

A comprehensive porewater survey of European peatlands reveals sustained elevated phosphorus levels after 10–20 years of rewetting

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ABSTRACT

Rewetting drained peatlands can lead to high nutrient mobilization, increased methane emissions, and a slow re-establishment of peat-forming vegetation. To guide effective restoration and management, understanding the temporal and spatial variability in porewater chemistry is essential. This study surveyed 64 natural and rewetted peatlands across Germany, Poland, Estonia, Sweden, Georgia, and Scotland from 1997 to 2017. A total of 812 anoxic porewater samples were collected using dialysis samplers (0–0.6 m depth). The rewetted fens exhibited a wide range of dissolved substances, spanning orders of magnitude for soluble reactive phosphorus (SRP: 0.1–18.9 mg L⁻¹), ammonium (NH₄⁺-N: 0.1–117.3 mg L⁻¹), and dissolved organic carbon (DOC: 13–313 mg L⁻¹). However, the mean concentrations were significantly higher than those observed in natural fens ($p < 0.05$). Depth-integrated mobilization rates for nutrients in rewetted fens were, on average, 23 times higher for SRP (1.8 mg P m⁻² d⁻¹) and 4.6 times higher for NH₄⁺-N (3.6 mg N m⁻² d⁻¹) compared to their natural counterparts (0.1 mg P m⁻² d⁻¹ and 0.8 mg N m⁻² d⁻¹). Seasonal variation was also evident in rewetted fens densely colonized by helophytes, with SRP concentrations being lower in the growing season. Notably, SRP concentrations remained elevated 10–20 years after rewetting; however, a 50–80 % decrease was observed at sites characterized by comparatively low iron content in the peat (< 20 mg g⁻¹ dry mass). Further investigations should explore how nutrient dynamics evolve over extended rewetting periods in different contexts, including climate change.

1. Introduction

Peatlands in their natural state are vital habitats for many highly specialized plant and animal species (Rydin and Jeglum, 2013). Beyond their ecological importance, they have stored vast amounts of carbon (C)

over millennia, dating back to the last glacial period or earlier, making them a significant repository in the terrestrial C cycle with a current storage up to 1,055Gt C (Nichols and Peteet, 2019). They also serve as nutrient sinks and hydrological buffers for downstream systems, earning them the term “kidneys of the landscape” (Mitsch and Gosselink, 2015).

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Based on their primary water source, peatlands are broadly classified into ombrotrophic bogs and minerotrophic fens. In addition, further classification distinguishes between poor and rich fens along gradients of acidity to alkalinity and oligotrophy to eutrophy (Rydin and Jeglum, 2013). These distinctions can be critical when designing management and restoration strategies and identifying goals and targets (Money et al., 2009).

Artificial drainage to enable different forms of land use lowers groundwater levels, introducing oxygen into peat layers and altering redox conditions. This oxygenation stimulates aerobic decomposition of organic matter (OM) accumulated over millennia, accelerating carbon dioxide (CO₂) emissions to the atmosphere and transforming peatlands from nutrient sinks into sources of nutrient pollution in adjacent watercourses (Kreyling et al., 2021).

Restoration and management efforts aim to recover the lost ecosystem functions of drained peatlands through rewetting to re-establish anaerobic, i.e., oxygen-free, water-saturated environments. Today, major attempts are being made to restore peatlands in Europe and other parts of the world to combat global challenges such as biodiversity loss (Meli et al., 2014; Tomscha et al., 2021), eutrophication of water bodies (Zak et al., 2017), and greenhouse gas emissions (Zou et al., 2022). However, restoring complete ecosystem functioning could take decades or more due to the irreversible changes of physicochemical soil characteristics and ongoing pressures, including aquatic and airborne pollution (Baumane et al., 2021; Kreyling et al., 2021).

Unlike in natural peatlands, nutrient and C mobilization in rewetted peatlands appear to intensify, even under restored oxygen-free, water-saturated conditions. Increased nutrient availability and low levels of enzyme inhibitors have been identified as drivers of higher mineralization and turnover during rewetting (Zak et al., 2019). In both rewetted peatlands and natural rich fens, porewater nutrient concentrations can vary by one to two orders of magnitude (Bourbonniere, 2009; Zak et al., 2010). Recent findings suggest that the wide range of P concentrations in rewetted organic soils is influenced by soil sorption capacity, which depends on the iron (Fe) and aluminum (Al) content as well as other potential sorbents (Florea et al., 2024). Elevated nutrient concentrations alter both plant productivity and soil respiration, with P pollution particularly responsible for driving species loss, more so than N pollution (van der Laan et al., 2024). In rewetted fens, P is the limiting factor for plant growth, and ongoing high P concentrations will hinder the recovery of plant biodiversity (Emsens et al., 2016). In summary, increased P availability in rewetted peat soils may hinder the restoration of key peatland functions, including biodiversity support, climate regulation, and water purification (Kreyling et al., 2021). While advances have been made in understanding the biogeochemical processes governing porewater chemistry, P mobilization, and restoration outcomes in rewetted peatlands (Gaffney et al., 2018; Zak et al., 2022), important aspects remain understudied. These include the long-term development (>10 years) of spatial and temporal patterns of porewater chemistry and C, N, and P dynamics in both natural and degraded peatlands (Hoffmann et al., 2011; Niedermeier and Robinson, 2009; Zak and Gelbrecht, 2007). Overall, there is a lack of comprehensive data on porewater chemistry across different peatland types, regardless of their natural or altered state (Zak et al., 2022). Here, we analyze data from an extensive survey of porewater chemistry in 64 natural and rewetted peatlands, including both groundwater-fed fens and rainwater-fed bogs in six European countries, to answer the following questions: (i) How does porewater composition vary across different peatland types, and how do rewetted peatland (bogs and fens) differ from their natural counterparts? (ii) How do different peat characteristics affect porewater composition in rewetted fens? (iii) Are there seasonal variations in P concentrations in the porewater of rewetted fens, and how do these concentrations change over time after rewetting?

2. Methodology

2.1. Data collection

The data was obtained during an international field survey supported by the Department of Environment of Mecklenburg-Vorpommern and the European Agriculture Guidance and the Guarantee Fund (EAGGF). Porewater and soil samples were collected in situ from 64 natural and rewetted European peatlands to assess porewater and soil chemistry. At selected sites, nutrient fluxes were calculated, while in others, seasonal variations in porewater chemistry and long-term changes over a 10–20-year post-rewetting period were recorded (Table 1).

2.2. Sampling sites

Porewater and soil samples were collected from peatlands in Germany (47 sites), Poland (5 sites), Estonia (6 sites), Scotland (3 sites), Sweden (2 sites), and Georgia (1 site) during 1997–2017 (Fig. 1). Based on the Köppen-Geiger climate classification system, the sites were in oceanic (Cfb, Cfc) and continental (Dfb, Dfc) climates (Peel et al., 2007). The peatlands under investigation included both minerotrophic fens and ombrotrophic bogs (see Table 2 for dominant plant species). Fens were further classified into poor and rich fens based on their acidity and floristic composition (Griffiths et al., 2019). The surface and near-surface porewater of rich fens has an elevated pH and higher calcium (Ca) concentrations due to the inflow of mineral-rich groundwater (Griffiths et al., 2019). However, some of the sampled fen sites, fed by mineral-poor groundwater, also had low pH values down to 4, comparable to those of bogs.

The investigated sites were additionally classified as either natural or rewetted. Natural peatlands are sites that have never been actively drained. At the time of sampling, all natural peatlands had a near-surface water table (± 0.05 m). Rewetted peatlands include bogs or fens that have experienced prolonged drainage, followed by re-wetting that raised the water level. The intensity of drainage and land use greatly varied between the peatlands, resulting in different degrees of decomposition in the upper peat layers (between 0–0.4 m depth). Sites experiencing drainage and agricultural use over several decades had highly decomposed peat in the upper 0.2 to 0.4 m layer (Zak et al., 2010). Due to peat loss and shrinkage, all rewetted fen sites remained inundated throughout the year, with water table levels ranging from 0.1

Table 1
Overview of investigations conducted in 64 European peatlands from 1997 to 2017. Porewater investigations were consistently conducted once, using at least three dialysis samplers. At selected sites, multiple samplings were carried out to monitor seasonal changes and long-term changes following rewetting (see bottom of the table). Sampling times are provided in the data repository.

| Peatlands | Bog | | Fen | | |
|-----------------------|----------------|----------------|----------------|----------------|-----------------|
| | Natural | Rewetted | Natural | | Rewetted |
| | | | Poor | Rich | Rich |
| Study site | 14 | 2 | 13 | 12 | 23 |
| Porewater chemistry | All | All | All | All | All |
| Peat chemistry | All | All | All | All | All |
| Vertical profile | 8 ^a | 1 ^b | 8 ^c | 8 ^d | 18 ^e |
| Seasonal changes | – | – | – | 1 ^a | 6 ^f |
| Years after rewetting | – | – | – | – | 5 [∞] |

^aNatural Bogs: Esäkaste, Koordi, Likstermossen, Moksi-Munsary, Cross Lochs II, Tellissaare, Umbusi, Vedelsoo; ^b Rewetted Bogs: Cross Lochs; ^c Natural Poor Fen: Großen Fuchskuhle, Halbe, Kablower Ziegelei, Kleiner Milasee, Luchsee, Zolwia Bloc (Schildkrötensee), Pastlingsee, Pätzer Hintersee); ^d Natural Rich Fen: Dagowmoor, Dollgen, Gützkow ^a, Löcknitztal, Rospuda, Rzecin, Triebschsee, Triebsees); ^e Rewetted Rich Fen: Anklam, Beestland ^f, [∞], Bugewitz, Demnitz Mergelbruch, Glieningsmoor, Jargelin Rand ^f, [∞], Jargelin Zentrum ^f, Menzlin ^f, [∞], Moor Maxsee, Rambowmoor, Sernitzniederung, Skaby, Stangenhagen (Nordpolder), Töpchin, Töpchin Süd, Wendewiesen I Süd, Wendewiesen II Nord ^f, [∞], Zarnekow ^f, [∞].

