RESTORATION ECOLOGY
The Journal of the Society for Ecological Restoration

SER SOCIETY FOR ECOLOGICAL RESTORATION

RESEARCH ARTICLE

Effects of riparian wetland restoration and grazing on CH_4 and CO_2 exchange more than a decade after rewetting

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Abstract

Introduction: Riparian wetlands provide several important ecosystem services, including carbon sequestration. Drained and degraded wetlands act as carbon sources, but rewetting might result in elevated methane (CH_4) emissions and does not always reestablish a carbon sink.

Objectives: This study examines the impacts of riparian wetland restoration and disturbance regime (grazing vs. no grazing) on CH_4 and CO_2 exchanges in wetlands 12–17 years post-restoration.

Methods: Greenhouse gas fluxes were measured using a static chamber at monthly intervals over a year to assess the effects of disturbance regime, groundwater level, and soil temperature on CH_4 and CO_2 exchange.

Results: Our results show no significant differences in CH_4 emissions between restored and near-natural sites. We demonstrate that grazed sites, both near-natural and restored, are net carbon sinks, while ungrazed sites are carbon sources. However, we did not capture the production from shrubs and trees which were abundant at near-natural ungrazed sites and would be expected to act as carbon sinks.

Conclusion: Our results suggest that ecosystem functioning with respect to carbon cycling was reestablished post-restoration, but that ecosystem function of the restored areas was contingent on the prevalent disturbance regime.

Implications for Practice: Wetland restoration aims at changing greenhouse gas (GHG) emission by altering the carbon cycling to a state similar to natural conditions. Grazing regime, affecting the vegetation trajectory toward open or wooded conditions, might affect carbon cycling and thereby the restoration outcome. Restored and near-natural sites with grazing had similar carbon cycling, implying that carbon cycling can be reestablished by restoration, although restoration might not restore all ecosystem properties (e.g. biodiversity and hydrology). Ungrazed sites showed higher GHG emissions, but studies assessing the carbon cycling in wooded wetlands, allowing for a separation of fluxes from woody vegetation, grazing animals, and herb layers, are needed to fully evaluate the consequences of the vegetation trajectory.

Key words: carbon cycling, ecosystem function, hydrology, methane, riparian wetlands, wetland restoration

Introduction

Wetlands are essential parts of natural landscapes and the habitat of a significant share of biodiversity. In addition, they provide a diverse array of ecosystem services such as carbon storage, flood control, and water purification. However, intensified human land use, especially drainage, has significantly impacted these environments, ranging from severe degradation and fragmentation to complete destruction (Fluet-Chouinard et al. 2023).

Throughout Europe, including Denmark, extensive drainage has been undertaken to convert wetlands to agricultural land during the last 200 years (Hughes 1995). These efforts included channeling rivers, digging ditches, and installing drainpipes to enhance run-off and lower the water table (Hoffmann & Baattrup-Pedersen 2007). Intact wetland soils are generally rich in organic carbon accumulated under anoxic conditions over hundreds to thousands of years. When wetlands are drained,

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Author contributions: MB, SJ, KS-J, HHB, JEK, LB-S conceived the study; JEK, MB, FF, KTM, TS, AKN, MERH collected the data: JEK, MB, AKN, MERH performed formal analysis; KTM designed the analysis software; JEK visualized data; JEK and LB-S drafted the manuscript; all authors revised it; KS-J, LB-S secured funding; JEK, MB share first-authorship.

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doi: 10.1111/rec.70185
Supporting information at:
http://onlinelibrary.wiley.com/doi/10.1111/rec.70185/suppinfo

oxygen availability increases and soil organic matter oxidizes, resulting in high CO_2 emissions (Mitsch & Gosselink 2015).

