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Incomplete recovery of a shallow lake from a natural browning event

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Abstract

1. Terrestrial loads of dissolved organic carbon (DOC) have increased in recent years in many north temperate lakes, leading to widespread brownification. This process can profoundly alter the relative strength of planktonic and benthic primary production in lakes due to changes in light and nutrient availability. While most existing in situ studies of brownification focus on gradual decadal trends, short-term flooding can induce rather sudden natural browning events in lakes.

2. We investigated the recovery of a small, temperate, groundwater-fed shallow lake from a strong natural flooding-induced browning and nutrient loading event. We hypothesised that along with a return to pre-flood lake water levels, DOC concentrations would return to pre-flood concentrations due to bacterial and photolytic mineralisation and flocculation, while total phosphorus (TP) concentrations would show a delayed and potentially incomplete recovery due to sustaining effects of phytoplankton dominance on nutrient dynamics in the lake. Phytoplankton gross primary production (GPP), which surged in response to higher nutrient concentrations and a compressed mixing depth, was expected to follow the same recovery pattern as TP. Benthic periphyton GPP was expected to recover in tandem with improving light conditions.

3. We measured post-flood water levels, water chemistry, and summer pelagic and benthic GPP. The lake water level declined gradually, returning to pre-flood levels within 4 years. As hypothesised, DOC concentrations initially declined rapidly, but remained 1.5-fold higher (*c.* 22 mg/L) than pre-flood values 3 years after peak browning. TP concentrations fluctuated greatly between seasons but remained generally elevated in subsequent years, being roughly double pre-browning values (*c.* 130 μg/L) 3 years post-flood. Measurements taken in 2019, 7 years after the initial browning event, showed both DOC and TP concentrations remaining at these elevated levels.

4. Across the intensive study period 3 years before and after peak browning (2010–2015), TP concentrations were positively correlated to summer phytoplankton biomass, while DOC and TP concentrations were negatively correlated to summer periphyton biomass and GPP. Accordingly, the lake's recovery period exhibited a

decline of pelagic GPP and a partial recovery of summer periphyton biomass and production, although a full return to pre-flood values was not recorded in either case. Whole-lake areal summertime GPP increased due to browning and remained higher than before the browning event.

5. This study provides a rare examination of differences in response rates between DOC, TP, and autotrophic structure in a shallow, temperate lake following a natural flood-induced extreme browning event. The available data provide compelling evidence that browning events can produce lasting changes in the water chemistry, trophic status, and productive pathways of a lake, persisting beyond the lake's return to pre-flood water levels. Such delayed or incomplete recoveries from flooding-induced browning and nutrient loading may have consequences for regional and long-term temporal trends in lake biogeochemistry, potentially contributing to the widespread phenomenon of incremental brownification.

KEYWORDS

dissolved organic carbon, periphyton, phosphorus, phytoplankton, primary production, water-level change

1 | INTRODUCTION

Dissolved organic carbon (DOC) concentrations in lakes and rivers have increased over the past decades in many regions (Evans et al., 2006; Meyer-Jakob & Smol, 2019; Williamsen et al. 2015), mostly due to additional terrestrial inputs (Monteith et al., 2007; Solomon et al., 2015). Increasing DOC concentrations can significantly impact the chemical, physical, and biological traits of aquatic ecosystems (Brothers et al., 2014; Hedström et al., 2017; Jones & Lennon, 2015; Solomon et al., 2015). Terrestrial organic carbon inputs contribute to basal resource availability (Pace et al., 2004; Solomon et al., 2011), but they can also reduce primary productivity via shading effects on phytoplankton and periphyton (Karlsson et al., 2009; Thrane et al., 2014). Increases in DOC concentrations can also physically alter small lakes by increasing the stability of thermal stratification, with multiple potential effects on algal biomass and productivity (Brothers et al., 2014; Fee et al., 1996; Houser, 2006). Above a concentration threshold of 5–15 mg/L, the negative influence of DOC shading on autochthonous primary production is believed to exceed the positive effects of DOC on resource availability via the direct supply of organic carbon and the potential fertilisation of autochthonous production (Jones et al., 2012; Karlsson et al., 2009; Kelly et al., 2018; Seekell et al., 2015).

Most in situ studies and observations to date have focused on a gradual and incremental upward trend in DOC concentrations in freshwater ecosystems, a trend that is widely referred to as *brownification* (e.g. Evans et al. 2006; Sepp et al., 2018; Williamsen et al. 2015). Nonetheless, DOC inputs and concentrations can also fluctuate significantly on shorter timescales. Such short-term browning events are most often described in lowland river systems, where sudden *blackwater* events can occur when flooding follows prolonged dry periods, transporting high quantities of accumulated terrestrial organic material. Raymond and Saiers (2010) calculated that 86% of the annual DOC flux in small forested catchments occurred in association with rising or falling stream-water hydrographs, and the released DOC can lead to severe anoxia, killing aquatic animals (e.g. Hladyz et al., 2011; Ning et al., 2015). Extensive flooding in the Murray–Darling Basin (Australia) following a decade of drought mobilised several hundred thousand tons of DOC and the plume of hypoxic water affected roughly 2,000 km of river channel for up to 6 months (Whitworth et al., 2012). While blackwater events in rivers may be common and severe, they are often short lived due to flushing, promoting a rapid recovery of both water quality and the affected fauna (Burford et al., 2008; Kerr et al., 2013). Similar short-term browning events can also occur in lakes (Brothers et al., 2014; Lenard & Ejankowski, 2017; Sadro & Melack, 2012). However, outside of a seasonal spring DOC loading context (e.g. Ågren et al., 2008; Berggren et al., 2010) short-term browning events are less commonly described in the literature. Such events are considered to be especially significant for shallow lakes featuring water retention times between 1 and 3 years in regions expecting increased precipitation due to climate change (Weyhenmeyer et al., 2016). Several mesocosm and microcosm studies have investigated the effects of an abrupt experimental addition of organic and/or humic matter on lake nutrient balances (Corman et al., 2018), macrophyte growth (Choudhury et al., 2019; Xu et al., 2018), phytoplankton composition (Lebret et al., 2018), and aquatic primary production (Feuchtmayr et al., 2019; Vasconcelos et al., 2018). These and other studies have found that browning in lakes, as with streams, can lead to anoxia and have strong effects on water chemistry, algal community composition, biomass and productivity, and the mortality of macrozoobenthos and fish (Brothers et al., 2014; Lenard & Ejankowski, 2017;