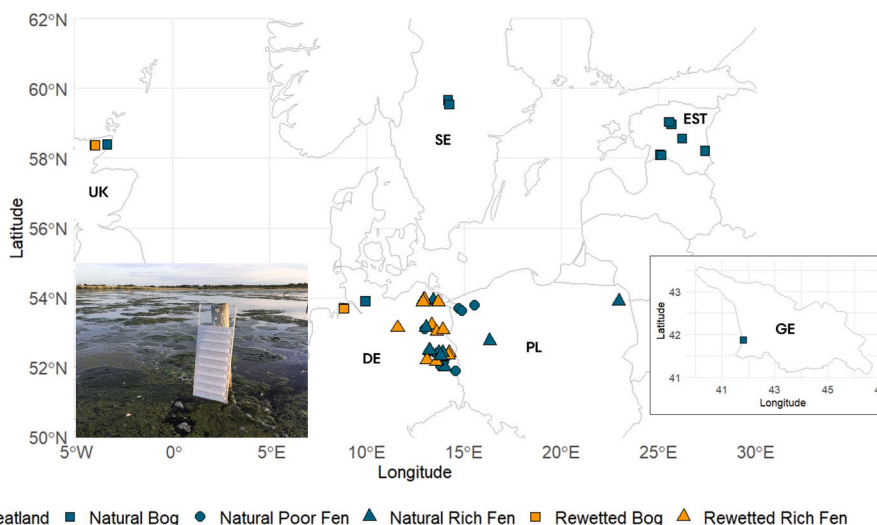


Fig. 1. Location of the 64 studied peatlands in Germany (GER), Poland (POL), Estonia (EST), Sweden (SE), Scotland in the United Kingdom (UK), and Georgia (GE), where both soil and porewater samples were collected to study nutrient composition after rewetting. Different colors indicate the type of peatlands, natural or rewetted bogs and fens. The photo in the lower left corner shows a dialysis sampler for obtaining anoxic porewater sampler from saturated peat soils as described in Zak et al. (2004).

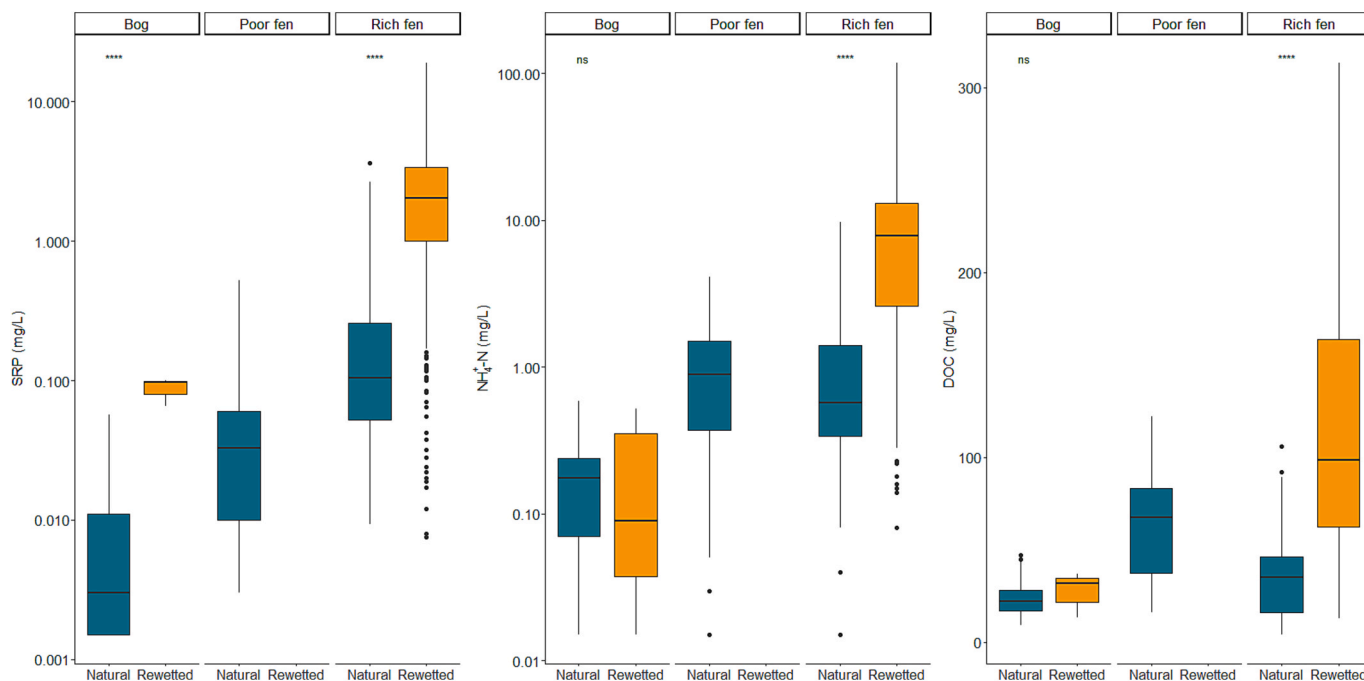


Fig. 2. Measured porewater concentration of soluble reactive phosphorus (SRP), ammonium ($\text{NH}_4^+\text{-N}$), and dissolved organic carbon (DOC) in natural and rewetted bogs and fens across all samples are presented in box plots. The line inside each box represents the median, the top and bottom edges correspond to the upper (75%) and lower (25%) quartiles, and the whiskers show the maximum and minimum values. Dots represent outliers. Note that SRP and $\text{NH}_4^+\text{-N}$ are plotted on a log scale. Asterisks denote statistical significance levels: **** indicates $p < 0.001$, ** indicates $p < 0.01$, and * indicates $p < 0.05$.

to 1 m above the soil surface, referred to as “highly degraded” in the following.

2.3. Sampling of porewater and peat

The dialysis sampling technique was used to conduct unbiased sampling of oxygen-sensitive dissolved solutes in the anoxic porewater of the study areas and to obtain vertical concentration profiles (Hesslein, 1976; Zak et al., 2004). This technique allows for the collection of porewater samples from specific depth ranges and provides vertical concentration profiles for dissolved solutes with a vertical resolution of

4 cm (Frank et al., 2014). The dialysis sampler used in this study consists of a transparent acrylic base plate with 14 chambers filled with deionized water (electrical conductivity $< 0.066 \mu\text{S cm}^{-1}$). The chambers were covered by a semipermeable HT-Tuffryn-200 Membrane made of polysulfone with a pore diameter of $0.2 \mu\text{m}$, fixed in place by a cover plate. Prior to sampling, the sampler was stored in a PVC container with deionized water and degassed with N_2 for about 24 h.

At all study sites, at least three dialysis samplers were placed in water-saturated upper peat layers (0–0.6 m) to collect anoxic porewater samples. Samplers were consistently placed at 10-m intervals along transects within distinct vegetation communities. Each sampling point

Table 2

Porewater composition of natural and rewetted bogs and fens (soil depth 0–0.6 m). The estimated marginal means ± standard errors based on generalized linear mixed model of dissolved solutes (SRP: Soluble Reactive Phosphorus, TDP: Total Dissolved Phosphorus, NH₄⁺-N: Ammonium, SO₄²⁻: Sulfate, DOC: Dissolved Organic Carbon, Fe: Total Iron, EC: Electrical Conductivity, K: Potassium, Na: Sodium, Mg: Magnesium, DIC: Dissolved Inorganic Carbon, NO₃⁻-N: Nitrate) are given in mg L⁻¹ and the electrical conductivity (EC) is in μS cm⁻¹. Superscript letters from multiple comparisons indicate significant differences (p < 0.05; for further statistical details [supplementary table 1](#)) between subcategories within each peatland type (but not across bogs and fens).

| Peatlands | Bog | | Fen | | |
|---------------------------------|---|--|---|--|--|
| | Natural | Rewetted | Natural | | Rewetted |
| | | | Poor | Rich | Rich |
| Study site | 14 | 2 | 13 | 12 | 23 |
| No. of samples | 49 | 11 | 37 | 65 | 562 |
| pH | 4.1 ± 0.1 ^a | 4.3 ± 0.2 ^a | 4.2 ± 0.1 ^a | 6.1 ± 0.2 ^b | 6.7 ± 0.1 ^c |
| EC | 48 ± 3.4 ^a | 68.3 ± 8.8 ^a | 70.5 ± 35 ^a | 344.5 ± 85.1 ^b | 1125.9 ± 109 ^c |
| Fe* | 0.1 ± 0.1 ^a | 0.3 ± 0.05 ^a | 1.7 ± 1.1 ^a | 2.6 ± 1.5 ^a | 20.1 ± 2.8 ^b |
| SO ₄ ²⁻ | 0.4 ± 0.1 ^a | 0.3 ± 0.1 ^a | 0.7 ± 0.3 ^a | 1.7 ± 0.9 ^{ab} | 8.7 ± 3.4 ^b |
| Ca ²⁺ | 0.4 ± 0.1 ^a | 0.4 ± 0.2 ^a | 2.7 ± 0.6 ^a | 36.5 ± 9.3 ^b | 147.5 ± 26.9 ^c |
| K ⁺ | 0.8 ± 0.6 ^a | 1.1 ± 0.1 ^a | 1.5 ± 0.3 ^a | 1.7 ± 0.3 ^a | 3.9 ± 0.5 ^b |
| Na ⁺ | 0.9 ± 0.2 ^a | 2.0 ± 0.4 ^a | 2.7 ± 0.6 ^a | 7.1 ± 1.9 ^b | 26.9 ± 5.5 ^c |
| Mg ²⁺ | 0.5 ± 0.1 ^a | 0.8 ± 0.1 ^a | 0.8 ± 0.3 ^a | 3.1 ± 1.1 ^b | 8.3 ± 1.6 ^c |
| SRP | 0.07 ± 0.01 ^a | 0.3 ± 0.03 ^b | 0.04 ± 0.1 ^a | 0.4 ± 0.1 ^a | 1.6 ± 0.2 ^b |
| TDP | 0.1 ± 0.01 ^a | 0.2 ± 0.04 ^a | 0.1 ± 0.1 ^a | 0.1 ± 0.1 ^a | 1.9 ± 0.5 ^b |
| NH ₄ ⁺ -N | 0.4 ± 0.04 ^a | 0.4 ± 0.1 ^a | 0.6 ± 0.3 ^a | 0.8 ± 0.4 ^a | 3.6 ± 0.7 ^b |
| NO ₃ ⁻ -N | 0.01 ^a | 0.01 ^a | 0.02 ^a | 0.05 ^a | 0.09 ^a |
| DOC | 3.1 ± 0.1 ^a | 3.3 ± 0.2 ^a | 52.1 ± 7.8 ^a | 34.5 ± 5.6 ^{ab} | 60.5 ± 7.0 ^b |
| DIC | n.d.** | n.d.** | 2.7 ± 1 ^a | 36.4 ± 9.3 ^b | 147 ± 26.9 ^c |
| Dominant plant species | <i>Sphagnum</i> spp. <i>Andromeda polifolia</i> <i>Drosera</i> spp. | <i>Phragmites australis</i> , <i>Carex</i> spp., <i>Juncus spec.</i> | <i>Carex</i> spp., brown mosses, <i>P. australis</i> | <i>Sphagnum</i> spp., <i>Eriophorum</i> <i>angustifolium</i> , <i>Vaccinium oxycoccos</i> | <i>P. australis</i> <i>Typha latifolia</i> <i>Ceratophyllum demersum</i> |
| Peat decomposition*** | Low (Fibric) | Moderate (Hemic) | Low (Fibric) | Low –Moderate (Fibric-Hemic) | Moderate-High (Hemic-Sapric) |