In recent decades, large funds have been allocated to wetland restoration; in Denmark alone, more than 200 wetlands with a total area approximately 13,000 ha have been restored under the Action Plans for the Aquatic Environment (Danish Environmental Portal 2025). These restoration projects often involved re-meandering rivers and removing drainage infrastructure, usually resulting in a raised water table. The aim was to reduce pollution to the aquatic environment from agriculture by promoting denitrification and phosphorus retention. Enhancing biodiversity was of secondary priority in the projects, effectively assumed to come along as a by-product (Baumane et al. 2021). Now the focus of wetland restoration in Denmark has shifted toward carbon sequestration and rainwater retention. Our overall aim was to investigate how the ecosystem functioning with regard to carbon cycling has developed in previously restored riparian wetlands.

When drained organic soils are rewetted, CO_2 emissions are significantly reduced due to rapidly declining oxidation (Nugent et al. 2019). However, the shift to predominantly anoxic conditions promotes the activity of methanogenic archaea, resulting in methane (CH_4) release. CH_4 is a potent greenhouse gas (GHG), with a global warming potential (GWP) 28–32 times greater than CO_2 on a 100-year timescale (Myhre et al. 2013; Etminan et al. 2016). Recently, modeling efforts by Günther et al. (2020) showed that despite higher radiative forcing from CH_4, rewetting sooner rather than later reduces the emission of GHGs overall and the radiative forcing as well, because of the short atmospheric lifetime of CH_4 (Myhre et al. 2013). Although CH_4 emissions should be reduced if possible, sustained CO_2 emissions from drained wetlands are much more harmful to the climate.

The main drivers of CH_4 fluxes from wetlands are the inundation regime, water table depth, and soil temperature (Tiemeyer et al. 2020; Koch et al. 2023). Other soil variables such as pH, oxidation status, and the magnitude and quality of organic matter, as well as vegetation composition, may also affect CH_4 emissions (Dias et al. 2010; Mitsch & Gosselink 2015). CH_4 can be emitted by diffusion and ebullition from the soil and stagnant surface water, and through root and stem aerenchyma, which is often well-developed in wetland plants (Baastrup-Spohr et al. 2015; Vroom et al. 2022). CH_4 release by ebullition and plant aerenchyma bypasses possible oxidation in upper soil and water layers and can constitute a substantial proportion of the total CH_4 flux (Sø et al. 2024).

The effect of rewetting on carbon cycling might change depending on the time frame in which it is observed. Several studies have shown that CH_4 spikes can occur in the years following rewetting, possibly due to widespread anoxia and die-back of vegetation after flooding, providing easily degradable organic material (Hahn-Schöfl et al. 2011; Hahn et al. 2015). Longer-term studies find contrasting results, ranging from gradual change from carbon source to sink and decreasing CH_4 emissions; while others find persistently high CH_4 emissions even decades after rewetting (Vanselow-Algan et al. 2015; Kalhori et al. 2024).

The disturbance regime may influence carbon cycling and GHG emissions in restored wetlands. In ungrazed wetlands, scrub encroachment and eventual development of swamp forest are part of the natural succession (Brunbjerg et al. 2022) and may result in substantial above- and belowground carbon stocks. An alternative successional trajectory is the development of reed beds and other tall-herb communities (Baumane et al. 2021). In grazed wetlands, low-growing meadows makeup a larger share of the plant cover, but often in mosaic with scrub and reeds. Traditional wetland use in northern Europe includes livestock grazing, haymaking, or both, along with cutting wood and reed and removing the cut biomass for firewood and roof thatch. Some research has indicated that grazing may increase carbon sequestration (Ward et al. 2007; Gomez-Casanovas et al. 2018; Schmitz et al. 2023) but we are far from a firm evidence base that includes data on animal density and comparative data on meadows, scrub, and reed beds. Grazing by large mammals, which is known to promote plant diversity by counteracting dominance by competitive species, may be considered a natural disturbance in most wetland systems (Fløjgaard et al. 2022). The influence of grazing on CH_4 emission is unclear, with studies showing either an increase or no effect at all (Gomez-Casanovas et al. 2018; DeLucia et al. 2019). However, tall herbs, such as *Typha* and *Phragmites*, which are limited by grazing, are expected to be associated with enhanced CH_4 emission through stem aerenchyma (Askaer et al. 2011). Another management strategy involves cutting and leaving the biomass to mulch, which can lead to both net release of CH_4 and CO_2 and also lower biodiversity (Kandel et al. 2019).

