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The unexpected long period of elevated CH_4 emissions from an inundated fen meadow ended only with the occurrence of cattail (*Typha latifolia*)

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Abstract

Drainage and agricultural use transform natural peatlands from a net carbon (C) sink to a net C source. Rewetting of peatlands, despite of high methane (CH_4) emissions, holds the potential to mitigate climate change by greatly reducing CO_2 emissions. However, the time span for this transition is unknown because most studies are limited to a few years. Especially, nonpermanent open water areas often created after rewetting, are highly productive. Here, we present 14 consecutive years of CH_4 flux measurements following rewetting of a formerly long-term drained peatland in the Peene valley. Measurements were made at two rewetted sites (non-inundated vs. inundated) using manual chambers. During the study period, significant differences in measured CH_4 emissions occurred. In general, these differences overlapped with stages of ecosystem transition from a cultivated grassland to a polytrophic lake dominated by emergent helophytes, but could also be additionally explained by other variables. This transition started with a rapid vegetation shift from dying cultivated grasses to open water floating and submerged hydrophytes and significantly increased CH_4 emissions. Since 2008, helophytes have gradually spread from the shoreline into the open water area, especially in drier years. This process was periodically delayed by exceptional inundation and eventually resulted in the inundated site being covered by emergent helophytes. While the period between 2009 and 2015 showed exceptionally high CH_4 emissions, these decreased significantly after cattail and other emergent helophytes became dominant at the inundated site. Therefore, CH_4 emissions declined only after 10 years of transition following rewetting, potentially reaching a new steady state. Overall, this study highlights the importance of an integrative approach to understand the shallow lakes CH_4 biogeochemistry, encompassing the entire area with its mosaic of different vegetation forms. This should be ideally done through a study design including proper measurement site allocation as well as long-term measurements.

KEYWORDS
cattail, fen, long-term data, methane emissions, peatland rewetting, wetland

1 | INTRODUCTION

Natural or pristine peatlands are among the most important soil carbon (C) stocks, despite their relatively small contribution of about 3% to the land mass (Joosten et al., 2012; Leifeld & Menichetti, 2018; Xu et al., 2018). In a pristine state, they have a slightly positive or neutral impact on the Earth's climate system through their function as a strong carbon dioxide (CO_2) sink, a weak methane (CH_4) source, and a very weak nitrous oxide (N_2O) source (Frolking et al., 2006; Whiting & Chanton, 2001). Meanwhile, globally about 11% of peatlands (in Europe about 50% and in Germany about 92%) have been drained mainly for land use (Joosten, 2009; Tanneberger et al., 2021; Tiemeyer et al., 2020). These peatlands are strong sources of CO_2 and N_2O as a result of aeration-induced mineralization processes within the peat body (Joosten, 2009; Joosten et al., 2016; Page & Baird, 2016). Globally, they constitute about 5%–10% of the anthropogenic greenhouse effect (Frolking et al., 2006; Smith et al., 2014; Strack et al., 2022; Tiemeyer et al., 2020). Not least for this reason, efforts have been stepped up worldwide for several decades to eliminate the negative climate effect of peatlands by restoring them through rewetting (Andersen et al., 2017; Bianchi et al., 2021; Humpenöder et al., 2020; Jurasinski et al., 2020). However, it is becoming increasingly clear that the restoration of peatlands, if it is possible at all, will take decades as drainage has often led to: (1) serious loss of typical peatland flora and fauna; (2) severe deterioration of the hydrological and physical peat properties; (3) extremely uneven and heavily subsided peat surface; and (4) sharp increase in the concentration of nutrients in the uppermost peat layers (Klimkowska et al., 2010, 2019; Kreyling et al., 2021). In particular, the restoration of formerly drained, nutrient-rich fens that are completely flooded in the course of rewetting, thus creating shallow lakes or smaller pools with open water areas (Beadle et al., 2015; Beyer et al., 2021), is considered to be potentially problematic. If the surface of the drained fens has dropped below the water level (WL) of the surrounding receiving waters, hydrological measures such as stopping to maintain or filling the drainage system as well as opening the dikes around those areas will lead to flooding of the adjacent fens. Shallow lakes and pools created by such low-cost, low-input dike opening can now be found in many regions with former valley fens (Beadle et al., 2015; Hemes et al., 2019) including Mecklenburg–Western Pomerania in NE Germany. Common to these sites is a broad and dynamic mix of highly productive emergent helophytes such as *Phragmites* sp., *Typha* sp. or *Carex* spp. and open waters (Steffenhagen et al., 2012; Zerbe et al., 2013). Here, the combination of permanently high inundation and contents of mineral and organic matter in the often brownish colored water or in the upper sediment layer is considered particularly critical in terms of net greenhouse gas (GHG) emissions (Zak et al., 2010, 2019; Zak & Gelbrecht, 2007). For example, a high WL (>0.5 m above soil surface) can substantially delay the establishment of CO_2-fixing helophytes, such as reeds or sedges (Zerbe et al., 2013) as prerequisites for the formation of a strong CO_2 sink. At the same time, high WL can lead to increased fluxes of CH_4, whose global warming potential is 28 times higher than that of CO_2 (IPCC, 2014). Due to the high WL, a stable anaerobic zone can form in the surface water above the sediment as well as within the sediment below. The further combination with the high nutrient concentration, the litter of the dead crops or grasses and the increased water temperature in summer due to the dark coloring leads to ideal conditions for CH_4 formation. This may also apply to the absence of emergent helophytes since their aerenchymatic system can promote CH_4 oxidation through the input of oxygen into the sediment or peat close to the roots (Bridgham et al., 2013; Hemes et al., 2018; Knox et al., 2021; Segers, 1998; Whalen, 2005). On the other hand, there is evidence that it is primarily plant litter from grasses and helophytes rather than old peat that serves as a C source for CH_4 formation (Hahn-Schöfl et al., 2011; McNicol et al., 2020; Tuittila et al., 2000). This ultimately means that the period of increased CH_4 emission may continue as long as fresh plant litter remains present and emergent helophytes remain absent. Irrespective of that, the high overall potential to mitigate GHG emissions through rewetting of peatlands is widely accepted (Günther et al., 2020). Indeed, there is evidence that CH_4 emissions from shallow lakes formed over formerly drained fens are initially very high, similar to other types of rewetted peatlands (Franz et al., 2016; Koebsch et al., 2015; Wilson et al., 2009). However, it remains to be clarified how the dynamics of CH_4 release from rewetted peatlands will develop in the longer term or if and when it will level even off to the stage of undisturbed peatlands. The few existing studies on the longer term effects of rewetting on CH_4 emissions were initiated years or decades after the implementation of the restoration measure, often explicitly or implicitly assuming that no changes in CH_4 emissions have occurred in the meantime (Hemes et al., 2018; Kandel et al., 2019; Nugent et al., 2018; Schaller et al., 2022; Vanselow-Algan et al., 2015; Wilson et al., 2016).

