate further from their natural trajectories even after the pulse ends. It is also important to stress that the absence of a total functional recovery at our last sampling date does not imply that it could not have occurred if the experiments lasted longer. However, our short-term experiments were not intended to determine whether there was a total recovery of plankton communities or not (which is still practically challenging even in longer experiments). Instead, our experimental design focused on providing insights on the variability of their recovery pace within a reasonable temporal scale for plankton communities and their short generation times, while still minimizing enclosure effects that can otherwise build up over time in longer experiments (Petersen and Kemp 2019). In this context, multiple factors and ecological traits can influence the pace of functional recovery from pulse disturbances in plankton, such as species-specific reproductive strategies (Ersoy et al. 2019), the replenishment of locally extinct taxa due to their dispersal and colonization from other undisturbed ecosystems (Leibold et al. 2004, Loreau et al. 2013), or the quantity and quality of resources available to grow on (Shade et al. 2012). Although it is beyond the scope of this study to determine the relative importance of all potential factors influencing the community recovery, our findings provide a first critical glimpse of the consistency in the recovery pace of plankton communities across a variety of environmental conditions in space and time.

Altogether, our modularized experiment across space and time provides a general view of how multiple trophic levels may react to the combined effects of pulse changes in fish densities and press changes in light availability. Although it is important to stress the context dependency of the observed responses to this particular combination of experimental perturbations, our results also identified ecological patterns that may be relevant to further our understanding of the effects of other perturbations. Lake food webs are increasingly experiencing a large variety of environmental changes that can take the form of either pulse or press perturbations, such as short- and long-term temperature changes (IPCC 2013, Seneviratne et al. 2014), storms (Stockwell et al. 2020), salinization (Kaushal et al. 2018), or altered biogeochemical cycles (Kritzberg et al. 2019). Response patterns of multiple trophic levels to other disturbances are likely to be different because of the different nature or intensity of the disturbance, but we may also expect similar temporal and spatial response dependencies for other bottom-up and top-down perturbations (e.g., see Rogers et al. 2020). Because many direct and indirect, abiotic (e.g., trophic status, temperature, dissolved organic carbon or light climate) and biotic factors (e.g., initial standing stock, biodiversity, or community trait composition) can potentially constrain local responses, further studies could focus on deciphering mechanisms driving site-to-site response differences by employing integrative statistical modeling (e.g., structural equation modeling; Grace et al. 2016). In addition, the identified dichotomy of effects that disturbances can have on the accumulated temporal turnover of community compositions highlights the potential of multiple disturbances to stabilize or destabilize biodiversity patterns over time. Exploring whether we find similar community patterns in response to other disturbance types is important because human interventions in management can be directed in one or another direction depending on whether implemented measures aim at stabilizing a particular community composition over time. At last, the observed specific response patterns from this study align with the emerging conception from a meta-analysis across ecosystem realms and multiple disturbances (Hillebrand and Kunze 2020) that functional recovery from pulse disturbances is generally frequent and rapid, whereas compositional change over time can often prevail and increase even after pulse disturbances end. These findings pose important implications for conservation schemes aiming at preserving biodiversity in its current state and highlight the need to identify drivers shaping the compositional stability of biological communities over time (Hillebrand and Kunze 2020).

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/ecy.3283/suppinfo

Data Availability Statement

Data are available in a collection on the SITES Data Portal. https://meta.fieldsites.se/collections/AYswWim7bxO3t1CUUIgQDNR