There is a scarcity of studies comparing restored and pristine riparian wetlands under different land disturbance regimes, as most studies compare farmland on drained wetland soils with only one restoration type. Our study aimed to compare ecosystem functions in terms of water level and carbon cycling (measured as CH_4 and CO_2 exchange with the atmosphere) between grazed riparian wetlands restored 12–17 years ago, similarly aged ungrazed wetlands, and near-natural wetlands. As few, if any, pristine wetlands are left in Denmark, we use the term "near-natural" to describe conditions with limited human alteration of hydrology and biota within the sites.

Studying the soil and herb layer using static chamber GHG measurements, we investigated two questions: (1) Is the carbon cycling in restored wetlands altered in comparison with near-natural counterparts? And (2) how is carbon cycling affected by different disturbance regimes (grazing vs. no grazing)?

Methods

Experimental Design and Site Descriptions

We conducted a factorial crossed design with four distinct riparian wetland types investigated in each of three river valleys across Denmark. The four wetland types were: restored grazed, near-natural grazed, restored ungrazed, and near-natural ungrazed (Fig. 1). The wetlands were in Jutland at river Omme, Funen at river Odense, and Zealand at river Tryggevælde (Fig. 1; Table S1). The river catchments are characterized by

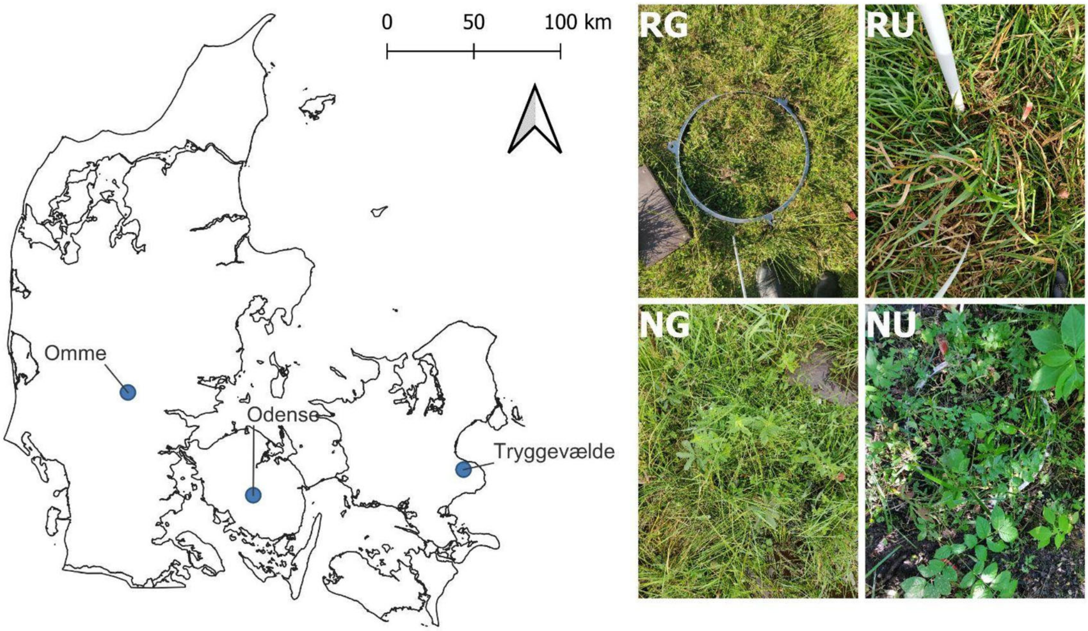

Figure 1. Map indicating the three catchment areas: Omme, Odense, and Tryggevælde, and example photographs of plots from restored grazed (RG), restored ungrazed (RU), near-natural grazed (NG), and near-natural ungrazed (NU) sites.