* photometric analysis has shown that most of the dissolved iron is in the reduced form (Fe²⁺). ** n.d.: not determined. *** degree of peat decomposition according to von Post scale in soil depth of 0–0.6 m (von Post, 1922). For further information about individual sites, see data repository.

was marked with a 2.5-m long wooden stake to facilitate later retrieval and enable repeated sampling for assessing temporal changes. These samples were collected during the main growing season (June to August) to compare porewater chemistry between sites and to observe temporal changes throughout the rewetting period, minimizing the influence of seasonal variation in both cases. In addition, selected peatlands were sampled at 1–3-month intervals to capture seasonal dynamics (Table 1). For all sites, detailed information on sampling times is provided in the data repository. The samplers were left undisturbed for a minimum of seven days to ensure equilibrium in the concentration of dissolved solutes within the chamber water and the surrounding area (Brandl and Hanselmann, 1991; Hesslein, 1976). Then, the chamber water was sampled with a multi-pipette (Eppendorf) and either combined into a composite sample or kept separate for one sampler. Each of the 14 chambers was individually emptied, and their contents were combined into a 1-liter polyethylene bottle filled with argon to minimize oxidation of redox-sensitive substances. The composite was gently agitated until fully homogenized, resulting in what is referred to as the composite sample. From these composite samples, aliquots of approximately 20 mL were immediately preserved with 0.3 mL of 2 M hydrochloric acid to avoid oxidation of dissolved Fe(II) and co-precipitation with P and other substances like dissolved OM (Zak et al., 2004). Samples were then transported in a cooled container to the laboratory and stored at 4 °C until further analysis. All chemical parameters were analyzed either the following day or, in the case of dissolved organic carbon (DOC), within two weeks, as no significant changes in concentration are expected within this time frame (Heinz and Zak, 2018).

Peat samples (about 0.5 L) were taken once from different decomposed peat layers at 0 to 0.6 m depth at all porewater sampling spots. All samples were obtained within 0.5 m of the designated spot, coinciding with the in situ porewater sampling period. This simultaneous sampling facilitated a direct comparison between in situ porewater concentrations and peat characteristics. The upper peat layer (about 5 cm) containing fresh plant tissue was not considered. The peat samples were stored in 3

L polyethylene bags at 5 °C for no longer than one week before further chemical analysis.

2.4. Flux calculations of dissolved nutrients

For 43 natural and rewetted study sites (Table 1), one sampler’s individual 14 chambers were sampled separately to obtain vertical concentration profiles for soluble reactive phosphorus (SRP) and ammonium (NH₄⁺-N) to calculate depth-integrated mobilization rates using the program Profile V1 (Berg et al., 1998), as shown in Fig. 3. Computation applied Fick’s first law of diffusion, considering pH, temperature, DM content, and loss on ignition of the peat (see data repository for single results). Diffusion constants for SRP and NH₄⁺-N under defined conditions (10–20 °C; pH 4.1–7.2) were sourced from Yuan-Hui and Gregory (1974) and adjusted using chemical equilibrium calculations that account for pH, temperature, and dynamic viscosity of water. The porosity of peat samples used to estimate tortuosity was derived from the water content and the composition of inorganic and organic matter content (Lewandowski et al., 2002). The calculations assumed steady-state conditions. Advective transport of dissolved solutes was excluded, particularly for rewetted peatlands, due to the low hydraulic conductivity of the decomposed peat layer. However, some bias might be present at natural fen sites. Since the peat samples were free of macro zoobenthos, variables for bio-diffusivity and bio-irrigation were not considered in calculating net mobilization rates (for further details, see Berg et al. (1998).

2.5. Chemical water analysis and peat characterization

Porewater chemistry was determined using standard methods. The concentration of SRP was analyzed by the molybdenum blue method (Cary 1E; Varian, Darmstadt, Germany) within 24 h after sampling, following Murphy and Riley (1962). With very few exceptions, porewater samples had SRP concentrations below the detection limit of 3 μg

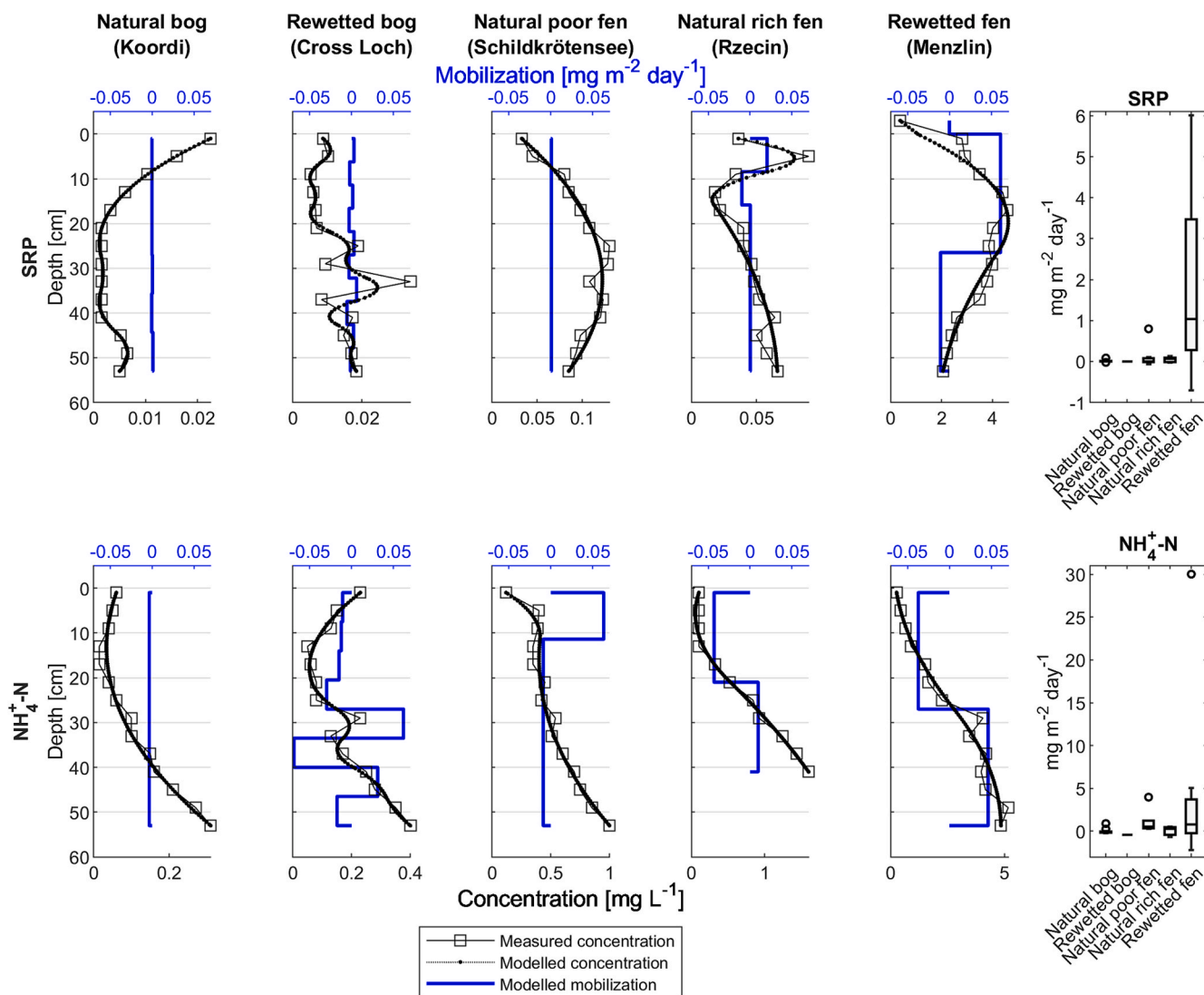


Fig. 3. Selected measured vertical concentration profiles for soluble reactive phosphorus (SRP) and ammonium ($\text{NH}_4^+\text{-N}$) and corresponding modelled mobilization rates (5 sites out of 43 sites, see data repository) in the sampled horizon (0–0.6 m depth) according to Profile V1 (Berg et al., 1998). For the natural sites, the entire depth was characterized by slightly decomposed peat, while for most of the rewetted sites, the upper 0.1–0.3 m were highly decomposed and the underlying peat was less decomposed. Data from all sites are presented in box plots (on the right), where the line inside each box represents the median, the top and bottom edges correspond to the upper and lower quartiles, and the whiskers show the maximum and minimum values. Note that the x-axis for the profile concentrations uses different scales across the selected sites.