The objective of our study was to address and clarify the following questions: (1) What are the dynamics and intensity of CH_4 fluxes after rewetting? (2) How long does it take for measurement site CH_4 emissions to return to the low levels of undisturbed peatlands? (3) Which factors besides the WL or factor constellations determine the development of CH_4 emissions? To fill this knowledge gap, we present the results of 14 continuous years of CH_4 flux measurements of a shallow lake in north-east (NE) Germany, which was created by the rewetting of a formerly drained fen meadow. CH_4 flux measurements were conducted at an inundated and non-inundated site using manual closed chambers. Thus, it allows to measure distinct vegetation types covering the manual chamber plots during the measurement period. Measurements at the inundated site covered

1 year prior to and 14 years after rewetting (2004–2017) while measurements at the non-inundated site covered 12 years (2004–2015).

2 | MATERIAL AND METHODS

2.1 | Study site

The study site area was established in a typical percolation peatland in the southern Baltic region (Succow & Joosten, 2001) near the village of Zarnekow in Mecklenburg–Western Pomerania, within NE of Germany. The study area is a part of the Polder Zarnekow-Upost (N53°52.5′, E12°53.3′) situated in the River Peene Valley southeast of the city of Dargun (see map in Figure 1). The entire polder encompasses an area of 550 ha (Schmidt, 2004). Peat thickness is up to 10.2 m. Drainage started during the 18th century. As a result of decades of drainage for intensive cropland or grassland use from the 1970s to the 1990s of the last century (Gelbrecht, 2008), surface subsidence (1 m), strong decomposition, and a shrinking of the upper peat layer (0.3 m) have occurred (Zak et al., 2008, 2015). The peat layers below had a medium degree of decomposition (Gelbrecht, 2008). The climate of the study area is moderately continental temperate (Hahn-Schöfl et al., 2011) with a mean annual air temperature of 9.2°C and annual precipitation of 583 mm (1991–2020, Teterow. German Meteorological Service, DWD).

Rewetting of the study area was initiated in autumn 2004 through different hydrological measures. At this time, two measurement sites were established, the first at a slightly higher (~0.35 m) landscape position, with an expected minor WL increase ("non-inundated site"), and the second within the polder at a lower landscape position, with an expected permanent inundation ("inundated site"). At both sites, WL, sediment (2, 5, and 10 cm depth), and water (5 cm above the sediment) temperatures were measured half-hourly using pressure probes (PDCR1830, Campbell Scientific) and thermocouples (T107, Campbell Scientific), connected to a Campbell science data logger (CR 1000, Campbell Scientific). Precipitation, wind speed, wind direction, air pressure, and air temperature were recorded by the climate station installed at the study area (WXT52C, Vaisala). In addition and to compensate for possible system failure, the daily mean air temperature (2 m height) and the daily sum of precipitation between July 2004 and December 2017 were obtained from the German Weather Service (DWD) in the nearby town of Teterow (25 km southwest).

2.2 | Vegetation dynamics

Habitat type mapping for the measurement site was performed in 2004, 2011, and 2022 (Tables S2–S4). A vegetation field survey of the entire study area was conducted in August and September 2020 (Table S7). Vegetation patches were visually discerned on an unmanned aerial vehicle (UAV) image taken shortly before and then visited in the field (Table S7). Annual vegetation maps from 2013 to 2020 were made based on Planet Labs satellite images. In total, 99 images of a high temporal resolution, a long temporal coverage, and a 5 × 5 m spatial resolution covering red, green, blue, and near-infrared bands were available. A retrospective classification was conducted assisted by a cluster analysis based on the temporal course of the vegetation indices: normalized difference vegetation index (NDVI) and near-infrared reflectance of vegetation (NIR_V) of each pixel. The resulting clusters were interpreted with the help of aerial or UAV images of higher spatial resolution. The accuracy of this method was assessed for 2020 and 2015 with an overall accuracy of 71% and 78%, respectively.

2.3 | CH_4 flux measurements

To measure CH_4 fluxes, five replicate round polyvinyl chloride collars (basal area: 0.194 m^3) were inserted next to each other at approx. 7 cm depth in the surface at both sites (Hoffmann et al., 2018). Due to inundation from autumn 2004 and onwards, the collars at the inundated site were replaced by fixed, floating collars using polystyrene plates. At both sites, the CH_4 flux measurements were conducted two to four times a month for 12–14 consecutive years (from 2004 to 2015 and 2017, respectively) using a manual chamber system: non-flow-through nonsteady-state (NFT-NSS) cone-shaped, white chambers (height: 0.395 m, volume: 0.063 m^3; Hoffmann et al., 2018; Livingston & Hutchinson, 1995). Each chamber was equipped with two vents at the top to connect evacuated glass bottles (60 mL) for air sampling. The initial sample was taken directly before chamber placement, followed by two more samples every 15 min over a total measurement time of 30 min. The sampled air was analyzed for CH_4 and CO_2 concentrations with a gas chromatograph (GC-14A and GC-14B, Shimadzu Scientific Instruments, Japan; detectors: flame ionization detector for CH_4, electron capture detector for CO_2). To prevent leakage, the collars had a channel for water sealing between the collar and the chamber. To obtain easy access to the collars and to avoid disturbances like triggered ebullition events during the measurements, wooden boardwalks were installed at both sites.

2.4 | CH_4 flux calculation and annual emission estimates

CH_4 fluxes were calculated according to the ideal gas law (Equation 1):

$$f = \frac{MpV}{RTA} \cdot \frac{dc}{dt} \tag{1}$$

where f is the CH_4 flux (CH_4-C in g m^{-2}), M represents the molar mass of CH_4-C (g mol^{-1}), p represents the ambient air pressure (Pa), V is the chamber volume (m^3), R is the gas constant (8.314 m^3 Pa K^{-1} mol^{-1}), T designates temperature (K) inside the chamber, A is inside-collar surface area (m^2), and dc/dt denotes the linear CH_4 concentration change during the