Sadro & Melack, 2012). However, the highest DOC concentrations reported in experimental studies are typically around 20 mg/L, while short-term browning events can result in lake concentrations several times greater than this (Brothers et al., 2014). Furthermore, little information is available on the recovery of shallow lakes from such events, despite longer water residence times probably resulting in more persistent ecological and biogeochemical effects on lakes compared to rivers.

Given that lake DOC and total phosphorus (TP) removal, and thus concentrations, are regulated by different mechanisms (described in detail below), their recovery rates in lakes following rapid flood-induced increases may be expected to differ as well. DOC removal in lakes lacking surface hydrological outputs is primarily facilitated by microbial mineralisation (Hanson et al., 2011), flocculation (von Wachenfeldt & Tranvik, 2008), photolytic mineralisation (Cory et al., 2014; Granéli et al., 1996), and dilution (depending on lake water residence times and inflowing DOC concentrations). In contrast, TP concentrations can only be permanently reduced via burial in the sediments or dilution, potentially delaying recovery time. Furthermore, phytoplankton and periphyton compete directly for nutrients in lakes, and a reduction in periphyton production and biomass can increase sediment fluxes of TP into the water column (Genkai-Kato et al., 2012), further delaying reductions of TP concentrations in lakes where phytoplankton and DOC have shaded out benthic primary producers (Vasconcelos et al. 2016). Therefore, through the above-described processes, DOC concentrations should theoretically decline more rapidly than TP concentrations following a sudden browning event. However, supportive information in the literature from long-term studies of actual lakes is sparse.

In this study, we analysed the recovery of a small, temperate, shallow, groundwater-fed lake to a sudden natural flood-induced browning event (previously described by Brothers et al., 2014). Due to high precipitation (Douinot et al., 2019; Heinrich et al., 2019) resulting in rising water levels in the lake and the surrounding peatlands, anoxic conditions established across the full lake water column, associated with DOC concentrations increasing five-fold, from c. 12 mg/L in 2010 to a maximum of c. 60 mg/L by 2012. Concurrently with increasing DOC concentrations, TP and iron (Fe) concentrations rose dramatically. Benthic and planktonic primary producers exhibited opposing responses to the browning. Increased nutrient availability and suppressed mixing depth promoted phytoplankton gross primary production (GPP), while shading by phytoplankton and DOC suppressed periphyton production (Brothers et al., 2014). We continued the examination of lake DOC and TP concentrations, as well as summertime primary production, for 3 years following peak browning (from 2012 to 2015) to investigate their recovery rates. Additional water samples were taken in 2019 for further examination of the long-term effects of browning on this lake. Along with declining precipitation and water levels after 2012, we anticipated a reduction of external DOC and TP loading due to the reduced flooding of the surrounding peatland. We expected a more rapid decrease in lake DOC concentrations compared to TP due to the ability of carbon to leave the lake via atmospheric fluxes.

Accordingly, we hypothesised that the lake's autotrophic community, which had featured significant benthic periphyton production (Brothers et al., 2013), might not fully return to pre-flood conditions if P concentrations remained elevated in the water column, as phytoplankton shading would prevent a full recovery of light conditions and thus benthic primary production.

2 | METHODS

2.1 | Study site

Kleiner Gollinsee (hereafter referred to as Gollinsee) is a small (0.03 km^2), shallow (Z_{mean}: 1.7 m, Z_{max}: 2.9 m; 2010 values), eutrophic lake located in north-eastern Germany (53°01′N, 13°35′E). The lake lacks surface in- or outflows. A net gain of 133 mm of groundwater was previously recorded from 8 June to 19 October 2010 (Rudnick, 2011) indicating a water residence time of approximately 5 years. Gollinsee is directly surrounded by degraded peat within a forested catchment and is sheltered from strong winds by a reed belt (*Phragmites australis* Trin. ex Steud.) and alder trees (*Alnus glutinosa* L.), resulting in lengthy, strongly stratified periods throughout the year. The lake lacks submerged macrophytes (Brothers, Hilt, Meyer, et al., 2013).

From November 2010 to November 2014, Gollinsee was divided into two similarly sized basins using a plastic curtain as part of an unrelated experiment examining food web uptake of controlled input of terrestrial particulate organic carbon (Attermeyer et al., 2013; Scharnweber et al., 2014). The flooding of the lake, and the resulting browning, occurred independently of this experiment, as evidenced by both basins exhibiting simultaneous and commensurate increases in DOC concentrations (Figure 1) following elevated precipitation rates in summer 2011 (Heinrich et al., 2019). Nevertheless, we present separate averages for each basin (hereafter referred to as north and south basins) during the years the lake was split (2011–2014). We here consider 2010 quality parameters to reflect the lake's preflood (baseline) state, as its water levels and water chemistry values reflect available data from earlier years (Figure S1; Table S1; Brennecke, 2008). 2011 marks the onset of the flooding (by rising groundwater stage and/or subsurface flow) and coincident browning event that reached its peak in summer 2012 (Brothers et al., 2014), and 2013 is here considered to represent the beginning of the lake's recovery period from the flooding and browning event. Given that the high regional precipitation levels of 2011 did not persist in the following years (Heinrich et al. 2019), the lake water residence time was estimated to remain approximately 5 years.