L^{-1} . In these cases, half of the detection limit was assigned to provide a data point. In some peatlands, porewater samples appeared brownish due to high concentrations of humic-like substances or contained hydrogen sulfide, which interferes with photometric P analysis. To address these issues, either a blank measurement (without adding ascorbic acid to a subsample, allowing later correction of the measured concentration) was performed, or hydrogen sulfide was removed by purging the acidified sample with air. Iron, Ca, and magnesium (Mg) concentrations were measured using flame atomic absorption spectrometry, while sodium (Na) and potassium (K) concentrations were determined by flame atomic emission spectrometry (PerkinElmer 3300). All metal concentrations were higher than the detection limit (0.2 mg L^{-1}). Ammonium was quantified using the indophenol method (Flow Solution III; Perstorp, Rodgau, Germany). The measured concentrations consistently exceeded the detection limit (0.03 mg N L^{-1}), and the acidified samples remained stable for several days when stored at $4 \text{ }^\circ\text{C}$. Dissolved organic carbon and dissolved inorganic carbon (DIC) were measured with a C analyzer (TOC 5000; Shimadzu, Kyoto, Japan), and SO_4^{2-} , chloride (Cl^-), and nitrate ($\text{NO}_3\text{-N}$) concentrations were

determined using ion chromatography (conductivity detection after electrochemical suppression, Dionex DX 100, Thermo Scientific, Germany). All DOC concentrations were consistently above the detection limit of 0.5 mg L^{-1} . Dissolved inorganic carbon (DIC) measurements were conducted either on the day of sampling or, at the latest, the following day. For repeated measurements using the sampling device, only the first value was considered, as subsequent readings (typically three per sample) showed a rapid decline in concentration within minutes due to supersaturation and degassing. To minimize CO_2 loss from porewater, measurement vials were filled without a headspace in the field and closed with airtight caps. Anion measurements were performed on non-acidified samples, which were pre-treated in the field using a chelate filter (IC-H sample preparation cartridge, Metrohm) to remove cations, including ferrous iron. This step prevented co-precipitation with anions and avoided clogging of the fine tubing in the ion chromatography (IC) analyzer. Detection limits for the anions were 0.5 mg L^{-1} for SO_4^{2-} and Cl^- , and 0.01 mg L^{-1} for $\text{NO}_3\text{-N}$; most study sites had concentrations below the detection limit for the latter. Porewater pH was measured immediately after collecting and combining individual

Table 3

Peat characteristics natural and rewetted bogs and fens. The table shows mean \pm standard error of solutes (C content: Carbon content, N content: Nitrogen content, P content: Phosphorus content, Fe content: Total Iron content, Al content: Aluminum content, Ca content: Calcium content). The contents are given in mg g⁻¹ dry mass). Superscript letters from multiple comparisons indicate significant differences ($p < 0.05$; for further statistical details [supplementary table 2](#)) between subcategories within each peatland type (but not across bogs and fens).

| | Bog | | Fen | | |
|------------------|-----------------------------|-----------------------------|-----------------------------|-------------------------------|-----------------------------|
| | Natural | Rewetted | Natural | | Rewetted |
| | | | Poor | Rich | Rich |
| C content | 483 \pm 5 ^a | 494 \pm 10 ^a | 445 \pm 11 ^b | 387 \pm 35 ^{ab} | 308 \pm 14 ^a |
| N content | 13.9 \pm 0.7 ^a | 18.6 \pm 1.0 ^a | 18.8 \pm 1.1 ^a | 19.6 \pm 3.6 ^a | 21.1 \pm 1.4 ^a |
| molar C/N ratio | 31.4 \pm 2.8 ^a | 41.7 \pm 1.9 ^a | 35.7 \pm 2.0 ^b | 27.4 \pm 6.4 ^{ab} | 19.1 \pm 2.6 ^a |
| P content | 0.2 \pm 0.02 ^a | 0.5 \pm 0.1 ^b | 0.7 \pm 0.1 ^a | 0.9 \pm 0.2 ^{ab} | 1.3 \pm 0.1 ^b |
| Fe content | 0.7 \pm 0.1 ^a | 1.5 \pm 0.2 ^b | 3.3 \pm 1.5 ^a | 8.6 \pm 4.9 ^a | 21.7 \pm 1.9 ^b |
| molar Fe/P ratio | 1.8 \pm 0.5 ^a | 1.9 \pm 0.1 ^a | 2.8 \pm 0.6 ^a | 6.1 \pm 2.0 ^{ab} | 9.0 \pm 0.8 ^b |
| Al content | 1.1 \pm 0.1 ^a | 2.0 \pm 0.3 ^b | 4.1 \pm 0.5 ^a | 3.4 \pm 1.6 ^a | 5.5 \pm 0.1 ^a |
| Ca content | 1.6 \pm 0.1 ^a | 1.0 \pm 0.3 ^a | 3.8 \pm 5.9 ^a | 19.7 \pm 18.9 ^{ab} | 58.5 \pm 7.8 ^b |

porewater samples into a composite, using pH probes (WTW, Weilheim, Germany). Otherwise, a shift of up to one pH unit is possible due to post-sampling chemical changes. Degassing of CO₂ can lead to a pH increase, while the precipitation of Fe(III) oxyhydroxides may cause a pH decrease (Elberling and Matthiesen, 2007; Zak et al., 2004).

From distinct soil layers out of the investigated depth of 0–0.6 m, a handful of peat was sampled to assess the degree of decomposition using the von Post method (von Post, 1922). This method assigns a decomposition index (H-value) on a scale from 1 (completely undecomposed) to 10 (fully decomposed), based on the physical consistency and plant residue content of the peat. While the von Post scale is a widely used and practical tool for rapid field assessment, it is not without limitations. Notably, it is subject to observer bias and can lead to inconsistent classification, particularly when distinguishing between adjacent categories (e.g., H1 vs. H2). Although efforts have been made to correlate von Post values with chemical peat properties influenced by decomposition, such correlations have shown limited consistency (Biester et al., 2014). Nevertheless, despite its subjectivity and semi-quantitative nature, the von Post method remains a valuable initial indicator of both chemical and hydrological characteristics of peat in the field. Crucially, it should always be supplemented by more precise laboratory-based analyses to provide a comprehensive understanding of peat properties and linked processes (Zak and Gelbrecht, 2007). As discussed earlier (Taufik et al., 2019), the von Post scale also aligns with broader qualitative categories of peat decomposition: fibric (low decomposition; H1–3), hemic (moderate decomposition; H4–6), and sapric (high decomposition; H7–10). For clarity and robustness, we refer to these grouped categories i) low, ii) moderate, and iii) high decomposition throughout this study, rather than relying on the full 10-point scale (Grover and Baldock, 2013). Dry matter (DM) content was calculated by drying three replicate samples (approx. 10 g each) at 105 °C to constant mass. OM content was assessed by loss on ignition at 550 °C for four hours. The loss of calcium carbonate during this process was negligible (<5%) in all peat samples (single results are not shown). For total content analysis of P, Fe, Al, Ca, C, and N, dried peat samples were homogenized using a stainless-steel mill. Total P was determined as SRP following an acid digestion procedure (10 mg dry sample + 2 mL 10 M H₂SO₄ + 4 mL 30 % H₂O₂ + 20 mL deionized water at 160 °C for 2 h). Fe, Al, and Ca contents were determined after digestion of 70 mg homogenized peat with 2 mL concentrated hydrochloric acid (36 %) and 6 mL nitric acid (76 %) in a high-pressure microwave digestion system (Gigatherm and GMS GmbH, Grub AR, Switzerland). C and N contents were determined using a CN analyzer (Vario EL; Elementar, Mt. Laurel, New Jersey, USA).

To assess the potential mobilization of P and Fe under anoxic conditions due to redox processes, 10 g of fresh (wet) peat were extracted with a 0.11 mol L⁻¹ bicarbonate–dithionite (BD) solution following an ammonium chloride extraction step, as described by Zak et al. (2008). Due to interference from humic substances in the BD extracts, dissolved P was typically measured after acid digestion as SRP, preventing

differentiation between inorganic and organic P.

2.6. Statistical data analysis

All statistical analyses were performed in R version 4.3.1 (R Core Team, 2020). Separate statistical models were applied for bogs and for fens to compare porewater chemistry and peat characteristics. For both bogs and fens, linear mixed-effects models (LMM) were used to account for random site-level variation. Model-estimated means (\pm standard error) of porewater chemistry and peat characteristics are presented in Table 2 and Table 3, respectively. Post-hoc pairwise comparisons were performed between natural and rewetted sites within each peatland type (bogs and fens) only, with no comparisons made between bogs and fens, using the estimated marginal means (emmeans) package (Lenth, 2022); significance was denoted by letter groupings (*multicomp*, Hothorn et al., 2008). Full model results are available in [Supplementary Tables 1 and 2](#).

Principal component analysis (PCA) was conducted on individual depth-integrated (“composite”) porewater samples from natural and rewetted sites to explore differences in composition parameters across all study locations (Fig. 4). Before running PCA, parameters were standardized to have zero mean and unit variance on the covariance matrix. Site differentiation based on classification was examined with a linear model with PC-scores from the first two dimensions as response variables and site hydrology (natural/rewetted) and years after rewetting as predictors.

Spearman correlations between the different variables in the porewater and peat composition datasets were explored. To examine the effect of peat variables on SRP concentrations in fen porewater, various combinations of peat variables were selected as predictors based on correlation analysis. Results from the correlation analysis (Fig. 5) guided the selection of predictor variables for linear mixed models (lmer, package *lme4*, Bates et al. (2015)), constructed to identify the best predictors for SRP. To account for site level variation, study site was included as random effect in mixed-effects models. SRP was square root-transformed to meet model assumptions. From candidate models informed by the correlation analysis, we used the Akaike Information Criterion corrected for small sample sizes (AICc) to select the best-fitting model (Wagenmakers and Farrell, 2004). The model with the lowest AICc value was chosen, indicating the optimal balance between model complexity and goodness of fit (Table 4).

To assess the seasonal and annual trends in SRP concentration variation in porewater, a generalized linear model with a Gamma probability distribution and log-link function was applied (glmmTMB, Brooks et al., 2017). For seasonal trends, both 3rd and 4th order polynomials for month (1–12) as a continuous predictor variable were tested. The results were similar for both orders, but a log-likelihood test indicated that the 4th order polynomial provided a better fit for most sites ($\chi^2 = 12.70$, df = 6, $p = 0.048$), explaining the maximum variance. Therefore, the 4th order polynomial was selected and is shown in Fig. 6.