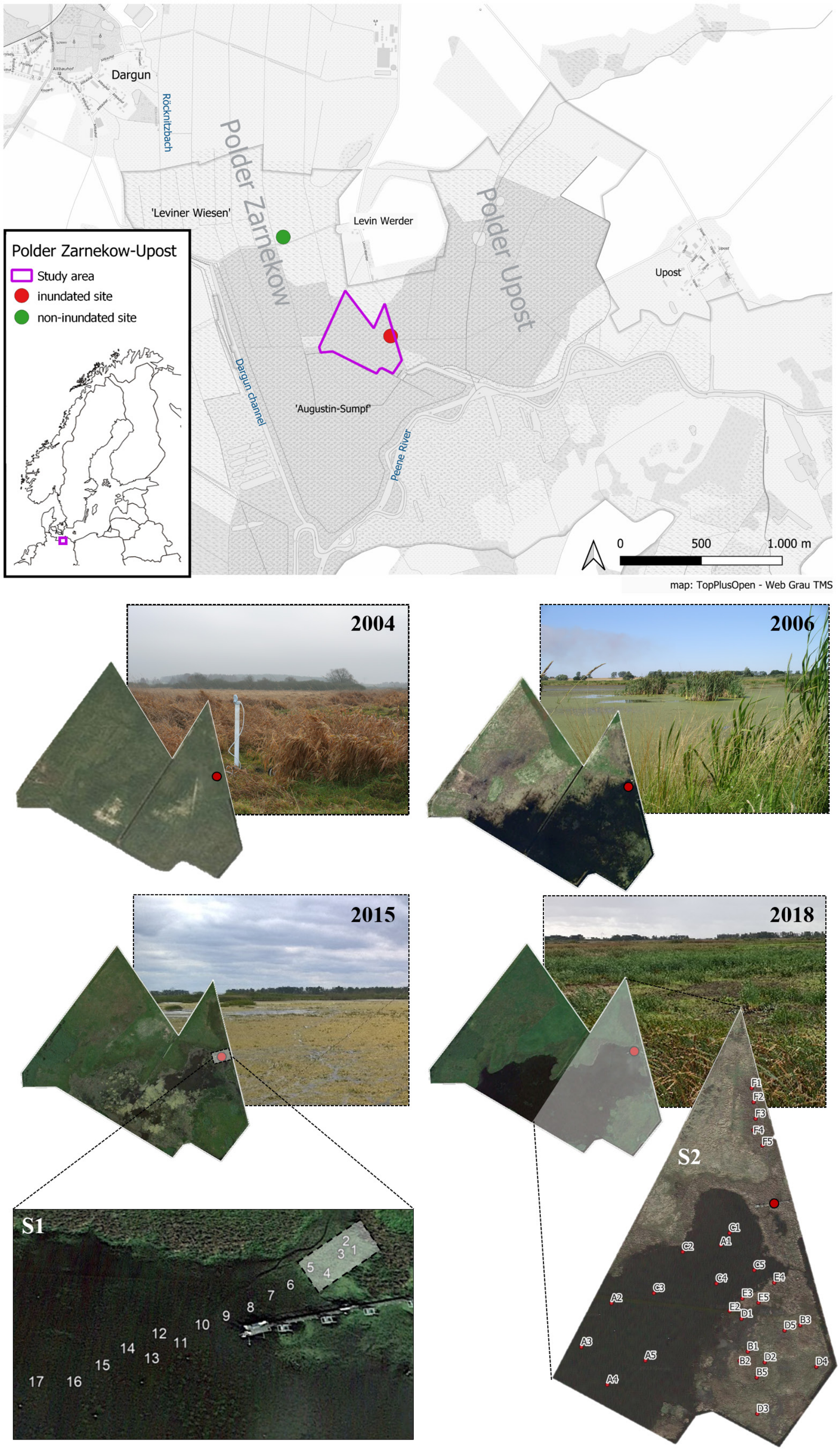

FIGURE 1 Map of Polder Zarnekow-Upost and satellite images showing the study area with the inundated (red dot) and non-inundated measurement site (green dot); Satellite images and pictures represent conditions at the study area prior to rewetting (2004) and 2, 11 and 14 years after rewetting, respectively. S1 and S2 show sampling points for sediment thickness and carbon stocks in 2011 (Table S5) and 2020 (Table S6). The squared area on S1 indicates approximate location of sediment sampling done by Hahn-Schöfl et al. (2011). Map lines delineate study areas and do not necessarily depict accepted national boundaries.

measurement time (s^{-1}). For a more robust calculation of CH_4 fluxes, in parallel concentration measurements from all five plots per site ($n=15$) were merged into one data set and used for further flux calculation (Huth et al., 2018). Prior to this, all measured concentrations originating from air samples flagged during GC-Analysis were removed. In addition, CH_4 concentration outliers within the merged data sets were excluded using sixfold of the interquartile range (IQR; Huth et al., 2018). To account for ebullition events right at the beginning of the measurement period, which may potentially bias the obtained flux, initial CH_4 concentration >5 ppm was also removed. Finally, CH_4 flux measurements were checked for consistency and corrected using parallel measured CO_2 concentrations. In case of negative CO_2 concentration changes >25 ppm during chamber closure, the measurements were excluded based on the assumption of a positive development of CO_2 concentration during opaque chamber measurements. In total, data processing resulted in a loss of less than 2.5% of all sampled CH_4 concentrations. Annual CH_4 emissions were finally obtained by simple linear interpolation of weekly to biweekly measured CH_4 fluxes (Huth et al., 2018).

2.5 | Statistical analysis

Annual emissions were checked for normal distribution using the Kolmogorov–Smirnov test (R package *dgof*). Since the fluxes were not normally distributed, the nonparametric Wilcox test (R package *stats*) was subsequently used to test for significant differences between annual CH_4 emissions obtained at the non-inundated and inundated sites, respectively. A cluster analysis (K means clustering; R package *cluster*) was performed to link possible clusters of annual CH_4 emissions and/or environmental variables such as WL with observed transitional stages. To determine the number of clusters, the Elbow method (R package *EBS*) was applied. Since principal component analysis (PCA) can cope with multicollinearity in underlying data input, a PCA (R package *stats*) was performed to explore multivariate relationships and patterns across measurement sites and years. The effects of transitional stages on annual CH_4 emissions as a response variable were tested using linear mixed effects model (LMM; R package *lmerTest*). In the LMM, WL was treated as a fixed effect and temperature as a random effect where slope of temperature effect on annual CH_4 emissions as well as its intercept could vary with transitional stage. A subsequent ANOVA was used to check for a significant effect of the variables. All statistical analyses were performed using the statistical program R (version 4.0.5; R Core Team, 2022).

3 | RESULTS

3.1 | Environmental conditions during the study period

Annual air temperature, precipitation, and WL are given in Table 1. The dynamics of air temperature, precipitation, and WL during the study period are shown in Figure 2a,b. The mean annual temperature during the study period was 9.4°C, the coldest year being 2010 with a mean annual temperature of 7.6°C. An overall trend of a slight increase in annual air temperature during the study period was observed. The highest annual temperature mainly occurred in the last 4 measurement years, exceeding 10°C of mean annual air temperature in 2014 and 2017 (Table 1). During the 14-year study period, the mean annual precipitation was 591 mm and included several, periodically severe flooding events. Wet years with high precipitation at the study area occurred in 2007, 2011, and 2017, with 687, 686, and 739 mm $year^{-1}$. The 2 years with the highest precipitation (2011 and 2017) are the years with the overall high WL of 0.59 and 0.52 m, respectively. During the same study period, the inundated site occasionally dried out such as in 2010 and 2012. 2012 and 2016 were the years with the lowest precipitation (473 mm). The WL fluctuated strongly at both sites. At the inundated site the WL was rarely lower than 0.1 m above the ground, and sometimes the site was inundated up to 1 m. The non-inundated site was flooded during winter and drained to 0.5 m below the ground during summer. In general, WL differed significantly between the non-inundated and the inundated sites, being, on average 0.5 m lower at the non-inundated than at the inundated site. Data on the chemistry of surface and pore water for the inundated site are presented in Appendix S1 (Table S1).