2.2 | Water sampling and water quality analysis

Integrated water samples (every 0.5 m from the water surface to just above the sediment) were retrieved using a Limnos water sampler (limnos.pl) about every 3 months from spring 2013 to summer 2015. Two additional water samples were taken in 2019 (on 27 April
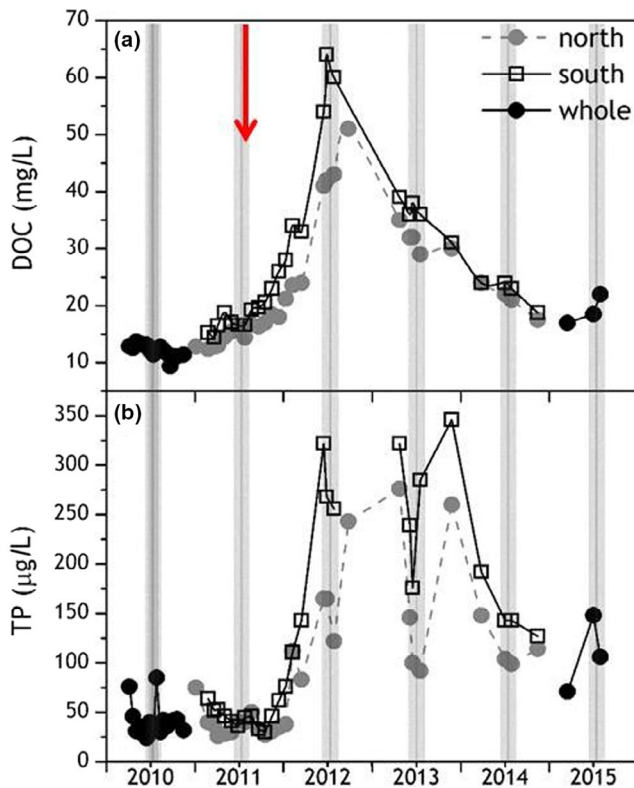
FIGURE 1 (a) Dissolved organic carbon (DOC, mg/L) and (b) total phosphorus (TP, µg/L) concentrations in Lake Gollinsee, from 2010 to 2015. Values for 2010 and 2015 represent that of the whole lake, whereas 2011–2014 values are shown for the two sides when the lake was split in half. Bars indicate annual benthic production sampling times (June–July). Data from 2010–2012 are taken from Brothers et al. (2014). An arrow shows the onset of flooding period. Refer to Figure S1 for water level dynamics [Colour figure can be viewed at wileyonlinelibrary.com]

and 14 August) to measure the DOC levels past the lake water residence period. Water samples were transported to the laboratory in cooling boxes and water chemistry parameters (listed below) were analysed the following day. During stratified periods, separate integrated samples were collected from the epilimnion and hypolimnion. To confirm whether the lake was stratified, mixing depths were determined using vertical profiles of dissolved oxygen (O_2) concentrations, pH, and water temperature, measured by a Yellow Springs Instruments multi-probe sonde. Water column light attenuation was measured every field campaign using two Underwater Spherical Quantum Sensors (LI-193, LI-COR) deployed 50 cm apart. We calculated the euphotic zone as the depth at which 1% of the surface light would remain available to primary producers. Water level was measured monthly by local conservation authorities (kindly provided by R. Michels, Biosphärenreservat Schorfheide-Chorin).

Although we primarily focused on DOC and TP concentrations, we also measured and report concentrations of total dissolved phosphorus (TDP), soluble reactive phosphorus (SRP), dissolved nitrogen (DN), ammonium (NH_4^+), dissolved iron (Fe^{2+} and Fe^{3+}), and manganese (Mn^{2+}) following German standard procedures (DEV, 2009), as both Fe and NH_4^+ are usually strongly linked with P mobilisation

in the sediment. Dissolved compounds were analysed in 0.45 µm filtrate. Total phosphorous and TDP were measured as soluble reactive P following Murphy and Riley (1962) after acid digestion at 150°C. We calculated particulate phosphorus by subtracting the values of TDP from TP. Dissolved organic phosphorus (DOP) was calculated by subtracting SRP from TDP values. DOC concentrations were measured with a Carbon-Analyzer (TOC 5000, Shimadzu), and Fe concentrations were analysed using an inductively coupled plasma optical emission spectrometer with an inductively coupled argon plasma unit (iCAP 6000-Duo, Thermo Fisher Scientific). Furthermore, to explore whether DOC had the same colouring and light attenuation effects throughout the years in the water column, we compared the fluorescence of filtered lake water at 470 nm (that we had already measured using a pulse amplitude modulated fluorometer [Phyto-PAM, Walz, Effeltrich, Germany] to estimate phytoplankton production), with lake water DOC concentrations.

To calculate a theoretical dilution of DOC from its peak concentrations reached in 2012, we used a simple mass balance approach based on estimated lake water retention time t_R, assuming a completely mixed lake, immediate intermixing of inflowing groundwater, no precipitation or evaporation and no DOC loss except for dilution:

$$DOC_t = DOC_0 \cdot e^{-\left(\frac{t}{t_R} \cdot \frac{DOC_{t-1} - DOC_{in}}{DOC_{t-1}}\right)}$$

with DOC concentrations at time t (DOC_t), at its peak (DOC_0) and of the inflowing groundwater (DOC_{in}). We here show calculations based on two scenarios: (1) no additional groundwater DOC input into the lake ($DOC_{in} = 0$), representing the potential maximum dilution effect; and (2) a groundwater inflow of DOC concentrations equivalent to pre-browning lake concentrations of 10 mg/L. Measurements taken from two wells near Gollinsee indicated that prior to 2011 groundwater DOC concentrations were typically 2.3–6.2 mg/L, and thus our groundwater DOC concentration of 10 mg/L may be considered a maximum post-flooding value (i.e. a conservative dilution effect estimate). The same approach was applied to TP but with $TP_{in} = 5$ µg/L. Wet DOC deposition via precipitation is considered minimal compared to other carbon fluxes in Gollinsee (Brothers, Hilt, Attermeyer, et al., 2013). To calculate theoretical DOC concentrations based on measured fluorescence at 470 nm, a linear regression was applied (calculated DOC = 0.0413 · fluorescence at 470 nm + 10.678; $r^2 = 0.95$).