different geologies, with sandy soil prevalent in Omme and clay-calcareous soils in Odense and Tryggevælde (Baumane et al. 2025). The restorations were initiated between 12 and 17 years ago (mean 15 years) and involved removal of drainage pipes, re-meandering, and raising of the stream bed. We demarcated six circular plots of 0.33 m^2 at each of the 12 sites (72 in total). The plots at each site were located to reflect the variation in vegetation and elevation within the site. Management was grazing (<0.5 livestock units/ha) from either May to October or the whole year (restored grazed, Omme) or no management, except restored ungrazed, Odense, which was cut in dry years, and in restored grazed, Tryggevælde, which was grazed until autumn 2021 and cut in summer 2022 (Table S1). The sites generally showed large variation in bulk density and organic carbon content (OC) both within and between sites (Table 1). The dominant vegetation type in near-natural grazed sites was rich fen, while species-rich willow scrub was prevalent in the near-natural ungrazed sites. In restored grazed wetlands, the vegetation mainly consisted of short stoloniferous grasses, e.g. *Agrostis stolonifera* and *Alopecurus geniculatus*, whereas restored ungrazed sites were dominated by tall graminoids, e.g. *Phalaris arundinacea* and *Phragmites australis*.

Fluxes of CH_4 and CO_2

We measured fluxes of CH_4 and CO_2 monthly from April 2022 to March 2023 (May 2022 to April 2023 for CH_4 measurements in Tryggevælde sites). While fluxes of CO_2 are primarily diffusive, emissions of CH_4 can occur as both diffusive and ebullitive (bubble) fluxes. The design of the current study with monthly flux measurements of short duration is not suitable for quantification of the often-erratic ebullitive CH_4 fluxes (Ramirez et al. 2017) and if observed, these were discarded (see below). We measured fluxes of CH_4 and CO_2 using a closed transparent chamber (height: 80 cm, ⌀: 63 cm) equipped with a fan, temperature sensor, and relative humidity sensor. To measure CH_4, air in the chamber headspace was circulated through a Los Gatos Ultraportable CH_4 analyzer (M-GPC-918, ABB, Sweden/Switzerland) through ¼″ (outer ⌀) polyvinyl chloride tubing. While the analyzer is also capable of measuring CO_2, we experienced that CH_4 cross-interfered with the CO_2 measurements and opted to measure CO_2 separately with a Senseair K30 FR CO_2 sensor (Senseair, Sweden) mounted inside the chamber, as previously done in floating chambers on lakes (Bastviken et al. 2015). During measurements, a rubber seal was placed on the chamber's collar to ensure an air-tight seal. The collars were pre-installed in summer and autumn 2021 and consisted of a circular aluminum collar with a flat outer edge for placement of the flux chamber (inner ⌀: 60.8 cm, area 0.3 m^2). Boardwalks were installed close to the collars, and during GHG measurements, field personnel moved as gently as possible around them to avoid provoking mass transport and CH_4 ebullition. In the case of ebullition visible as a sudden, steep concentration increase in the trace on the CH_4 analyzer, we repeated the measurement whenever possible. To avoid overpressure, the chamber was fitted with a small vent (inner ⌀: 3 mm) to equalize the headspace pressure with the surrounding atmosphere. We randomized the visit order to the different sites to account for different light conditions and hours of measurement. The average time of day for measurements varied between 12.30 and 14.00 hours for the different sites. Measurements were performed in daylight and always after 8:00 hours and

Table 1. Soil characteristics and groundwater chemistry of the investigated sites. Mean values ± 95% CI. BD, dry bulk density; G, grazed; N, near-natural; OC, organic carbon; OD, Odense; OM, Omme; R, restored; TR, tryggevælde; U, ungrazed.