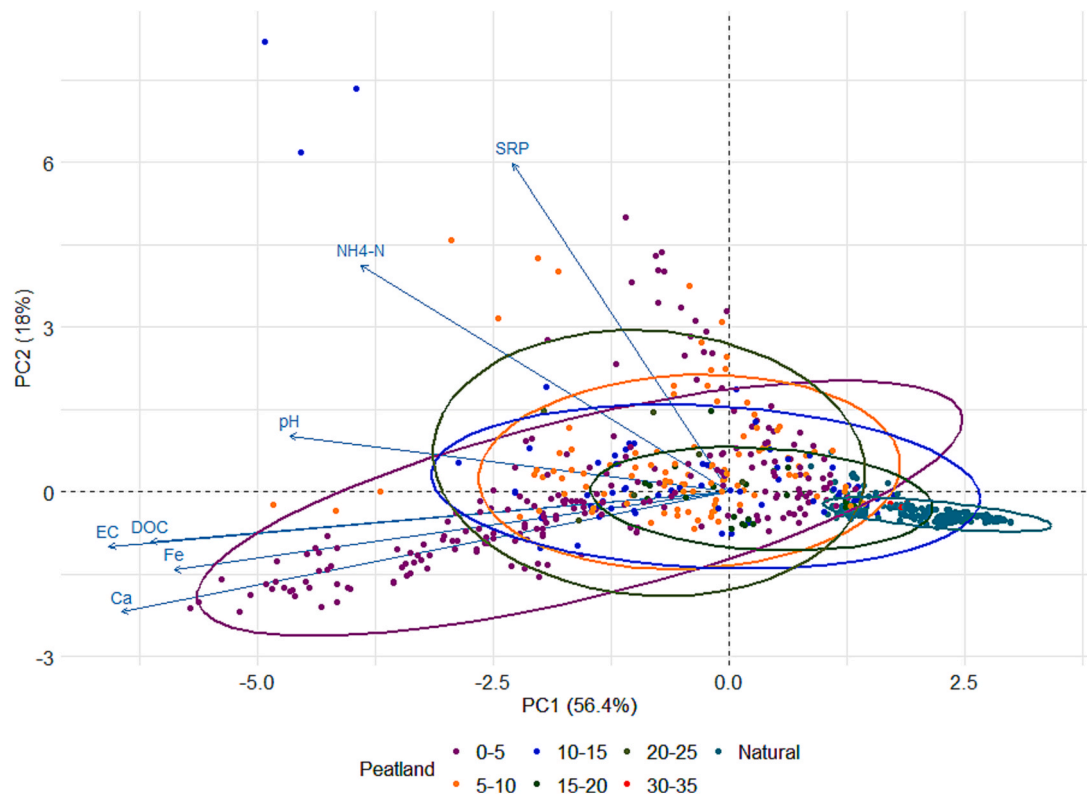


Fig. 4. Principal Component Analysis (PCA) biplot of porewater nutrient composition across all sampling sites ($n = 64$ peatlands) under natural and rewetted conditions. Rewetted sites are further categorized based on the number of years since rewetting: 0–5, 5–10, 10–15, 15–20, 20–25, 25–30, and 30–35 years. Principal Components (PC1 and PC2) refer to the first and second principal components in PCA. Ellipses represent 68 % confidence intervals for each years category group.

However, summary and statistical comparison of both the 3rd and 4th order polynomials are provided in [Supplementary tables 3 and 4](#). Estimated marginal means and trends were evaluated using the `emmeans` function (`emmeans`, [Lenth \(2022\)](#)). Temporal and spatial SRP seasonal variations were modeled only for six selected German sites (Jargelin-Rand, Jargelin Zentrum, Wendewiese Nord, Menzlin, Beestland, and Zarnekow) with at least four samplings within a year (see [Supplementary table 5](#)).

Similarly, “years after rewetting” is included in the model for annual trends. Study site and its interaction with time were added as fixed factors, with sampling year as a random effect. Long-term variability in porewater SRP concentrations over several decades ([Fig. 7](#)) was modeled for five selected German sites (Jargelin-Rand, Wendewiese Nord, Menzlin, Beestland, and Zarnekow), where sampling was conducted for more than ten years post rewetting (see [Supplementary tables 6 and 7](#)).

3. Results

3.1. Porewater and peat chemistry in natural and rewetted peatlands

Natural bogs had the lowest electrical conductivity (EC; $48 \pm 3.4 \mu\text{S cm}^{-1}$), which is consistent with low ion concentrations ([Table 2](#)). Both natural and rewetted bogs exhibited low levels of dissolved solutes (Fe^{2+} , SO_4^{2-} , K^+ , Na^+ , Mg^{2+}), whereas rich fens had much higher solute and ion concentrations. Rewetting significantly increased pH and EC in rich fens from 344.5 ± 85.1 to $1125.9 \pm 109 \mu\text{S cm}^{-1}$ leading to marked increases in Fe^{2+} , SO_4^{2-} , K^+ , Na^+ , and Mg^{2+} ($p < 0.05$; [Table 2](#)). For example, the Fe concentration rose to $20.1 \pm 2.8 \text{ mg L}^{-1}$ compared to $2.6 \pm 1.5 \text{ mg L}^{-1}$, and SO_4^{2-} reached up to 2000 mg L^{-1} at the Zarnekow site shortly after rewetting (see data repository) – about 1000-fold higher than under natural conditions ([Table 2](#)).

Porewater nutrient concentrations differed clearly between natural

and rewetted sites ([Fig. 2](#)). Rewetting significantly increased SRP in both bogs and fens ($p < 0.001$) and $\text{NH}_4\text{-N}$ in fens ($p < 0.001$). The SRP concentrations were about ten times higher at the rewetted sites, reaching 1.6 mg L^{-1} in rich fens compared to $0.1\text{--}0.4 \text{ mg L}^{-1}$ in natural fens. $\text{NH}_4\text{-N}$ rose from 0.8 mg L^{-1} in natural fens to 3.6 mg L^{-1} in rewetted rich fens. In contrast, DOC concentrations, remained consistently low across both natural and rewetted bogs ([Fig. 2](#)).

The concentrations of SRP in rewetted fens were often highest in the upper, highly decomposed peat layer (0–0.3 m) and decreased with depth, while $\text{NH}_4\text{-N}$ tended to increase with depth – patterns clearly observed in the rewetted fen Menzlin ([Fig. 3](#)). These vertical gradients were less distinct or absent in other rewetted fens and natural peatlands. When integrated over the full sampling depth (0–0.6 m), SRP and $\text{NH}_4\text{-N}$ mobilization rates were substantially higher in rewetted fens – on average, 23 and 4.6 times higher, respectively – than in natural fens, with mean rates of 1.8 vs. $0.1 \text{ mg P m}^{-2} \text{ d}^{-1}$ and 3.6 vs. $0.8 \text{ mg N m}^{-2} \text{ d}^{-1}$. However, mobilization rates were sometimes near zero or negative, particularly in natural peatlands. Elevated SRP mobilization was mostly confined to degraded upper layers, while deeper, less decomposed layers often showed negative rates, explaining the lower depth-integrated values in some rewetted fens.

Carbon content in peat was comparable between natural and rewetted bogs (483 and $494 \text{ mg g}^{-1} \text{ DM}$, respectively), while rewetted rich fens had the lowest C content ($308 \text{ mg g}^{-1} \text{ DM}$) ([Table 3](#)). Nitrogen content did not differ significantly between natural and rewetted bogs ($p > 0.05$) and both had similar C/N ratios. The rewetted rich fens, however, had the lowest C/N ratios (19.1 ± 2.6). The contents of P and Fe were markedly higher in rewetted bogs and fens than their natural counterparts. The Fe/P ratio was approximately 1.3 times higher in rewetted rich fens (9.0 ± 0.8) compared to natural rich fens (6.1 ± 2.0), although the difference was not statistically significant ($p > 0.05$). In contrast, Al content differed significantly in rewetted bogs ($p < 0.05$) but remained consistent between natural and rewetted fens. Overall,