2.3 | Biomass and production of phytoplankton and periphyton

For phytoplankton biomass, aliquots of the water samples were filtered onto three 25-mm Whatman glass fibre filters, used to measure chlorophyll a (chl-a) concentrations via high-performance liquid chromatography following Shatwell et al. (2012). For phytoplankton GPP measurements, rapid photosynthesis-irradiance (P-I) curves of phytoplankton were measured using a Phyto-PAM fluorometer following a dark adaptation period of at least 15 min. Additionally, a lake-centre weather station recorded and transmitted global

radiation continuously at regular intervals of 10 min in 2011, hourly in 2012, and every 30 min in 2014. Due to technical problems with the weather station, data from January to mid-September 2013 and all of 2015 were retrieved from a nearby weather station (at Döllnsee, 3.5 km southeast of Gollinsee). Chlorophyll-*a* concentrations (from high-performance liquid chromatography) were paired with P-I parameters, photosynthetically active radiation at the water surface (I_0), and water column light attenuation (ε) to calculate phytoplankton production for each 10 cm of the water column following Brothers, Hilt, Meyer, et al. (2013), using the equation:

$$P_z = P_{max} \cdot chla \left(1 - e^{-\alpha \cdot I_z \cdot P_{max}^{-1}} \right)$$

where P_z is the production at depth z, P_{max} and α are P-I parameters representing PAM-measured light-saturated photosynthesis and photosynthetic efficiency at low light, respectively, and I_z is photosynthetically active radiation at depth z, calculated for every 10 cm depth following the Lambert–Beer equation:

$$I_z = I_0 \cdot e^{-\varepsilon \cdot z}$$

Each calculated P_z value was then multiplied by the estimated water volume at corresponding depth. The total sum of these values constituted daily whole-lake phytoplankton production.

To measure summer periphyton biomass accumulation and GPP, we incubated artificial plastic substrates in Gollinsee for a month in June and July of every year between 2010 and 2015. During this period, GPP approaches maximum values in shallow lakes (Brothers, Hilt, Meyer, et al., 2013; Liboriussen & Jeppesen, 2003). We used sets of transparent polypropylene strips with textured surfaces (IBICO, GBC, Chicago, IL, U.S.A.) installed 10 cm below the water surface and subsequently every 50 cm until the sediment was reached. Each set consisted of three large (15 × 2 cm) and small (4.5 × 1.3 cm) strips. The large strips were transported to the laboratory in plastic cylinders deposited in dark and humid coolers, whereas the small ones were stored in 15- ml plastic tubes filled with filtered lake water to avoid zooplankton grazing during transportation. We used the small strips with a Phyto-PAM Emitter Detector Fiberoptics unit to measure rapid photosynthesis-light curves of periphyton. Periphyton grown on the large substrates was scraped using a toothbrush and filtered lake water, then filtered onto 25-mm Whatman glass fibre filters to determine chl-*a* content, following the protocol described above for phytoplankton. Periphyton GPP was calculated for the different depths of biofilm strips harvested using the equation described above for phytoplankton, multiplied by the estimated colonisable surface area corresponding to each depth (taken from lake tachymetry measurements).

2.4 | Statistical analyses

Spearman's ρ correlation indices were calculated to test for a relationship between primary producer biomass or production and DOC or TP concentrations in the water column. All statistical analyses were performed using R version 3.4.2 (R group).

3 | RESULTS

3.1 | Lake water parameters and quality

The lake water level began declining gradually back to the pre-flood state in summer 2013, returning to pre-flood levels by 2016 (Figure S1). Lake water DOC concentrations, having also reached maximum values during the summer of 2012, decreased more rapidly than water levels (Figure 1a). Within 1 year following peak values (i.e. by summer 2013), DOC concentrations had already fallen by roughly 40% at a rate of 30 mg L^{-1} year^{-1}, even though water levels had decreased only marginally (5%) over that same period. Thereafter, the decline in DOC concentrations slowed down to a rate of about 10 mg L^{-1} year^{-1} (declining another 29% by summer 2014) despite a stronger concurrent water level decline (19%), while in the last year of sampling, the DOC concentration remained at roughly 17.5 mg/L, about 50% greater than 2010 pre-brownification values. DOC concentrations declined exponentially by 0.55 per year between summer of 2012 and the end of 2014 ($r^2 = 0.93$).

Concentrations of TP initially increased strongly in 2011, then fluctuated greatly through 2012 until the end of 2013. After this delay, TP declined exponentially until the end of 2015, although with much scatter, by 0.44 per year ($r^2 = 0.32$), remaining generally low thereafter (Figure 1b). Total phosphorous concentrations seemed to stabilise by the end of 2014 at concentrations around double those measured prior to brownification (127 μg/L in July 2015, compared to 58.5 μg/L in 2010). Two additional water samples taken in April and August 2019, past the lake's calculated water residence time, showed that DOC (21.6 and 23 mg/L) and TP (131 and 111 μg/L) concentrations remained well above pre-flood values measured at the same time of year. Concentrations of SRP, P_{part}, DOP, DN, NH_4, Fe, and Mn followed roughly the same trend: exhibiting a sharp increase during the browning event, without a smooth, rapid decline in its aftermath (Figure 2). SRP, DN, NH_4, Fe, and Mn concentrations showed additionally strong peaks in autumn 2013 (Figure 2a, d, e–g). By July 2015, concentrations of SRP, DOP, DN, NH_4, Fe, and Mn were back to pre-browning concentrations (Figure 2), while concentrations of P_{part} remained elevated (Figure 2; Figure S2).