Site	*BD (g/cm^3)*	*$CaCO_3$ (%)*	*NO_3 (mg/L)*	*OC (%)*	*pH*	*PO_4 (mg/L)*
ODNG	0.82 ± 0.37	21.13 ± 30.21	0.09 ± 0.20	5.60 ± 3.90	7.50 ± 1.50	0.04 ± 0.05
ODNU	0.46 ± 0.22	17.27 ± 17.61	1.01 ± 1.78	13.26 ± 7.76	7.34 ± 1.01	0.19 ± 0.13
ODRG	0.74 ± 0.36	4.79 ± 8.36	2.14 ± 2.57	17.09 ± 8.80	5.39 ± 0.36	3.70 ± 2.05
ODRU	0.77 ± 0.23	3.78 ± 2.41	0.41 ± 0.21	10.78 ± 3.64	7.20 ± 0.64	1.64 ± 0.58
OMNG	0.94 ± 0.34	1.05 ± 0.79	13.38 ± 7.88	3.94 ± 4.60	5.46 ± 0.42	0.45 ± 0.23
OMNU	0.83 ± 0.69	1.61 ± 2.28	40.11 ± 7.24	6.94 ± 6.06	5.39 ± 0.46	0.01 ± 0.01
OMRG	1.15 ± 0.45	0.96 ± 0.60	2.72 ± 4.65	3.91 ± 5.31	5.20 ± 0.20	3.01 ± 0.87
OMRU	1.31 ± 0.29	0.51 ± 0.19	0.34 ± 0.20	2.23 ± 1.62	5.38 ± 0.76	3.11 ± 0.56
TRNG	0.24 ± 0.05	3.33 ± 2.16	9.02 ± 16.84	32.57 ± 4.44	6.38 ± 0.51	0.83 ± 0.28
TRNU	0.20 ± 0.12	4.68 ± 3.32	3.55 ± 2.81	32.85 ± 8.03	6.46 ± 0.86	0.23 ± 0.08
TRRG	1.02 ± 0.25	3.65 ± 2.20	0.37 ± 0.62	5.05 ± 1.98	7.18 ± 0.39	0.09 ± 0.06
TRRU	1.32 ± 0.25	7.76 ± 4.39	6.45 ± 14.02	3.19 ± 1.45	7.26 ± 0.44	0.00 ± 0.32

before 19:00 hours. There were a few instances (January 2023: all plots in restored managed, Odense two plots in near-natural ungrazed, Odense. February 2023: three plots in restored grazed, Odenes) of excessive flooding (>30 cm) during winter, preventing GHG measurements with the used chamber. The plots were not fenced off or restricted in other ways, meaning that cattle were free to graze inside the installed collars.

At the monthly measurement campaigns, the GHG flux from each plot was measured twice, once in light and once in darkness. Each measurement cycle lasted 180–300 seconds and first measurement always started with measuring of CH_4 and CO_2 under ambient light conditions (net ecosystem exchange [NEE]). Following the measurement in daylight, the chamber air was vented until GHG concentrations had returned to atmospheric background levels, at least 30 seconds later. We then covered the chamber using a thick, black polyester fabric cover and measured CH_4 and CO_2 in darkness (ecosystem respiration, R_{eco}), thereby conducting the second GHG measurements of the plot at the given measurement campaign.

The slope of CH_4 and CO_2 concentration change over time was calculated by linear regression, where a representative greater than 30 seconds period was selected based on a visual assessment. Fluxes were calculated as:

$$F(t) = \frac{\Delta C}{\Delta t} \frac{VP}{RK} \frac{1}{A} \qquad (1)$$

where $\Delta C/\Delta t$ is the concentration change of the gas (dry fraction) over time in seconds, V is the volume of the chamber (L), P is pressure (atm), R is the universal gas constant (L atm K^{-1} mol^{-1}), K is the average chamber temperature during measurement (in ^oK) and A is the footprint of the chamber (m^2). To indicate the direction of CH_4 and NEE and R_{eco} fluxes, we used the atmospheric science sign convention: negative values indicate an uptake by the ecosystem, and positive emission to the atmosphere. Note that for gross primary production (GPP) values are reported as positive and thus not following the atmospheric sign convention. This approach was chosen for clarity, as positive values more intuitively reflect production, with higher values corresponding to greater production.