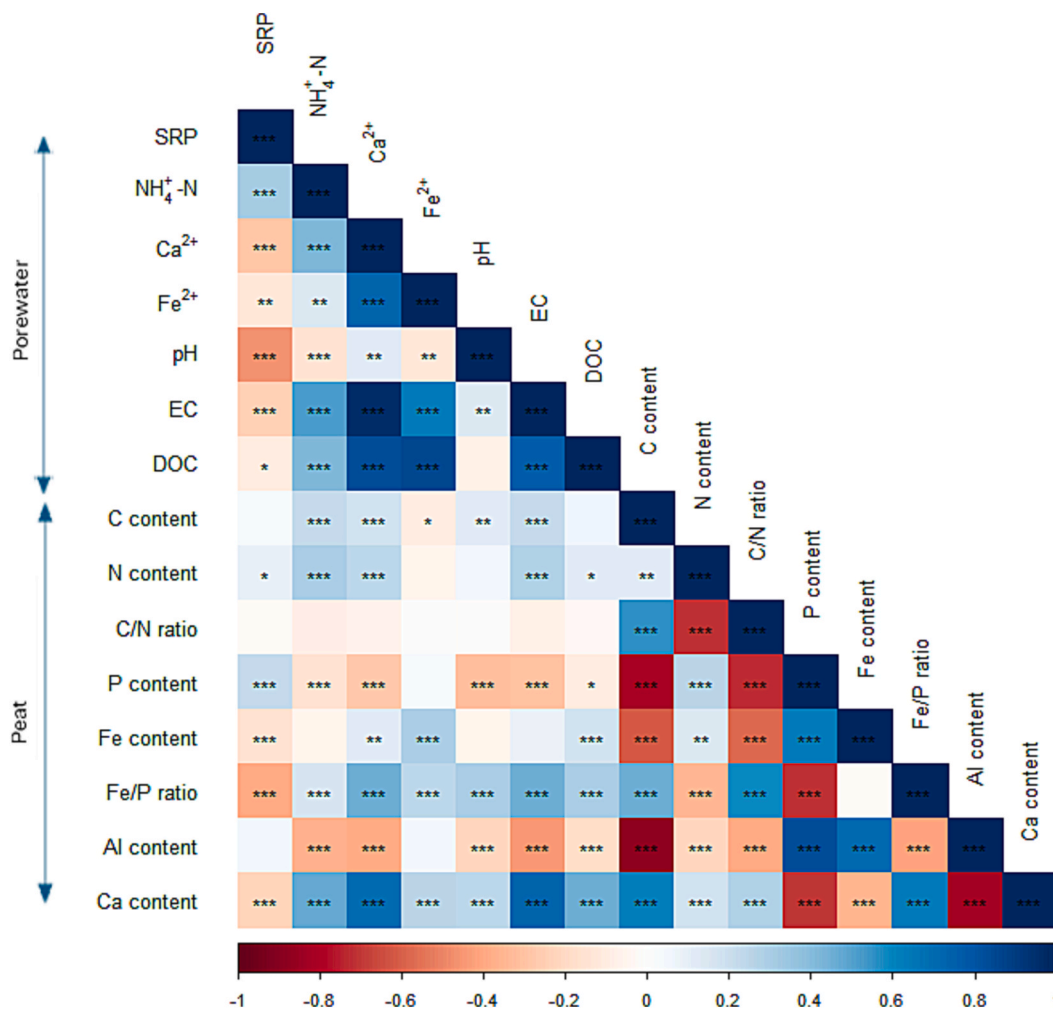


Fig. 5. Correlation matrix illustrating the relationships between porewater characteristics and peat properties in fens: Dark red represents strong negative correlations, while dark blue indicates strong positive correlations. (SRP: Soluble Reactive Phosphorus, NH₄⁺-N: Ammonium, Ca²⁺: Calcium, Fe²⁺: Iron, pH, EC: Electrical conductivity, DOC: Dissolved organic Carbon are porewater characteristics and C: Carbon, N: Nitrogen, C/N ratio, P: Phosphorus, Fe: Iron, Fe/P, Al: Aluminum, Ca: Calcium contents are peat bulk properties). Asterisks denote statistical significance levels: *** indicates $p < 0.001$, ** indicates $p < 0.01$, and * indicates $p < 0.05$. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Comparison of different models for predicting soluble reactive phosphorus (SRP) concentration using a linear mixed model (lmer) incorporating study site variability.

| Model | Variables | ΔAICc* |
|---------|--|--------|
| Model 1 | Fe content, Al content, pH | 0 |
| Model 2 | Fe content, Al content, pH, Ca content, Fe/P ratio | 22 |
| Model 3 | Fe content, Al content | 33 |
| Model 4 | Fe content, Al content, Ca content | 43 |
| Model 5 | Fe content, Al content, Fe/P ratio | 44 |

*Akaike Information Criterion corrected for small sample sizes (AICc) assesses the relative fit of statistical models, with lower values indicating better model fit. ΔAICc represents the difference between the AICc of a given model and the best-fitting model, with smaller ΔAICc values suggesting a closer fit to the data. The AICc values range from 1955 to 1999. Note that Fe/P ratio is on a molar basis.

rewetted rich fens exhibited elevated nutrient and metal concentrations in the peat.

The first two principal components (PC1 and PC2) explained 74.4 % of the variance in porewater composition across natural and rewetted peatlands (PC1: 56.4 %, PC2: 18.0 %; Fig. 4). The PCA biplot shows a clear separation along PC1 ($F = 721.51$, $df = 1$, $p < 0.001$), with rewetted sites displaying greater variability. PC1 reflects differences in

chemical properties, with high loadings of EC, Ca²⁺, DOC, and Fe²⁺. PC2 ($F = 33.90$, $df = 1$, $p < 0.001$) captures nutrient mobilization and temporal changes, showing strong positive loadings for SRP and NH₄⁺-N. Recently rewetted sites (0–5 years) clustered with higher PC1 scores, indicating elevated ion and organic matter concentrations, while natural sites formed a distinct cluster with consistently lower nutrient and solute levels.

3.2. Effect of peat characteristics on porewater composition

The correlation analysis aimed to identify peat properties influencing SRP concentrations in the porewater of rewetted fens. Contrary to expectations, peat Fe and Al contents showed only weak correlations with SRP. However, SRP was strongly negatively correlated with the molar Fe/P ratio ($p < 0.001$), suggesting that P release is influenced by the degree of P saturation in Fe(III) compounds (Fig. 5). SRP also correlated negatively with porewater pH and, to a lesser extent, with peat Ca content.

Overall, SRP showed relatively weak individual correlations with peat and porewater variables, except for pH. To better explain SRP variability, linear regression models were tested using combinations of variables (Table 4). Model 1, which included Fe content, Al content, and pH, had the lowest AICc and offered the best balance between

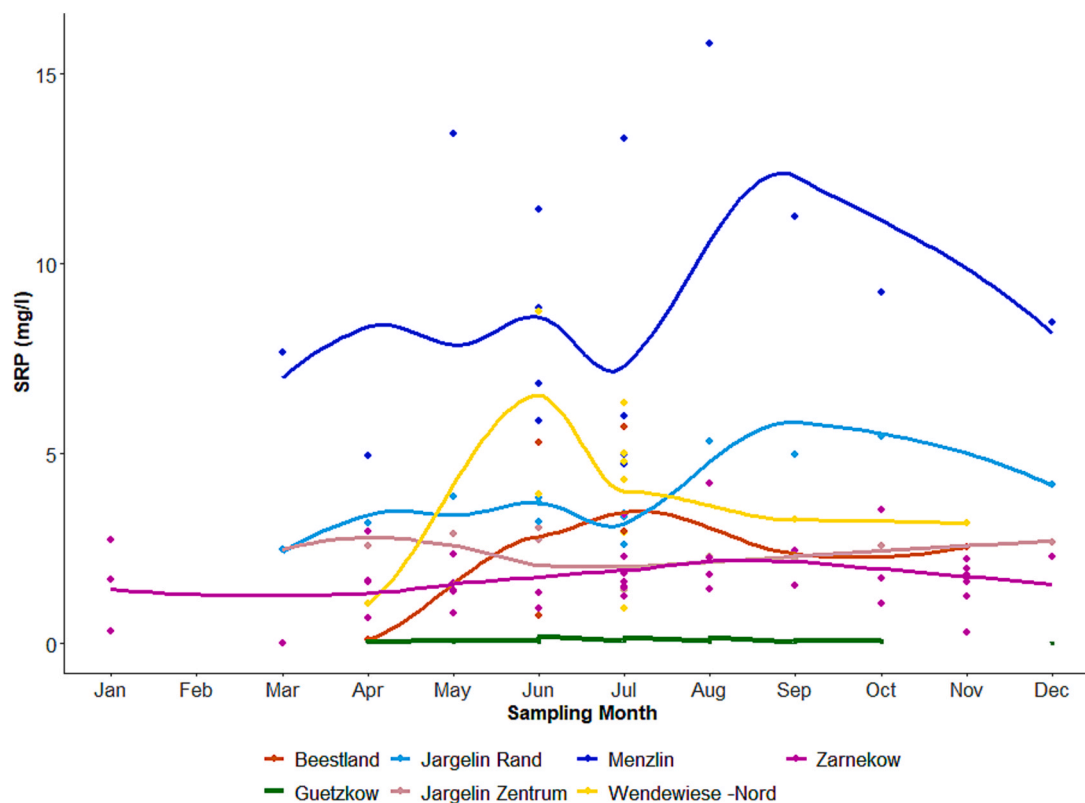


Fig. 6. Monthly variation in soluble reactive phosphorus (SRP) concentration over a year at the selected sampling sites of rewetted fens– Beestland, Jargelin Rand, Jargelin Zentrum, Wendewiese Nord, Menzlin, and Zarnekow. The points represent the observed SRP concentrations, and the lines show the modeled linear variation of SRP. A linear mixed model (glmmTMB) with a polynomial order of 4 was used to model SRP concentration changes. The natural site, Guetzkow, is included as a baseline but was not part of the model.

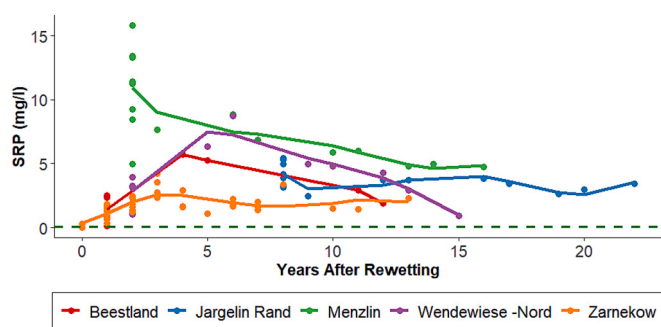


Fig. 7. Change in average soluble reactive phosphorus (SRP) concentration over the years after rewetting at the selected sampling sites – Beestland, Jargelin Rand, Wendewiese Nord, Menzlin, and Zarnekow. Sampling was conducted within the vegetation period to avoid seasonal effects. Points represent the observed SRP concentrations, and lines show the modeled linear variation of SRP. Dotted lines represent the average concentration of SRP in natural fens. A linear mixed model (glmmTMB) with a polynomial order of 4 was used to model SRP concentration change.

explanatory power and simplicity. Although more complex models (e.g., including Ca content and the Fe/P ratio) slightly improved fit, they posed a risk of overfitting. Thus, Model 1 emerged as the most parsimonious and effective model for predicting SRP concentrations.

3.3. Seasonal variation of P concentration and change over the rewetting years

Seasonal SRP variation across the rewetted fen sites showed distinct site-specific patterns (site × season interaction: $F = 53.3$, $df = 20$, $p <$

0.001; Fig. 6). Menzlin consistently exhibited the highest SRP levels (6.9 mg L^{-1}), about three times higher than other sites. In contrast, Jargelin Zentrum (1.2 mg L^{-1}) and Zarnekow (1.9 mg L^{-1}) had the lowest and most stable concentrations. Beestland, Wendewiese Nord, and Jargelin Rand showed intermediate SRP levels ($3.0\text{--}3.7 \text{ mg L}^{-1}$) with moderate seasonal variation. The natural rich fen Guetzkow had the lowest and most stable SRP levels throughout the year.