3.2 | Vegetation dynamics

Before rewetting, the vegetation of the study area was largely dominated by reed canary grass (*Phalaris arundinacea*) at both sites. In addition, grasses also typical of meadow use such as tufted grass (*Dactylis glomerata*), tall fescue (*Festuca arundinacea*), and couch grass (*Elytrigia repens*) occurred (Huth et al., 2013; Zerbe et al., 2013). As a result of rewetting in October 2004, WL rose above the soil surface, creating a shallow polytrophic lake (Gelbrecht, 2008; Steffenhagen et al., 2012) or an inundated site (Zak et al., 2015). During the same period, the non-inundated site was transformed into a semi-humid meadow where mostly the same dominant vegetation was observed as prior to rewetting.

Due to permanent flooding at the inundated site, the former vegetation died off soon after the rewetting and was transformed into a new up to 0.3 m thick sediment layer (Hahn-Schöfl et al., 2011). From 2005, the open water area of the shallow lake was colonized by floating and submerged hydrophytes such as, for example, *Ceratophyllum* sp. and *Lemna* sp. (Hahn-Schöfl et al., 2011; Steffenhagen et al., 2012; Zak et al., 2015), which dominated the site only 2 years after rewetting. From 2008, emergent helophytes such as broadleaf cattail (*Typha latifolia*), bur-reed (*Sparganium* sp.), and tall manna grass (*Glyceria* sp.) gradually began to spread from the shoreline into the established shallow lake. This is substantiated by annual vegetation maps starting in 2013 (Figure 3). Succession was, however, periodically delayed by exceptional floodings, such as in 2011, 2012, and 2015. For instance, Figure 3 shows a distinct decrease in shoreline vegetation in 2015, while during the year 2014 as well as the year 2016 shoreline vegetation further extended into the shallow lake.

TABLE 1 Environmental variables and annual methane (CH_4) emissions during the study period. Mean annual air temperature (°C), cumulative annual precipitation (mm), and mean annual WL (m) are given for both measurement sites. Dominant vegetation coverage and cluster groups are added for the inundated site.

			Non-inundated inundated					
Year Unit	Cumulative annual precipitation mm	Mean annual air temperature °C	Mean annual WL m	Annual CH_4 emissions gCH_4-$Cm^{-2}year^{-1}$	Mean annual WL m	Annual CH_4 emissions gCH_4-$Cm^{-2}year^{-1}$	Vegetation cover	Cluster
2004	568	8.7	NA	0.4 ± 0.1	NA	0.8 ± 0.1	Grassland	2
2005	565	9	−0.10	3.2 ± 1.2	0.22	32.9 ± 8.6	Floating hydrophytes	2
2006	500	9.8	−0.22	0.5 ± 0.3	0.21	79.3 ± 7.4		2
2007	687	10	0.10	4.7 ± 0.8	0.37	25.9 ± 2.7		2
2008	582	9.7	−0.08	10.9 ± 1.5	0.25	26.9 ± 4.1		2
2009	524	9.1	−0.18	0.1 ± 0.5	0.15	150 ± 12	Submerged hydrophytes	1
2010	670	7.6	−0.11	0.1 ± 0	0.32	47.1 ± 7.5		2
2011	686	9.5	−0.03	15.2 ± 2.1	0.59	157 ± 12.5		1
2012	473	8.9	−0.28	0.1 ± 0	0.55	48.6 ± 3.8		2
2013	631	8.9	−0.22	0.0 ± 0	0.52	137.8 ± 8.8		1
2014	595	10.2	−0.31	0.6 ± 0	0.45	229.2 ± 11.7		1
2015	587	9.8	NA	0.2 ± 0.1	0.54	199.9 ± 13.7		1
2016	473	9.7	NA	NA	0.39	27.5 ± 5.2	Helophytes	2
2017	739	10.1	NA	NA	0.52	11.8 ± 1.1		2
Mean	591	9.4	−0.14	3 ± 0.6***	0.39	83.9 ± 7.1***		

Note: Asterisks indicate significant difference between mean CH_4 emissions between indudated and non-inundated measurement site.
Abbreviation: NA, not analyzed.

Therefore, the succession of emergent helophytes from the shoreline into the open water areas of the shallow lake, increasingly covering the inundated measurement site, did not start before 2015. As a result of this succession, from 2016 till the end of the vegetation mapping period in 2020, the inundated measuring site was dominated by cattail (Franz et al., 2016; Koebsch et al., 2020; Zak et al., 2015), still representing a transitional stage toward a near-pristine percolation peatland (Figure 3). Thus, the vegetation forms at the end of CH_4 flux measurement period (2017) still prevailed and continued developing until 2020 and further into 2022. The latter has been confirmed by an additional habitat type mapping conducted in 2022 (Table S4). Although the proportion of the area covered by open water declined substantially during the observation period due to the colonization and succession of different emergent helophytes, wider areas with open water still persist at the study area even years after CH_4 flux measurements were completed (Figure 3).

3.3 | CH_4 flux dynamics and annual emissions

Annual CH_4 emissions at the non-inundated site were significantly (p-value: <.01; Wilcoxon test) lower compared to the inundated site (Figure 2c,d). With an average of $3 \pm 0.6\,gCH_4$-$Cm^{-2}year^{-1}$, the non-inundated site was only a small CH_4-C source. The daily CH_4-C fluxes varied between <0.1 and $0.3\,gm^{-2}day^{-1}$. The highest CH_4-C fluxes at the non-inundated site were recorded right after the summer floodings in 2007, 2008, and 2011. In contrast, the inundated site was a strong CH_4-C source during most of the study period, with, on average, $83.9 \pm 7.1\,gCH_4$-$Cm^{-2}year^{-1}$. The CH_4 fluxes varied between <0.1 and $3\,gm^{-2}day^{-1}$. Unlike the non-inundated site, a clear seasonal pattern with higher emissions during the summertime and lower emissions during the wintertime could be traced at the inundated site (Figure 2d). Distinct interannual variability was also only recorded at the inundated site (Figure 2d). Following the autumn 2004 rewetting, increasingly high CH_4 emissions were observed during the years 2005 and 2006. While the annual CH_4 emission in 2007 was followed by another decline, the CH_4 emissions further generally continued to increase between 2008 and 2015, peaking in 2014 with $229\,gCH_4$-$Cm^{-2}year^{-1}$. Exceptions from the increasing emissions are the years 2010 and 2012, which showed a temporary sharp decline. Only in 2016 and 2017, the annual CH_4 emissions finally declined for a period of two consecutive years showing with $11.8\,gCH_4$-$Cm^{-2}year^{-1}$ in 2017 the lowest annual emissions since the rewetting.