Ancillary Measurements

To monitor the groundwater level, shallow wells were installed 10–20 cm from each collar used for GHG measurements. The exceptions were the restored ungrazed at Tryggevælde, where only one well was installed, as well as near-natural grazed and restored ungrazed at Odense, which each missed one well. The wells consisted of a 1 m polyethylene tube with a diameter of 54.6 mm (outer) and 50 mm (inner), along with a 30 cm screen placed 0.5–0.8 m belowground level. These wells were installed using a casing with a 10 cm diameter (Hand bailer auger set, Eijkelkamp 01.12.SA, The Netherlands), and gravel-packed with 0.9–1.6 mm quartz sand (per EN12904) and they were sealed with bentonite-cement from the scree's top to the soil surface. The groundwater level was measured with a water level meter (Solinst 101 P2, Georgetown, Canada) each time we measured GHGs. Negative values correspond to a groundwater level below the soil surface, while positive values indicate inundation. We measured soil temperature using a digital thermometer at a 5 cm depth, and soil moisture using a handheld soil moisture meter (SM150 Soil Moisture Kit, Delta-T Devices Ltd., Cambridge, U.K.). We took four temperature and moisture measurements per plot, each 10 cm from the inside of the collar in the four cardinal directions, and used the mean value in further analysis.

Groundwater chemistry sampling was performed by clean pumping the wells by three times its volume, using a peristaltic pump. The water samples were collected approximately every third month, starting in autumn 2022 and ending in autumn 2023. A PE syringe was used to collect water, which was then filtered (Sartorius Minisart CA, 0.20 µm, Göttingen, Germany) into polypropylene vials. For nitrate (NO_3^-), 9 mL samples were conserved by freezing until they were analyzed using ion chromatography (930 Compact IC Flex, Short column METROSEP A Supp 19-100/4.0, Metrohm AG, Herisau, Switzerland). Three milliliters of water were collected for the phosphate

(PO_4^{3-}) sampling and preserved in-field with 0.12 mL 1 M sulfuric acid (H_2SO_4). The samples were stored refrigerated until spectrophotometric analysis (HACH DR 2800, Loveland, CO, U.S.A.), which was conducted using the molybdenum blue method (Koroleff 1983).

Sediment cores were collected with a hand auger (Eijkelkamp, model 04.15.SB, Giesbeek, The Netherlands) and round plastic liners (Ø5 cm, length 30 cm). The sediment cores were collected once during the study period, approximately 1 m from each of the GHG observation plots. Bulk density (BD, g/cm^3), calcium carbonate ($CaCO_3$, %) and OC, % were determined through the loss on ignition (LOI) method (Heiri et al. 2001; Santisteban et al. 2004). The pH of the sediment was determined by mixing a 2 g sample with 10 mL of a 0.01 M NaCl solution. After 15 minutes mixing time, the pH was measured using a KCl-saturated glass electrode.

Data Processing and Interpolation

We recorded 1526 CH_4 fluxes (760 daylight, 766 dark). Fluxes with r^2 less than 0.7 and an apparent flux greater than $|0.001|$ μmol m^{-2} s^{-1} were discarded following visual inspection for irregularities (e.g. sudden concentration spikes), resulting in 148 removals. As light and dark measurements did not differ significantly (both averaging 0.06 μmol m^{-2} s^{-1}; Wilcoxon test, $p = 0.34$), the mean of available pairs was used, yielding 717 data points.

For CO_2, we collected 1651 fluxes (831 daylight, 820 dark). Fluxes higher than $|0.5|$ μmol m^{-2} s^{-1} with an r^2 below 0.7 were flagged; 138 were discarded due to low r^2 or visual anomalies. Additionally, in computing GPP (GPP = –NEE + R_{eco}), negative values were excluded, resulting in 549 GPP, 766 NEE, and 742 R_{eco} observations. The higher discard rate was attributed to the limited precision of the substitute K30 CO_2 sensor, especially in low-productivity and winter conditions (see Figs. S1 & S2).