Our dilution effect calculations indicate that in the absence of active DOC removal via flocculation and degradation, and with no additional DOC loading from groundwater inputs, DOC concentrations should decline by roughly 50% from their peak browning concentrations within approximately 3 years (i.e. by summer 2015; Figure 3a). If groundwater inputs continued to load DOC into the lake at calculated pre-flood rates, the dilution effect would result in a decrease of about 37% of the DOC concentrations within the water column in 3 years and about half of its peak concentrations within 5 years. The predicted dilution effect on TP closely matched the observed decline in TP concentrations (Figure 3b). Oxygen profiles
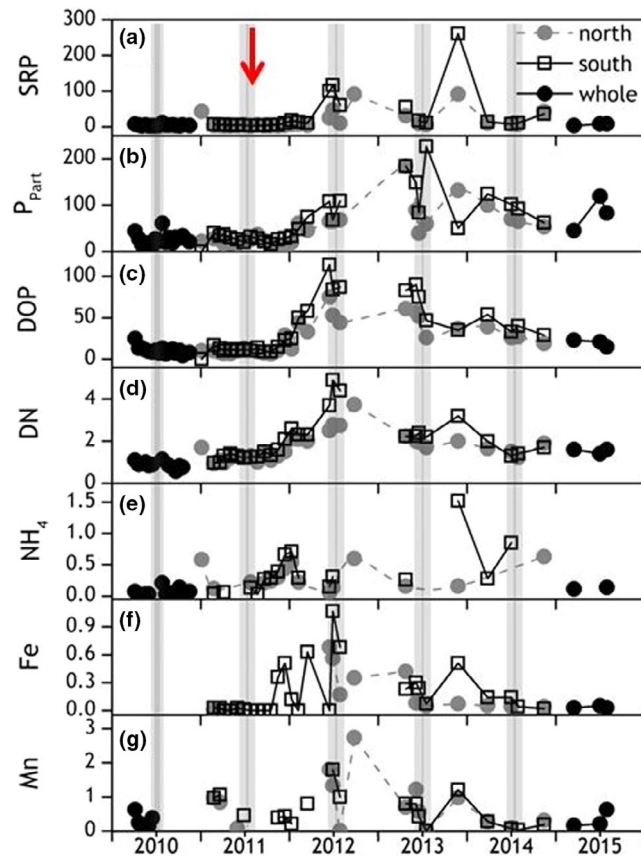
FIGURE 2 Concentrations of (a) soluble reactive phosphorus (SRP, in μg/L), (b) total particulate phosphorus (P_{part} = TP – TDP, in μg/L), (c) dissolved organic phosphorus (DOP = TDP -SRP, in μg/L), (d) dissolved nitrogen (DN, in mg/L), (e) ammonium (NH_4^+, in mg/L), (f) iron (Fe, in mg/L), and (g) manganese (Mn, in mg/L) in Lake Gollinsee from 2010 to 2015. Values for 2010 and 2015 represent that of the whole lake, whereas 2011–2014 values are shown for the two sides when the lake was split in half. Grey bars indicate annual benthic production sampling times. An arrow shows the onset of flooding period. Refer to Figure S1 for water level dynamics [Colour figure can be viewed at wileyonlinelibrary.com]

indicated that the lake was strongly stratified during the summer, and fully mixed by November (Figure S3).

3.2 | Biomass and production of phytoplankton and periphyton

Throughout the study, Gollinsee was dominated by phytoplankton production, although the biomass and GPP of the primary producers varied between years and with changes in DOC, TP concentrations, and light attenuation (Figure 4). Gollinsee's two basins experienced roughly similar water chemistry trends over time (Figures 1, 2) although there were some differences between the timing of their changes in algal biomass and GPP. Phytoplankton biomass reached its peak value in 2013 in the southern basin (191 μg chl-*a*/L in the epilimnion), before decreasing four-fold in 2014. In 2015, phytoplankton biomass remained much higher than 2010 values (104.5 vs.
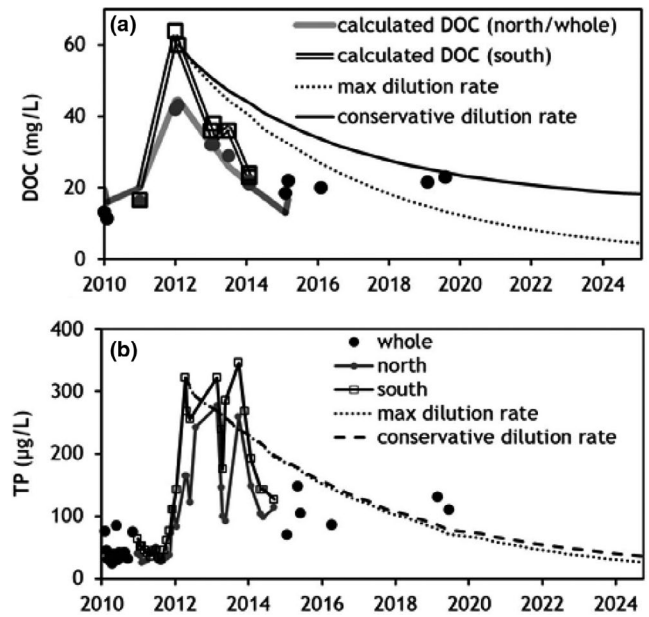