Seasonal trends followed a 4th-order polynomial pattern ($\chi^2 = 15.2$, $df = 4$, $p = 0.004$), with a spring peak, a secondary early-summer peak at helophyte-dominated sites (e.g., Menzlin, Wendewiese Nord), followed by a decline during midsummer and a rise from late summer into fall. SRP variability was lowest at Zarnekow, likely reflecting its first year of rewetting.

The SRP concentrations showed a significant nonlinear temporal trend following rewetting ($\chi^2 = 26.7$, $df = 4$, $p < 0.001$), with most sites following a similar pattern over the first five years (Fig. 7). SRP levels generally increased post-rewetting, peaking within 3–5 years, before gradually declining. Despite site-specific differences ($\chi^2 = 24.75$, $df = 4$, $p < 0.001$), Menzlin consistently showed the highest SRP values (peaking above 10 mg L^{-1}) and an earlier peak compared to the other fens.

After peak concentrations, SRP declined by $3\text{--}6 \text{ mg L}^{-1}$ over the following five years, except at Jargelin Rand and Zarnekow. Jargelin Rand exhibited low interannual variability but lacked early post-rewetting data. By 8–22 years after rewetting, SRP levels had stabilized between $3\text{--}5 \text{ mg L}^{-1}$ at all sites. Wendewiese Nord showed the steepest decline, from 7.3 mg L^{-1} (year 4) to 1.2 mg L^{-1} (year 15). Zarnekow maintained the lowest and most stable SRP concentrations, peaking at 2.9 mg L^{-1} around year three and decreasing gradually for another three years thereafter.

Overall, SRP levels across the rewetted fens remained elevated

compared to natural peatlands, with stabilization typically occurring 10–15 years post-rewetting.

4. Discussion

This study, encompassing 64 natural and rewetted peatlands, shows that rewetting fens leads to increased concentrations of dissolved solutes, including P, N, and C, whereas changes in bogs were minimal, with only SRP showing a significant increase (Table 2). This aligns with previous findings (Schoumans, 2015; Lundin et al., 2017; Menberu et al., 2017; Gaffney et al., 2018; Vroom et al., 2020; Florea et al., 2024; van der Laan et al., 2024). However, data on rewetted bogs remain limited, both in this study and in the literature. Reported SRP concentrations in rewetted bogs from comparable climatic zones (Cfa, Cfb, Cfc, Dfb) range from 0.01 to 1.1 mg L⁻¹, consistent with our results (Urbanová et al., 2011; Wertebach et al., 2014; Gaffney et al., 2018; Hjelm, 2021; Howson et al., 2021; Nachtigall and Giani, 2022). Although sampling methods differ, the influence of technique and depth on porewater chemistry remains unclear. Bogs may recover more rapidly post-rewetting, likely due to lower P accumulation compared to nutrient-rich, calcareous fens (Frank et al., 2014; Säurich et al., 2019). The distinct hydrological and nutrient regimes of bogs and fens explain their differing responses to rewetting, with fens typically undergoing more pronounced changes (Jauhainen et al., 2002; Maltby and Barker, 2009). Eventually, P remobilization during rewetting can elevate the risk of downstream eutrophication, depending on site-specific chemical characteristics and hydrological connectivity (Zak et al., 2010).

4.1. Porewater chemistry in natural and rewetted peatlands

Natural bogs and poor fens showed similar porewater chemistry, despite differing water sources: rainwater in bogs and groundwater in fens (Wheeler and Proctor, 2000). This similarity likely reflects the sampling focus in poor fens on central zones dominated by *Sphagnum* and other bog-associated species (Table 2), where water has undergone natural purification along the hydrological gradient. In contrast, fen margins are more influenced by groundwater inflow, dense vegetation, and nutrient-rich litter, typically supporting species like *Phragmites australis*, which indicate more eutrophic conditions (Rydin et al., 1999). Rich fens, particularly those that have been rewetted, exhibited greater variability in porewater chemistry (Fig. 2). Rewetted fens with heavily decomposed surface peat, resulting from long-term drainage and agricultural use, showed significantly elevated concentrations of SRP and NH₄⁺-N – sometimes 10 to 100 times higher than those in natural peatlands. Less degraded fens, however, were more similar to their natural counterparts. The degree of peat decomposition, which depends on the duration and intensity of past drainage, plays a key role in nutrient release (Klimkowska et al., 2019; Kreyling et al., 2021). Field studies alone cannot fully explain the causes of these elevated solute concentrations, nor can they predict how long such effects will persist or their potential impact on nearby water bodies. This uncertainty arises from the complexity of interacting factors, including temperature, hydrology, microbial processes, and plant dynamics (Maltby and Barker, 2009). Despite the limitation of field data interpretation, the following processes and drivers are relevant to substance release in rewetted fens based on current understanding:

1. Elevated Fe concentrations in heavily degraded rewetted fens indicate that P release is primarily due to the reductive dissolution of redox-sensitive Fe(III) compounds and the P bound to them (Kjaergaard et al., 2012; Emsens et al., 2016; Kaila et al., 2016; Florea et al., 2024). Additionally, P may be released through the ongoing decomposition of particulate organic matter via hydrolysis or fermentation (Turner et al., 2003).
2. The highest porewater P concentrations in rewetted fens are typically found at the peat surface, where decomposition is most advanced

(Liu and Lennartz, 2015; McCarter et al., 2020). Elevated levels of NH₄⁺-N in the porewater further suggest increased release of substances by microbial processes. The higher P and N release in rewetted fens with highly decomposed peat compared to natural fens may be due to: (a) greater organic matter availability within the decomposed peat layer (McCarter et al., 2020; Arsenault et al., 2024), possibly fueled by root residuals from former grassland use (Hahn-Schöfl et al., 2011), (b) higher availability of oxidizing substances like SO₄²⁻ or Fe(III) oxyhydroxides for microbial redox processes (Zak and Gelbrecht, 2007; de Jong et al., 2020), (c) high levels of redox-sensitive Fe-P compounds, resulting from previous peat mineralization and P fertilization, which release P and other substances under reducing conditions (Florea et al., 2024), and (d) the absence of microbial inhibitors (Xiong et al., 2023).

3. The high DOC concentrations, reaching up to 200 mg L⁻¹, are similar to P and NH₄⁺-N, associated with increased release from decomposed peat at the soil surface (Zak and Gelbrecht, 2007). It is likely that a significant portion of this DOC originates from the reductive dissolution of Fe(III)-bound organic C (Riedel et al., 2013). However, the relative importance of this and other contributing processes requires further investigation.
4. High SO₄²⁻ concentrations, particularly during the initial phases of fen rewetting, originate from the oxidation of organic S forms and Fe sulfides like pyrite during drainage (Vermaat et al., 2016). At calcareous sites, SO₄²⁻ may accumulate as gypsum, which re-dissolves after rewetting (Litaor et al., 2004), causing higher SO₄²⁻ and Ca²⁺ concentrations (Table 2). Unlike fens with calcareous catchments where pyrite oxidation has led to extremely high SO₄²⁻ concentrations (van Dijk et al., 2004), the calcareous fens of the young glacial northeastern German lowlands did not experience acidification due to sufficient carbonate buffering. This contrasts with fens in older glacial landscapes, such as the southern part of the Lusatian region (last glaciation > 100,000 years ago), where carbonate depletion has made them more susceptible to acidification (Roessel and Zak, 2022).
5. Anaerobic SO₄²⁻ decomposition and hydrogen sulfide formation can increase P mobilization through reductive dissolution of Fe(III)-bound P (Lamers et al., 2012). However, high SO₄²⁻ concentrations do not always correlate with high P release; it depends on the abundance of redox-sensitive P-binding forms and the availability of organic substances as electron donors. In some SO₄²⁻-rich fens (> 200 mg L⁻¹), SRP concentrations remained low (< 0.1 mg L⁻¹), comparable to those in natural fens.

Overall, we found that SRP concentrations were positively associated with mobilization rates across the investigated sites. The greatest P mobilization occurred in the upper highly decomposed peat layer (Fig. 3), which is usually only two or three decimeters thick and rich in "redox-sensitive P" or P mobilization potential (Zak et al., 2008). Over time, rewetting has led to even higher P mobilization rates in the newly formed mud layer (Zak et al., 2018), a factor not fully accounted for in our profile calculations. This mud layer, typically only a few centimeters thick, lies above the decomposed peat at the inundated study sites and contains a large proportion of redox-sensitive P and fresh or more labile organic P forms (data not shown, but see (Cabezas et al., 2014). The 4 cm vertical resolution used in our analysis was insufficient to capture nutrient release from the newly formed active soil layer. A finer resolution of 1 cm or less is recommended for better calculation of nutrient mobilization, as demonstrated in previous studies on peat cores from rewetted fen peatlands (Zak et al., 2010).

4.2. The influence of peat properties on porewater phosphorus

The peat Fe content pool in the upper layer of rewetted fens significantly impacts P mobilization to porewater (Table 3). A large pool of Fe(III) hydroxides in the peat prevents mass P mobilization by providing sorption surfaces and forming redox-sensitive Fe-P compounds,

resulting in a moderately negative correlation between peat Fe content and P concentrations in porewater (Fig. 5). In the case of human-induced rewetting, water levels rarely remain stable throughout the year. Even rewetted fens, though frequently inundated, can desiccate during prolonged summer droughts, leading to topsoil aeration (Zerbe et al., 2013; Negassa et al., 2020). These fluctuating redox conditions shifting Fe between the ferric (Fe(III)) and ferrous (Fe(II)) state are crucial for C and nutrient cycling, as labile organic matter acts as an electron donor in the microbe-mediated Fe-reduction reactions (Negassa et al., 2020). Large pools of Fe(III) oxides in the upper peat layers of drained fens can hinder the restoration of the fen's ability to store nutrients and C after rewetting (Zak et al., 2004; Kjaergaard et al., 2012). Raised water levels in rewetted fens induce reducing conditions, generating Fe(II) and releasing P bound to these compounds. Net P mobilization depends on the residual sorption capacity (Florea et al., 2024), i.e. the availability of P-binding partners that remain unsaturated. As indicated by the selected Model 1, P concentrations are depending on Fe content, Al content, and pH (Table 4). Menzlin, a Fe-poor fen with relatively low Al content (ca. 4 mg g⁻¹ DM) and a pH range of 6.3–6.7, exhibited substantially higher SRP concentrations, on average, three times higher than those in other rewetted fens (Fig. 7). Moreover, a strong negative correlation ($p < 0.001$) was observed between pH and SRP. Inorganic P forms bind strongly to Fe and Al at pH values around 6, a process relevant for fens (Lijklema, 1980). When pH drops below 4, Fe-P and Al-P compounds dissolve, increasing P availability. On the other hand, rewetting of peatlands shifts porewater pH towards neutrality, decreasing P fixation due to deprotonation of chemical functional groups (Lamers et al., 2002). However, a higher pH (> 6–7) also promotes the precipitation of P minerals such as vivianite (Fe₃[PO₄]₂·8H₂O) or different calcium phosphates, thereby reducing P concentrations in the porewater (Florea et al., 2024).