4 | DISCUSSION

4.1 | Uncertainty of CH_4 emission estimates

On a single flux basis, CH_4 measurements might be biased due to changes in microclimate or pressure disturbances caused by chamber deployment affecting the gas exchange from the peat surface

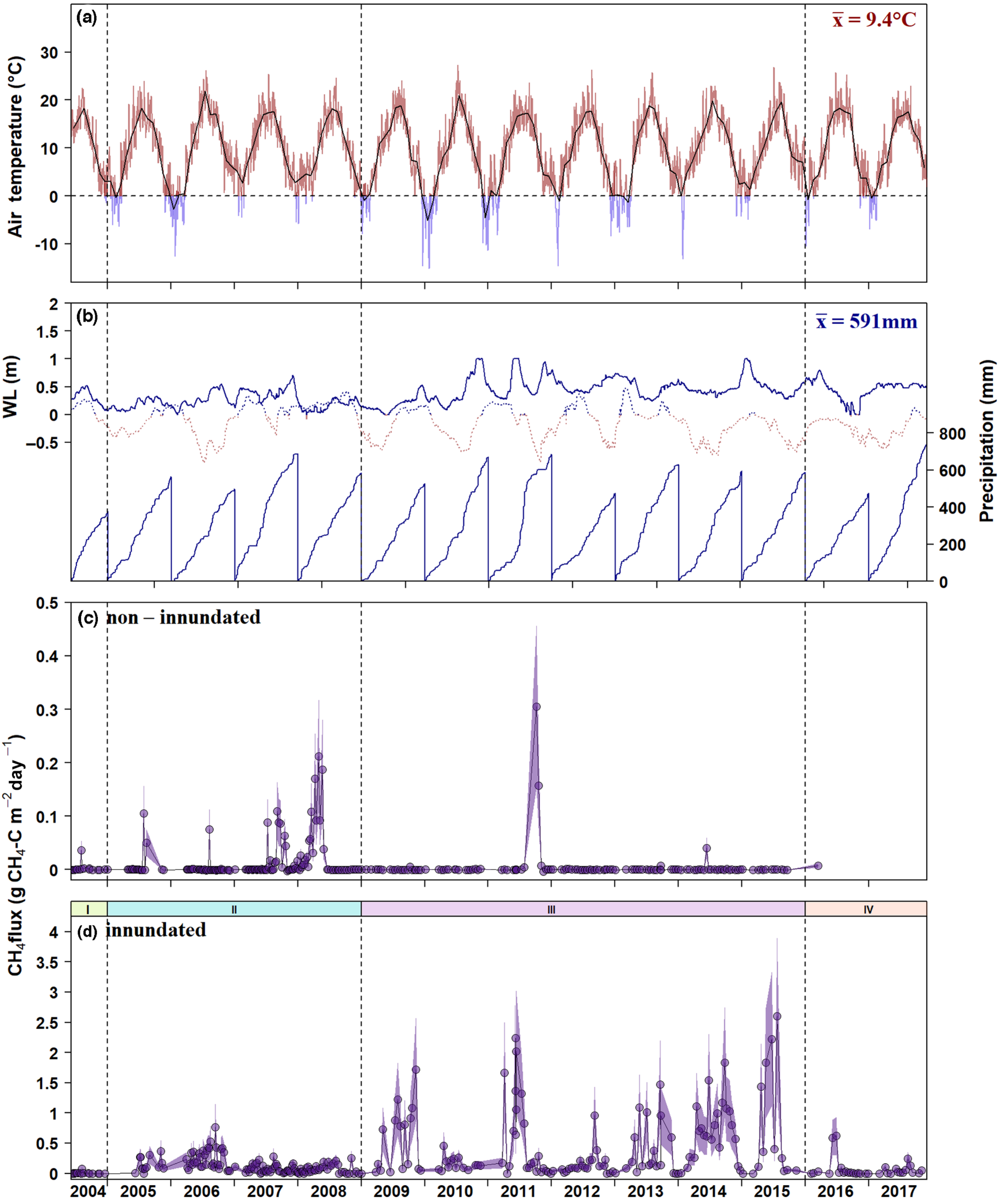

FIGURE 2 Time series of environmental variables: mean daily (red line above, blue line below 0°C) and monthly (black line) air temperature (a); daily cumulative precipitation per year (blue line), water level (WL) at the inundated (blue line above, red line below surface), and non-inundated site (dashed blue line above, dashed red line below surface) (b); in the top right corner is shown mean annual air temperature (a) and mean annual precipitation (b) for the period 2004–2017 (b); temporal dynamics (c, d) of measured (purple dots) and interpolated (purple line) daily methane (CH_4) fluxes (CH_4-C g m^{-2} day^{-1}) at the non-inundated (c) and inundated (d) study sites. Change in dominant vegetation cover at the inundated site is described in the figure (d) header: I—grassland, II—floating hydrophytes, III—submerged hydrophytes, and IV—helophytes.

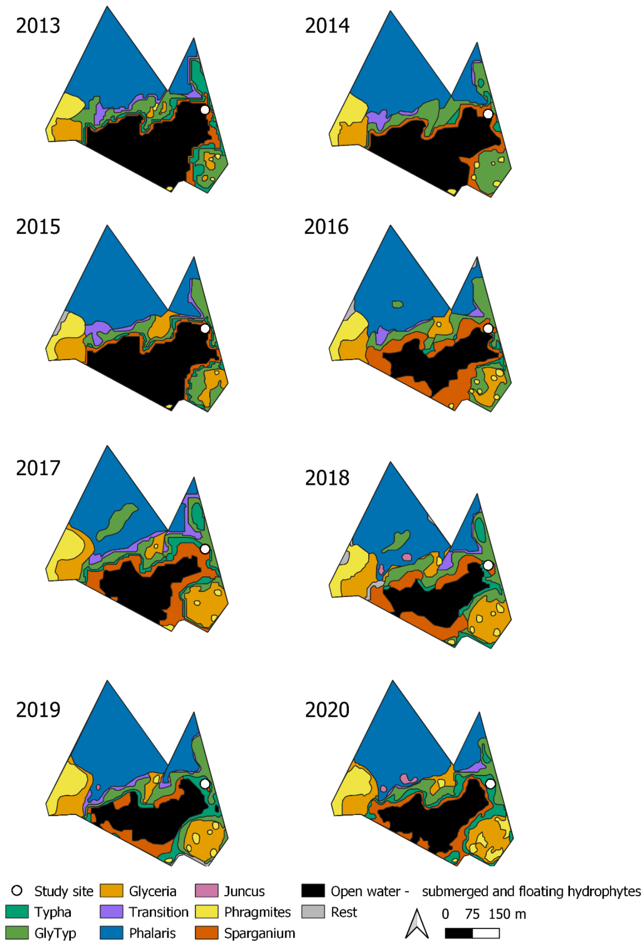

FIGURE 3 Annual vegetation maps of the study area displaying spatio-temporal dynamics of the different dominant vegetation types from 2013 to 2020. The white dot indicated the location of the measurement site.