FIGURE 3 (a) Measured dissolved organic carbon (DOC, markers) compared to calculated DOC from fluorescence (lines). Theoretical decrease of DOC from its peak concentrations (2012) solely due to dilution based on estimated lake water retention times, assuming no further DOC input (C_{in} = 0 mg/L; solid line) or a conservative estimate with groundwater inflow containing 10 mg DOC per L (dotted line). (b) Theoretical decrease of TP from 2012 solely due to dilution, assuming no further TP input (0 μg/L; dotted line) and TP input equivalent to pre-brownification state (5 μg/L; dashed line)

13.28 μg chl-*a*/L, respectively). Phytoplankton GPP rates peaked at 4.9 g C m^{-2} day^{-1} in the southern basin in 2013 and dropped three-fold the following year. Phytoplankton biomass was positively correlated with TP concentrations. Periphyton biomass and GPP showed an inverse relationship to DOC, TP concentrations, and light attenuation (Table 1; Figure 4d–f), being at their lowest during peak browning. Periphyton biomass ranged from about 4.98 μg chl-*a* per cm^2 in 2010 to 0.67 μg chl-*a* per cm^2 and 0.58 μg chl-*a* per cm^2 in the southern basin in 2012 and the northern basin in 2013, respectively. Neither basin's periphyton community recovered fully to its pre-browning status by 2015.

3.3 | Light availability

Mean global radiation values measured at the surface of Gollinsee during our periphyton study periods (June–July) decreased in 2011 but increased gradually every year from 2011 to 2014 (Figure 5a). Light attenuation values were highest in 2012 (Figure 5b), leading to the most reduced euphotic zone depth during that same year (Figure 5c). Thereafter, despite increasing light conditions every year, the water column did not fully return to its pre-browning light attenuation levels (1.8 per m in 2010 vs. 2.9 per m in 2015) and euphotic zone depth (2.6 m in 2010 vs. 1.6 m in 2015; Figure 5b, c). Background fluorescence and DOC concentrations were strongly correlated (Spearman's

FIGURE 4 Summer gross primary production (GPP: phytoplankton [a–c] and periphyton GPP [d–f] in g C m^{-2} day^{-1}) and water dissolved organic carbon (DOC, in mg/L), TP (in μg/L) concentrations, and light attenuation coefficient K_d (in m^{-1}) in Lake Gollinsee from 2010 to 2015. Filled symbols represent values from the northern basin, empty symbols correspond to values from the southern basin. A single symbol from each of 2010 and 2015 represents whole-lake calculations. Pre-flooding values (2010) are indicated in red [Colour figure can be viewed at wileyonlinelibrary.com]
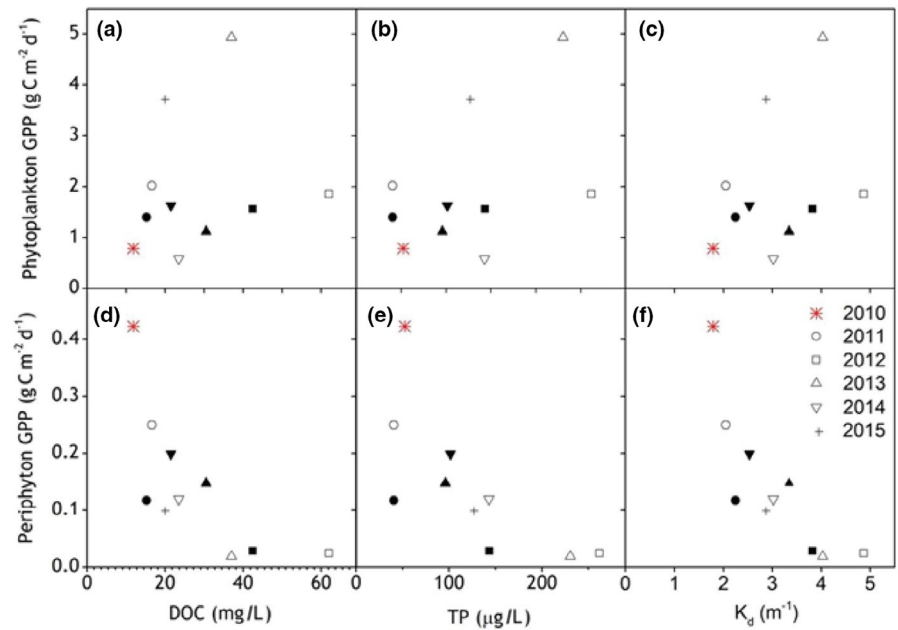

TABLE 1 Spearman's correlation indices and P-values of phytoplankton and periphyton biomass and gross primary production (GPP) values with water dissolved organic carbon (DOC) and total phosphorus (TP) concentrations in Gollinsee between 2010 and 2015. Significant values are represented in bold

	DOC		TP	
	Spearman's ρ	p-value	Spearman's ρ	p-value
Phytoplankton biomass	0.527	0.123	0.748	**0.013**
Phytoplankton GPP	0.236	0.514	0.300	0.403
Periphyton biomass	−0.745	**0.018**	−0.651	**0.042**
Periphyton GPP	−0.721	**0.024**	−0.784	**0.007**

rho = 0.958, p = 0.0002, Figure S4). The background fluorescence of filtered water (probably caused by coloured humic substances) was higher in 2012 and 2013 than in previous years, but values in 2014 were similar to those in 2011 (Figure 3a), and values had returned to pre-brownification levels by 2015.

4 | DISCUSSION

Our results show that the recovery of a shallow temperate lake from a natural, flood-induced, browning event can be more rapid for DOC concentrations compared to TP concentrations. However, the recoveries of DOC, TP, and autotrophic structure were all delayed or incomplete. Short-term or sudden browning events can thus produce lasting changes in the water chemistry, trophic status, and productive pathways of a lake, persisting beyond the lake's return to pre-flood water levels.