4.3. Seasonal variation of P concentration and change over the rewetting years

Porewater chemistry in peatlands is the result of complex interactions among hydrological, geochemical, and biological processes (Griffiths and Sebestyen, 2016), all of which vary across space and time. Seasonal fluctuations in the water table, along with associated changes in oxygen dynamics, further influence porewater composition by controlling the mobility of elements such as S, N, and P released during organic matter mineralization (Albert-Saiz et al., 2025; Frank et al., 2014). Several interacting factors such as temperature changes, plant growth cycles, microbial activity, watershed hydrology, and P availability together cause seasonal variability of P within peatlands (Griffiths et al., 2019). For example, study sites with dense helophyte stands, such as Jargelin Rand and Menzlin, exhibited high P uptake from porewater during peak summer growth, up to 30 kg P ha⁻¹ (Zak et al., 2014). This corresponded with a noticeable decline in porewater P concentrations, a pattern not observed at Beestland and Zarnekow, which were not colonized by helophytes at the time of sampling (Fig. 4). In fall and winter, decreased biological demand and plant die-off lead to higher P concentrations in the porewater (Walton et al., 2020). On the other hand, heavy rainfall and high inflow of ground- and surface water from adjacent rivers dilute dissolved solutes in the porewater (Palihakkara et al., 2025). The concentration of P in ditches of the rewetted fen exhibit similar seasonal variations, corresponding with water table level fluctuations (Niedermeier and Robinson, 2009). Higher temperatures combined with increased C availability during the summer have led to significant seasonal shifts in the community composition of eukaryotes (fungi, protists, and microbial metazoa) in rewetted fens (Wang et al., 2021). These shifts can influence porewater chemistry via accelerated decomposition processes (Reuter et al., 2024). Additionally, nutrient uptake by dominant vegetation, including helophytes versus hydrophytes (Steffenhagen et al., 2012), and oxygen transport through plant root aerenchyma also affect local porewater chemistry (Zhou et al.,

2024).

In addition to seasonal dynamics, the effect of time since rewetting on P concentrations in rewetted fens remains uncertain. Is a decline after just a few years to be expected, or is a timescale of decades more realistic, as suggested by Kreyling et al. (2021). It is likely that processes controlling the P concentration in porewater of rewetted fens may change significantly. The rate of P release into porewater following rewetting of peatlands is influenced by interconnected abiotic and biotic factors, including moisture levels, porosity, peat decomposition, hydraulic conductivity, temperature, mineral-rich water inflow, microbial activity, and chemical soil characteristics (Tiemeyer et al., 2005; Florea et al., 2024). In the early years after rewetting, high decomposition and lowered porosity of upper peat layers affect water saturation and movement, promoting Fe(III)-oxide reduction and intense P release. Decomposition and temperature further influence microbial activity, accelerating organic matter breakdown and P release.

Phosphorus release typically peaks when pore spaces are fully saturated, releasing trapped P from all pores. Differences in peak SRP release times (from 2–5 years, as shown in Fig. 6) reflect the varying times required for complete pore saturation and establishment of steady state redox conditions across sites. The subsequent decline in SRP concentrations may result from recolonization by dense vegetation stands following a stage dominated by hydrophytes (Zerbe et al., 2013), as rooted plants absorb and store P in newly forming peat (Schwieger et al., 2022). In our study, the oldest rewetted sites clustered with natural peatlands, indicating a recovery of “natural-like” water chemistry over time.

In Jargelin Rand, SRP concentrations fluctuated slightly over the monitored rewetting period, similar to Zarnekow after P concentrations peaked in the third year. Processes of Fe reduction, P resorption, and other P linked processes have stabilized or reached steady states, respectively, compared to other fens (Fig. 7). Previous studies indicate that Fe-rich fens may exhibit lower SRP concentrations in porewater. However, a decline of SRP concentrations may take longer in Fe-rich fens than in Fe-poor fens (Emsens et al., 2016) due to the initially larger mobile P pools and the ongoing “eternal iron wheel” cycle of P trapping and re-dissolution during its gradual release (Emerson et al., 2012).

4.4. Implications for peatland restoration from the vegetation perspective

Nitrogen can be the primary limiting factor for plant growth in the early stages following rewetting. However, over time, P may become limiting, and in some cases, co-limitation by both N and P, as well as potassium, may occur (Emsens et al., 2017).

Elevated porewater nutrient concentrations, particularly of SRP and NH₄⁺-N, indicate increased nutrient availability for plants. However, the effects of these nutrient levels on plant uptake and vegetation composition can vary substantially across species and wetland types (Bedford et al., 1999). Despite these variations, consistent evidence shows that plant biomass production tends to be substantially higher in rewetted peatlands compared to their near-natural or pristine counterparts (Walton et al., 2020). In such nutrient-rich environments, fast-growing, nutrient-tolerant species often dominate, while native peat-forming species, such as *brown* mosses and sedges, may be absent for years or even decades after rewetting (Kreyling et al., 2021).

Furthermore, high nutrient levels can alter the chemical composition of plant tissues, including changes in the concentration and quality of polyphenolics – compounds that inhibit microbial enzymes (Zak et al., 2019). These shifts can influence the decomposability of plant litter and, consequently, affect C sequestration and greenhouse gas emissions in rewetted peatlands (Zak et al., 2015).

The trajectory of vegetation recovery is governed not only by nutrient availability but also by broader physicochemical conditions. These include hydrological changes, altered redox conditions, and the frequent absence or degradation of viable seed banks at formerly

drained sites (Baumane et al., 2021).

Taken together, these factors underscore the importance of detailed assessments of porewater chemistry in combination with hydrological and ecological monitoring. An integrated understanding is crucial for predicting vegetation dynamics, managing nutrient retention, and minimizing nutrient losses in rewetted agricultural peatlands. It is also essential for assessing C cycling and associated greenhouse gas fluxes across different stages of vegetation transition following rewetting (Antonijević et al., 2025).

To accelerate re-oligotrophication of rewetted peatlands, ongoing management interventions such as plant harvesting or removal of nutrient-enriched topsoil may be necessary. However, this approach is controversial due to its costs, energy consumption, and potential climate impact if degraded peat is exposed to oxic conditions and continues to mineralize. These effects, however, have not yet been investigated in detail (Zak et al., 2022).

5. Conclusions

Based on the analysis of spatial and temporal variability in porewater chemistry across 64 different degraded bogs and fens, several general conclusions can be drawn regarding nutrient release in rewetted peatlands:

- 1) Influence of peatland type and rewetting: The porewater chemistry of natural bogs and poor fens, unlike that of rich fens, showed little variation across the surveyed sample sites. The most pronounced differences in porewater chemistry are observed between rewetted rich fens and their natural counterparts. Rewetting of highly decomposed topsoil layers, resulting from previous drainage and intensive land use, often leads to elevated nutrient and DOC concentrations in the upper soil layers.
- 2) P release mechanisms: Elevated P concentrations in porewater of rewetted fens are primarily linked to reductive dissolution of Fe(III) oxyhydroxides. However, peatlands with high Fe/P ratios or significant Al content tend to exhibit comparatively lower porewater SRP concentrations.
- 3) Seasonal variability and long-term trends: Porewater P concentrations fluctuate seasonally, with lower concentrations during the growing season in rewetted fens colonized by dense stands of helophytes such as *Typha latifolia* due either to nutrient uptake or oxygen release and concomitant precipitation of Fe(III)-P compounds in the rhizosphere. Phosphorus concentrations in rewetted fens tend to decline by up to three-fold over 5 to 10 years after rewetting. However, natural baseline levels are unlikely to be reached within 20 years – or even longer – without additional human intervention. The decline rate is faster in peatlands with relatively low Fe content compared to P.

Our findings provide important insights into the biogeochemical processes driving nutrient dynamics in rewetted peatlands and highlight the long-term challenges of restoring these ecosystems to their natural states. This includes the recolonization of lost peatland vegetation adapted to nutrient-poor conditions like brow mosses, low sedges, and adapted endangered animal species (Fraixedas et al., 2017).

CRedit authorship contribution statement

Nimisha Krishnankutty: Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Jörg Gelbrecht:** Writing – review & editing. **Rasmus Jes Petersen:** Writing – review & editing, Software, Formal analysis. **Dylan Rayner:** Writing – review & editing, Conceptualization. **Maximilian P. Lau:** Writing – review & editing, Methodology, Investigation. **Stefan Frank:** Writing – review & editing, Methodology, Investigation. **Roxane Andersen:** Writing – review & editing, Methodology, Investigation. **Jaan Pärn:**

Writing – review & editing, Methodology, Investigation. **Ülo Mander:** Writing – review & editing, Methodology, Investigation. **Wiktor Kotowski:** Writing – review & editing, Methodology, Investigation. **Haojie Liu:** Writing – review & editing, Methodology, Investigation. **Bo V. Iversen:** Writing – review & editing, Conceptualization. **Goswin Heckrath:** Writing – review & editing, Conceptualization. **Hans C.B. Hansen:** Writing – review & editing, Conceptualization. **Carl C. Hoffmann:** Writing – review & editing. **Maarit I. Mäenpää:** Writing – review & editing, Validation, Formal analysis. **Tobias Goldhammer:** Writing – review & editing, Methodology, Investigation. **Ain Kull:** Writing – review & editing, Methodology, Investigation. **Adrian-Florin Florea:** Writing – review & editing, Conceptualization. **Dominik Zak:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2025.117554>.

Data availability

Data will be made available on request.

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