(Denmead, 2008; Kutzbach et al., 2007; Lai et al., 2012). Pressure fluctuations can induce a mass flow of CH_4-enriched gas from the soil pore space into the atmosphere (Maier et al., 2010) enclosed by the chamber, which, in the case of flooded areas, usually takes place as a result of ebullition events (Tokida et al., 2007). On the basis of annual CH_4 emission estimates, a systematic bias might arise as a result of a low temporal measurement resolution (Meijide et al., 2011; Parkin, 2008; Savage et al., 2014). Several studies have reported that CH_4 fluxes measured using manual closed chambers tend to be higher than those measured by EC (Chaichana et al., 2018; Hendriks et al., 2010; Meijide et al., 2011; Werle & Kormann, 2001; Yu et al., 2013). Thus, for the same study area, Franz et al. (2016) reported an EC-based annual CH_4 emission of 39.5 g CH_4-C m^{-2} $year^{-1}$ (May 2013 to May 2014), which is substantially lower than the 163 g CH_4-C m^{-2} $year^{-1}$ reported in our study for the same period of time. One might argue that this might be due to the inability of chamber measurements to cover high temporal variation and transient, for example, ebullition or frost/thaw-related, CH_4 emission peaks (Courtois et al., 2019; Minamikawa et al., 2012; Pihlatie et al., 2010; Raz-Yaseef et al., 2017). However, differences between EC- and chamber-based (placed within the EC footprint area) emissions can also result from deviating CH_4 source strengths of the areas covered by the EC (>ha) and chamber measurements (<m^2). Unlike the spatially distinct chamber measurements, EC measurements cover a much bigger area, thus aggregating over present spatial heterogeneity (Franz et al., 2016; Morin et al., 2017) within the area, resulting in a mixed CH_4 emission signal of, for example, areas of open water and areas covered with emergent helophytes. However, possible limitations in the precision and accuracy of the manual chamber method do not change the fact that unusually high CH_4 fluxes were recorded at the inundated measurement site over a long period of time.

4.2 | Open water areas as a typical component of flooded fen grasslands

As shown by the results, the structure, composition, and development of the vegetation in the polder Zarnekow correspond very well to the conditions of a large number of other shallow lakes, which developed after rewetting of fens (e.g., Beadle et al., 2015; Hemes et al., 2019; Koch et al., 2017; Schulz et al., 2011; Steffenhagen et al., 2012; Zerbe et al., 2013). Often, a broad mosaic of partly extremely productive vegetation is formed in a very short distance, which is subject to fast temporal dynamics. Typical for all these sites is the large proportion of open water areas from the beginning, which showed a rapid change in the occurrence of submerged hydrophytes (Steffenhagen et al., 2012; Zerbe et al., 2013). It is also a common characteristic that the extent of these areas shrinks over the course of time, that is, within years to decades, because of the colonization with diverse forms of emergent helophytes.

There are contradictory estimations about the future development of vegetation on flooded fens like the Zarnekow-Upost polder. On the one hand, the formation of cattail could mark the final vegetation stage of the shallow lake before silting up (Zak et al., 2015). On the other hand, there is also evidence that subsequently reed or sedge meadows might establish (Steffenhagen et al., 2012; Zerbe et al., 2013). This is probably determined by nutrient supply in addition to water level development (Schulz et al., 2011). However, the time span of this development is fairly unknown. In addition to dense *Typha* stands, a relatively large share of open water areas still remained (>30% of the total area) at the study area even 5 years after the end of the CH_4 flux measurements and 18 years after the rewetting of the area.

4.3 | Response of actual annual CH_4 emissions to environmental variables

Environmental conditions such as WL and temperature often explain the dynamics of CH_4 emissions in peatlands (Moore & Dalva, 1993; Morin, 2019; Strack et al., 2004; Turetsky et al., 2008). Flooding conditions favor the anaerobic decomposition of organic matter and