4.1 | Dissolved organic carbon and TP recovery dynamics

The fact that DOC concentrations declined much more rapidly (by a rate of 0.55 per year) than explainable by dilution (0.2 per year)

from peak concentrations in summer 2012 to the end of 2014 indicates that active DOC removal mechanisms probably accelerated the removal of DOC from Gollinsee during its recovery period. Such likely removal mechanisms include bacterial (von Wachenfeldt & Tranvik, 2008) and photolytic mineralisation (Bertilsson & Tranvik, 2000; Granéli et al., 1996), as well as flocculation resulting in burial in the sediments (Skoog & Arias-Esquivel, 2009; von Wachenfeldt & Tranvik, 2008). The observed rates of DOC removal measured in Gollinsee are roughly equivalent to those reported for other eutrophic lakes featuring elevated bacterial growth efficiencies (32. 1 mg C L^{-1} year^{-1}; Biddanda et al., 2001), and a study from a nearby eutrophic lake (Schulzensee) also found that rising DOC concentrations can increase bacterial DOC consumption rates by up to 68% when nutrients are not limiting (Attermeyer et al., 2014). However, photolytic mineralisation is also an effective pathway for removing terrigenous organic carbon (Obernosterer & Benner, 2004), potentially explaining roughly half of our observed decrease in DOC concentrations (9.4 mg C L^{-1} year^{-1}, following Bertilsson & Tranvik, 2000, and using the mean global radiation at Gollinsee for the year 2012, assuming that the top 2 cm water layer was subject to photolysis).

While the rapid decline of DOC concentrations during Gollinsee's recovery period indicates that passive dilution and export was not the only recovery mechanism, it is difficult to determine the relative
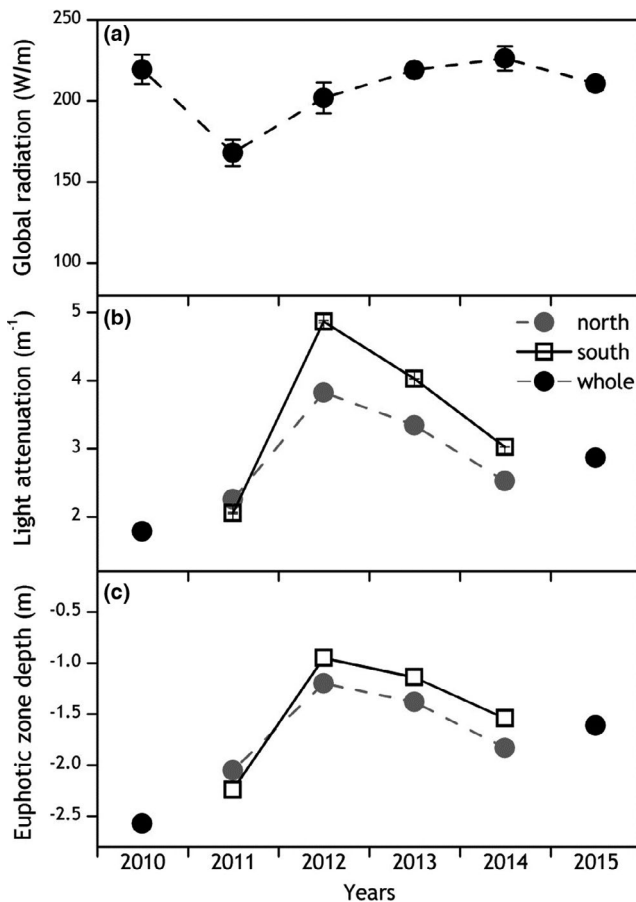
FIGURE 5 Differences in global radiation at the water surface (a, ± standard error), water column light attenuation levels (b, ± standard error) and euphotic zone depth, defined as 1% of photosynthetically active radiation (c) at Lake Gollinsee in June and July between 2010 and 2015. Global radiation was measured continuously at regular intervals of 10 min in 2011, hourly in 2012, and every 30 min in 2014. On-site 2013 and 2015 data are lacking due to weather station malfunction, and we thus show global radiation measurements from Döllnsee instead (3.5 km from Gollinsee). Light attenuation values represent the average of two direct measurements per year, at the start and end of the study period

strength of permanent carbon removal via export to the atmosphere as carbon dioxide (CO_2) versus burial in the sediments. Gollinsee's CO_2 emissions to the atmosphere reportedly increased by an order of magnitude from 2010 (mean = c. 50 g C m^{-2} $year^{-1}$) to 2012 (c. 400 g C m^{-2} $year^{-1}$) (Brothers et al., 2014). Other processes such as flocculation probably also contributed to the permanent removal of DOC from the water column. Concomitant decreases of DOC and Fe concentrations indicate that the co-precipitation of DOC with iron-containing minerals (namely iron sulfide) could have played a major role in DOC removal (as hypothesised by Skoog & Arias-Esquivel, 2009) and a return to greater DOC storage in the lake sediments. Prevailing anoxic conditions during peak browning (summer 2012; reported in Brothers et al., 2014) would have presumably driven sulfide concentrations to increase in the water column, which in turn would have led to iron sulfide precipitation. After

2013, DOC concentrations declined more slowly and eventually stabilised at concentrations which were roughly 50% greater than pre-brownification values. This appeared to extend beyond the end of our initial study period, given follow-up measurements in 2019 which described the same DOC concentrations as in 2015.

As predicted, TP concentrations exhibited a longer delay in recovery than DOC concentrations and appeared to have been largely driven by dilution effects. Phosphorus released from both catchment soils and sediments during anoxic conditions was probably taken up by phytoplankton when pelagic production was boosted during the browning event. This is corroborated by evidence from the lake's south basin in summer 2013, where the highest recorded values of particulate P (237 µg/L) coincided with peak phytoplankton GPP rates and biomass (191 µg chl-a/L). Assuming a mean P content of phytoplankton of about 1 µg P/µg chl-a, phytoplankton probably contained most of the particulate P that contributed 64 ± 11% to TP (all data without winter samples). Phosphorous uptake of phytoplankton was certainly even higher because part of the produced biomass sank out of the pelagic zone. This phytoplankton uptake probably delayed the rapid sequestration of P into the sediments by iron co-precipitation when oxic conditions returned in the water column. Subsequent peaks in SRP and NH_4^+ in autumn 2013 were probably due to the mineralisation of the phytoplankton bloom. Minor peaks in concentrations of Fe, and Mn during autumn 2013 were probably caused by the mixing of the nutrient-rich and anoxic hypolimnion with the epilimnion following a strong summer stratification. This may indicate an increased availability of P for phytoplankton growth in the lake during recovery from the browning event. Substantial increases in N and P associated with DOC increases have also been recorded in many seepage lakes and may generate future water-quality concerns (Corman et al., 2018).

4.2 | Response and effects of primary producers during post-flood recovery period

Phytoplankton and periphyton biomass and GPP responded in opposing manners through the lake's post-flood recovery period. Phytoplankton GPP had been enhanced by browning due to elevated TP concentrations and compressed mixing depths (Brothers et al., 2014), exacerbating the shading of periphyton by DOC and Fe (Jones, 1992). During recovery, pelagic and benthic primary producers also responded differentially to declining DOC and TP concentrations, supporting theoretical predictions by Vasconcelos et al. (2016). While gradual changes in DOC and TP concentrations coincided with a gradual decrease in phytoplankton biomass and production, decreasing light attenuation within the water column resulted in a more sudden increase in benthic GPP once a critical threshold was passed.

Gollinsee experienced only a partial recovery in DOC and TP concentrations despite lake water levels (and presumably loading rates) returning to pre-flood conditions by 2016. The available evidence indicates that this probably reflects the interacting effects between DOC,

TP, and the autotrophic community structure of the lake. Specifically, periphyton GPP never returned to pre-browning (2010) rates despite the reprieve from DOC and Fe shading following 2012. This continued suppression of periphyton production thus probably resulted from phytoplankton shading, analogous to the classic stable state relationship between planktonic and benthic primary producers described for shallow lakes (e.g. Genkai-Kato et al., 2012). The elevated phytoplankton community established from the browning event (Brothers et al., 2014) was able to continue to suppress periphyton through the lake's recovery period, resulting in higher TP in the water column and decreasing the P-binding capacity of epiphyton in the sediments (Lu et al., 2016).

Given an initially rapid decline in DOC concentrations, which exceeded hydrological dilution rates, it is less clear why DOC concentrations had not returned to pre-browning values by the end of the study period (2015), or even 4 years later during a follow-up sampling campaign. We acknowledge the possibility that the scarcity of our data in later years may indicate that minor seasonal fluxes in DOC concentrations were not captured in our measurements, although note that values measured in 2019 remained well above the range of values measured in any pre-flood years, across all seasons. We also consider the possibility that DOC concentrations are continuing to decline to pre-browning levels, but at an extremely slow pace. Measurements of background fluorescence of filtered water indicate a strong correlation with DOC concentrations. However, in 2015 fluorescence measurements provided values that were equivalent to those measured during the pre-flood period, despite DOC concentrations being 1.5-fold higher. This might indicate that the DOC at the end of the study period was of a less humic (and coloured) nature, potentially signifying a different source. Indeed, the linear relationship between fluorescence and DOC concentrations provided an X-intercept of *c*. 10 mg/L, indicating that a large fraction of DOC in this system is probably colourless. A possible explanation is that a significant proportion of the water column DOC in 2015 was exuded by phytoplankton (Nguyen et al. 2005). We considered the most likely to be explanation for this trend to be the lower concentrations of total DOC and perhaps depletion of the most labile DOC in the initial years. However, fluorescence data do not support that the most coloured fraction of DOC was remaining in the lake (Brandão et al., 2018). Potential alternative possibilities might be colourless DOC exuded by phytoplankton or a decreased biodegradability of algal DOC due to interactive effects of UV radiation and humic matter (Tranvik & Kokalj, 1998).

The incomplete return of DOC concentrations to pre-flood levels might imply that the long-term effects of extreme rainfall events could contribute to the observed general trend of increasing DOC concentrations (brownification) in groundwater-fed freshwater systems of the northern hemisphere. A study of 120 Swedish lakes predicted that an increase in precipitation would result in greater terrestrially derived DOM concentrations and diminish the influence of in-lake processing on DOM quality (Kellerman et al., 2014). DOC concentrations and its quality can also have significant positive effects on bacterioplankton communities (Crump et al., 2003; Kritzberg et al., 2006), which in turn impact DOC mineralisation rates

in the system (Attermeyer et al., 2014). With higher frequency of extreme rain events expected in the region (Meehl et al., 2001; van den Besselaar et al., 2012), the trends and impacts of such browning events will further intensify (de Wit et al., 2016), increasing carbon export from terrestrial to aquatic sources, altering aquatic primary production and greenhouse gas emissions.

We conclude that shallow, eutrophic lakes can exhibit a delayed or incomplete recovery from a short-term browning event, as indicated by a delayed or incomplete return of DOC and TP concentrations, as well as planktonic and benthic primary production to pre-browning levels. With a projected increase in extreme rainfall events coupled to global warming (Berg et al., 2013), sudden browning events might become an increasingly common phenomenon, particularly in small shallow lakes. Our findings that hydrological changes due to extreme precipitation have long-term, sustained effects on lakes and their food webs may thus have far-reaching consequences for trends in water quality and aquatic biogeochemical cycling in the face of ongoing climate change.

CONFLICT OF INTEREST

None of the authors have any conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data analysed during the current study are available from the corresponding author on reasonable request.

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SUPPORTING INFORMATION

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

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