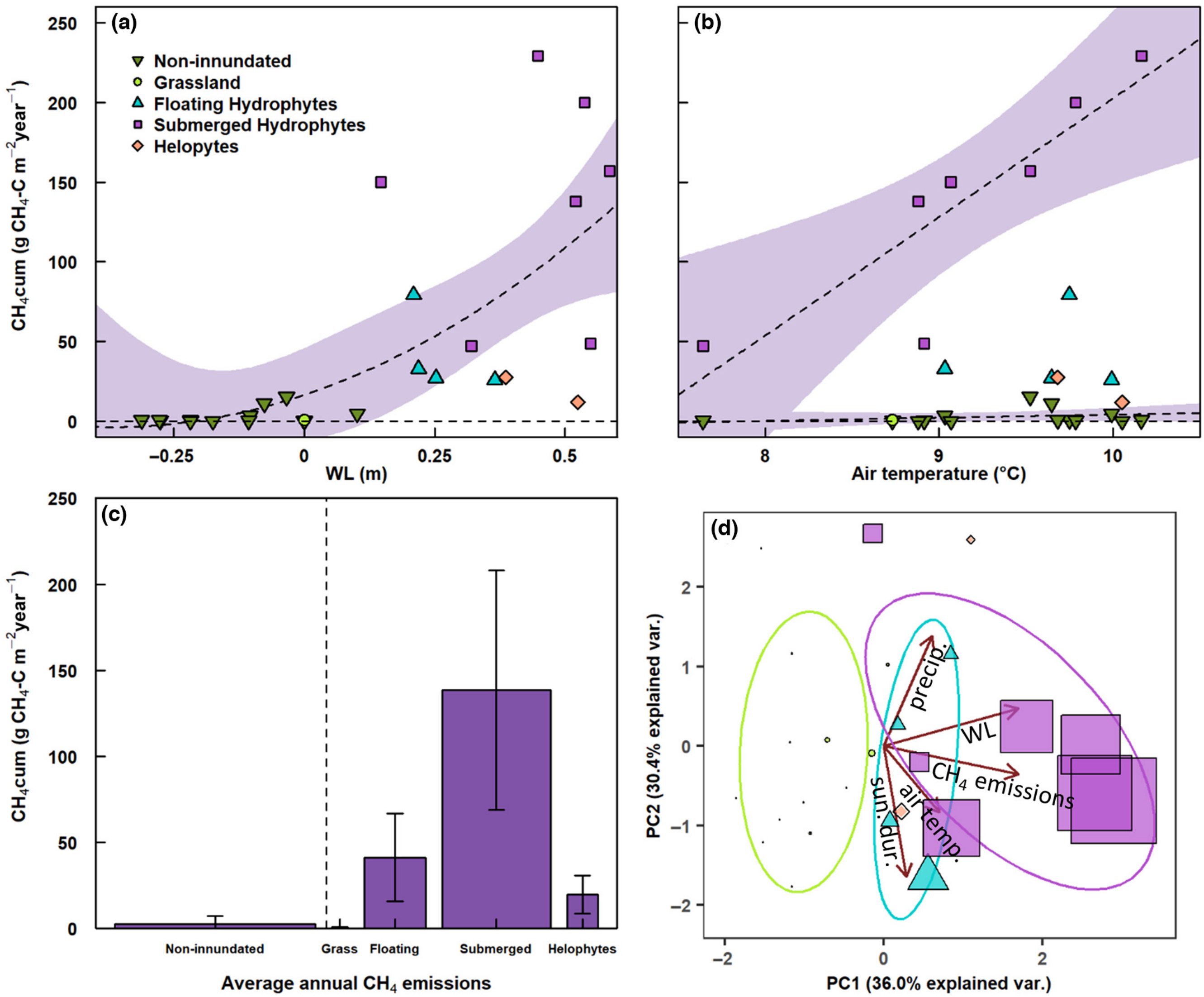

FIGURE 4 Correlation of annual methane (CH_4) emissions ($g\,CH_4$-$C\,m^{-2}\,year^{-1}$) with environmental variables (a) water level (WL) and (b) temperature; (c) average annual CH_4 emissions for the non-inundated site and different transitional stages of the inundated site (width of bars indicates measurement years of each transitional stage): error bars indicate ±SD; (d) principal component analysis (PCA) of 26 measurement years (14 on inundated and 12 on non-inundated measurement site), displaying eigenvectors and PC scores in the plane of principal components 1 and 2. Measurement years cluster into different transitional stages. The variance in-between transitional stages is explained by environmental conditions (PC1; e.g., WL and CH_4), while the variance within a transitional stage is largely explained by weather conditions (PC2; e.g., precipitation and air temperature).

thus CH_4 production by methanogenic archaea, while higher temperatures generally increase microbial activity (Hopple et al., 2020; Turetsky et al., 2008; Zinder, 1993). A significant positive dependence of annual CH_4 emission with WL (p-value <.1) was also observed in this study (Figure 4a), with low emissions during years at WL<0m and increasing, but strongly variable, annual CH_4 emissions at WL>0m. For example, the highest emissions were recorded during the period dominated by submerged hydrophytes from 2009 to 2015, while lower emissions finally occurred after cattail succession into the measurement site, starting at the end of 2015.

Although seasonal pattern of CH_4 fluxes at the inundated site with water abundance throughout the year appeared (low fluxes during colder winter and higher fluxes during warm summer), no such clear temperature dependency emerged in the annual CH_4 emission estimates (Figure 4b). One reason for this could be the shifts in dominant vegetation cover during the different transitional stages throughout the 14-year study period, which may cloud an underlying temperature dependency. This was evident during periods of similar vegetation cover, representing certain transitional stages. For example, during the years 2009–2015, when the dominant vegetation cover was submerged hydrophytes, a positive significant dependence (ρ=0.96, p-value <.01) of annual CH_4 emission estimates with mean annual air temperature could be seen (Figure 4b).

In summary, mean WL is of central importance for the CH_4 emission potential (Evans et al., 2021; Tiemeyer et al., 2020); however, its effect is modified not only by the temperature driving the interannual variability, but, more importantly, the vegetation cover, which might alter microclimatic conditions, such as the water temperature, through shading and determines the magnitude of CH_4 emissions (Figure 4). This is substantiated by the performed LMM ANOVA, which showed a significant effect of WL (p-value = .011) on annual CH_4 emissions. Figure 5 shows the 1:1 agreement plot of annual estimated (interpolation of manual chamber measurements) and predicted (using LMM) annual CH_4 emissions. No correlation could be observed for CH_4 emission with dissolved organic carbon (DOC) concentration measured either in pore or in surface water (Table S1).

4.4 | Cause of the extremely high CH_4 emissions, their long duration and decline

Annual CH_4 emissions at the inundated measurement site were much higher than those traced by data from other peatlands, an example being the study of 41 peatlands in the United Kingdom and Ireland by Evans et al. (2021) who reported maximum annual CH_4 emissions of 18.8 g CH_4-C m^{-2} $year^{-1}$. Similarly, much lower, annual CH_4 emissions were observed in fen peatlands in Sweden (3.7 g CH_4-C m^{-2} $year^{-1}$; Nilsson et al., 2001), Finland (24.7 g CH_4-C m^{-2} $year^{-1}$; Nykänen et al., 2003), and Poland (29.2 g CH_4-C m^{-2} $year^{-1}$; Juszczak & Augustin, 2013). Nevertheless, single years with high annual CH_4 emissions from peatlands with eutrophic conditions based on periodic closed chamber measurements were also reported by other authors, for example, Minke et al. (2016) and Godin et al. (2012), who observed annual CH_4 emissions as high as 101 and 154 g CH_4-C m^{-2} $year^{-1}$, respectively. In addition, the up to seven times lower average annual emission rates of 19.7 g CH_4-C m^{-2} $year^{-1}$ observed in 2016 and 2017 are comparable to those reported by van den Berg et al. (2016) for a minerotrophic peatland in southwest Germany (22.5 g CH_4-C m^{-2} $year^{-1}$) as well as an inundated fen area in NE Germany (15.8 g CH_4-C m^{-2} $year^{-1}$; Günther et al., 2014). However, to our knowledge, until now, no long-term observations of similar high CH_4 emissions exist from polytrophic fen peatlands. This is especially true for open water areas at these sites. This may be due to the fact that long-term measurements have not been made at similar sites so far. After all, eddy measurements conducted in 2013/2014 by Franz et al. (2016) on the Zarnekow-Upost polder also showed that annual CH_4 emission rates on the open water area were higher by a factor of four than on the surrounding sites with emergent vegetation (53 g CH_4 m^{-2} $year^{-1}$ vs. 13 g CH_4 m^{-2} $year^{-1}$). Moreover, in a mesocosm study with rewetted peat, the presence of *Typha* sp. reduced the CH_4 emission rate to less than one tenth of the unvegetated control (Vroom et al., 2018).

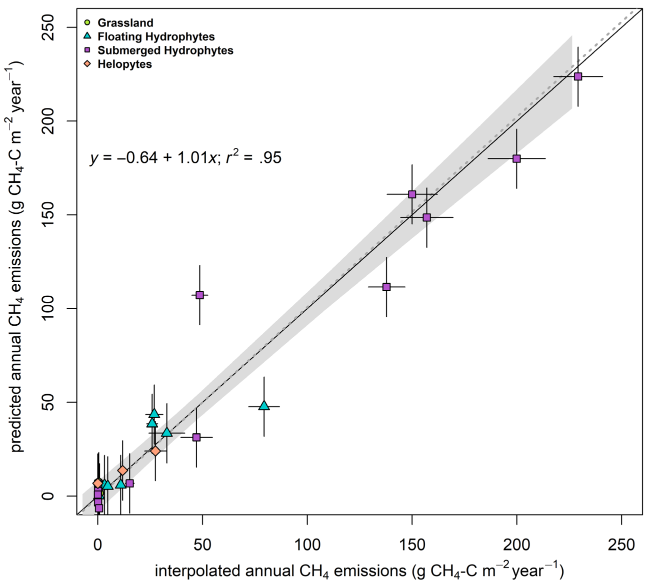

FIGURE 5 1:1-agreement plot between interpolated (measured) and predicted (LMM) annual methane (CH_4) emissions at the inundated and non-inundated site. The LMM consists of a quadratic fixed term for WL and a linear random (intercept and slope) term for temperature (Figure 4). Symbols are color coded and shaped according to the different transitional stages. The black line shows 1:1 agreement and the dashed gray line the correlation between interpolated and predicted annual CH_4 emissions. Error bars indicate the estimated error (interpolated CH_4 emissions) and the standard error from the fitted LMM (predicted CH_4 emissions).

The increased annual CH_4 emissions at our inundated measurement site during the first years after rewetting might be due to the high input of fresh plant litter through initial plant die-back. The same had earlier been hypothesized by Hahn-Schöfl et al. (2011) and later by McNicol et al. (2020), who suggested that this fresh plant litter might be a major contributor to higher CH_4 emissions. Hence, in the years following rewetting, until the end of 2015, when the measurement site remained free of emergent helophytes analogous to the entire central open water area (Figure 3), the litter of aquatic plants like *Ceratophyllum demersum* and *Lemnaceae* floating mats have apparently been potent C sources for the very high CH_4 emissions. Decomposition experiments showed that *Ceratophyllum* litter was converted to CH_4 up to three times more than litter of emergent helophytes such as *T. latifolia* or *P. australis* (Zak et al., 2015). Consistent with this, EC measurements of CO_2 exchange over the open water surface performed by Franz et al. (2016) and Koebsch et al. (2020) from 2013 to 2017 showed net CO_2 losses, that is, no CO_2-C accumulation in the form of new sediment. However, sediment and peat analyses carried out in 2020 showed that considerable C accumulation rates occurred after flooding in the open water surface, which were much higher than in the areas covered by emergent helophytes (Figure 1 (S2), Table S6). This can only be explained by ongoing lateral C transfer in the form of solid or liquid plant remains into the open water areas from the surrounding vegetation belt with emergent helophytes. In the case of the inundated measurement site, the predominant wind from southwest (2013–2017) and periods of extraordinary inundations (e.g., 2011) probably were favorable factors for this transfer. Therefore, lateral transfer likely represents the third major C source—after initial plant die-back and litter of newly established aquatic plants—for CH_4 formation within the open water areas. However, the question of how much these two C sources contributed to CH_4 formation can only be answered with the help of targeted

^{13}C- or ^{14}C-isotope studies to label and separate C substrates. The strong decline in annual CH_4 emissions in the last 2 years of the study (2016 and 2017) coincides with the establishment of helophytes, mainly *T. latifolia*, outcompeting the submerged hydrophytes at the inundated measurement site (Figure 3). This distinct change of vegetation patterns could explain the decline of CH_4 emissions by the interaction of four processes: (1) lowering the substrate availability for CH_4 producers, (2) higher CH_4 oxidation in the rooted sediment layer, (3) changing microclimatological conditions favorable for CH_4 production, and (4) reducing lateral transport of fresh organic matter from the open water body. Regarding the first point, the aforementioned laboratory study by Zak et al. (2015) revealed that the CH_4 production potential by *T. latifolia* was three times lower compared to *C. demersum* despite the substantially higher annual biomass production of *T. latifolia*. This is worth mentioning as helophytes in general might increase the input of fresh organic material and thus accelerate anoxic decomposition and CH_4 production (Chanton et al., 1993; Tuittila et al., 2000). Second, the aerenchymatic tissue of *T. latifolia* creates a transport pathway for oxygen into the anoxic sediment layers, promoting the oxidation of CH_4 by methanotrophs and inhibiting methanogenesis (Fritz et al., 2011; Vroom et al., 2018). However, at the same time, the plant aerenchym might also act as a direct diffusion pathway for CH_4 from anoxic sediment layers into the atmosphere (Chanton et al., 1993; Vroom et al., 2018). Finally, regarding the third and fourth points, the dense stands of helophytes likely lower the temperature in the sediment and water as a result of shading (Franz et al., 2016) and might furthermore hamper the transport of allochthonous fresh organic material into the measurement site. The first is in alignment with an observed drop (for 0.3°C) of the average annual soil temperature (10 cm depth; standardized as difference to average annual air temperature) from 2014 and 2015 compared to 2016 and 2017 at the measurement site.

As shown so far, the different transitional stages following rewetting evidence different but high annual CH_4 emissions (see Section 4.2) that only started to decrease during the last two measurement years after establishment of emergent helophytes (e.g., *Typha* sp., *Carex* sp.). However, given the uncertainties regarding the further plant succession, the future CH_4 dynamics at the inundated measurement site remain speculative and thus need further investigation.

5 | CONCLUSIONS

Thanks to the long-term measurements of CH_4 emissions and vegetation development, which started prior to rewetting, it could be clearly shown that open water areas have a special significance for CH_4 emissions from shallow lakes that arise after flooding of fen grasslands. Both the long-term extremely high CH_4 flux rates and the high proportion of these open water areas in the total extent of flooded fen grasslands over a period of more than a decade contribute to this. In addition, long-term measurements have also helped to elucidate the potential response variables affecting CH_4 emissions, such as shifts in dominant vegetation cover. Such observations need to be accompanied by investigations of processes relevant for CH_4 formation and their emission regulation in order to distinguish between CH_4 emissions resulting from the recreation of hot spots or temporary hot moments, both of which are a major uncertainty factors within the annual CH_4 emission budget (Morin, 2019; Wilson et al., 2016). As there are indications that colonization of the open water areas with other emergent helophytes such as *Phragmites* sp. and *Carex* sp. could also lead to a reduction of the extremely high CH_4 emissions (e.g., Couwenberg et al., 2011), these should also be included in future studies.

Last, but not least, the study also suggests that it is quite important for the understanding of the CH_4 biogeochemistry of the shallow lakes that an integrative approach is taken, encompassing the entire area with its mosaic of different vegetation forms. An example of this is the apparently great importance of plant litter from former grass vegetation and the surrounding highly productive helophyte belt for the high CH_4 fluxes of the open water areas. Accordingly, harvesting of grass before rewetting could lower initial high CH_4 emissions. If operable drainage systems with weirs and, perhaps, a pumping station still exist, a more controlled and progressive "slow rewetting" strategy accompanied by the rapid coverage of the entire area with helophytes is proposed as an alternative to spontaneous inundation of long-term drained peatlands (Zak & McInnes, 2022).

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DATA AVAILABILITY STATEMENT

The data of the study can be accessed at doi: https://doi.org/10.4228/zalf-f1sj-0156.

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