Fluxes (CH_4, R_{eco}, GPP, and NEE) were converted to g m^{-2} h^{-1} and linearly interpolated to estimate hourly rates per plot. Day and night lengths, based on site latitude and calculated using the R package *geosphere*, were used to compute daily NEE (daytime NEE + nighttime R_{eco}) and GPP (daytime R_{eco} – daytime NEE). Assuming no diurnal variation for R_{eco} and CH_4, daily totals were summed to derive annual and seasonal values, with seasons defined as spring (March–May), summer (June–August), fall (September–November), and winter (December–February).

Statistical Analysis

To test the effects of restoration and disturbance regime, we fitted linear mixed models (LMMs) with soil temperature, groundwater level, and annual groundwater level amplitude as response variables, including sites nested within regions (Jutland, Funen, Zealand) as random factors. Similarly, we tested the overall effects on annual GHG fluxes (CH_4, GPP, and NEE) using LMMs that allowed interaction between disturbance (grazed/ungrazed) and restoration status (near-natural/restored) with sites nested within river valleys as random factors. Because near-natural ungrazed sites differ by not being dominated by herbaceous vegetation, we also ran GPP and NEE models excluding these sites; here, the missing combination of disturbance and restoration meant that only main effects were estimated, and to avoid overfitting, only river valley was used as a random effect.

For the environmental soil variables, we tested for correlation between bulk density and organic content using a Spearman rank correlation and tested for the effect of restoration using Mann–Whitney *U* tests.

To assess the influence of measured environmental variables on CH_4 and CO_2 fluxes, we fitted LMMs with individual (i.e. not annual) fluxes as response variables. Due to high intercorrelation between soil moisture and groundwater level (Pearson $r = 0.50$, $p < 0.001$), soil moisture was excluded. The final models for CH_4 flux, R_{eco}, and GPP included standardized (by subtracting the variable's mean and dividing it by the standard deviation) groundwater level and soil temperature as continuous predictors, status and disturbance as factors, and allowed interactions between groundwater level and soil temperature, and between status and disturbance. For CH_4, a fully nested design (plots within sites within river valleys) was used, while for R_{eco} and GPP, nesting was reduced to sites within river valleys to avoid overfitting. A separate GPP model excluding NU sites was also fitted.

To achieve homoscedasticity and a normal distribution of the residuals, we transformed the response variable in some of the models. For the annual models, we $\log_{10}$ transformed the groundwater level amplitude and CH_4 fluxes (first adding a constant to all CH_4 values, 0.294, due to negative values in the dataset). To model individual GHG fluxes, we $\log_{10}$-transformed the CH_4 fluxes (first adding a constant, 0.0012, to account for negative fluxes) and square-root transformed R_{eco}. However, for the CH_4 model, we still did not achieve a normal distribution of the residuals; therefore, we made a model using a truncated dataset, where values outside the 2.5th–97.5th percentile range were removed, producing a dataset of 674 points for analysis. Here, the data was also $\log_{10}$-transformed (with 0.0027 as an added constant). The models using the truncated dataset and the full dataset (Tables S3 & S4) yielded very similar parameter estimates and *p* values, and the more valid truncated model is presented in the results section. For GPP, we first square-root transformed the absolute values, which was followed by additive inversion.

All LMMs were fitted using the R package lme4 while using lmerTest to calculate *p* values for lme4 model outputs (Bates et al. 2015; Kuznetsova et al. 2017). We calculated estimated marginal means using the R package emmeans to perform post hoc pairwise comparisons of the categorical predictors (restoration status and disturbance regime). Tables presenting the model' results were generated using the R package sjPlot. We used a significance level (α) of 0.05 for hypothesis testing.

To investigate the temperature sensitivity of the ecosystem respiration, we fitted a non-linear model:

$$R_{eco}^{T} = a \times \exp^{T \times b} \qquad (2)$$

where R_{eco}^{T} is the ecosystem respiration at a given temperature, a and b are fitted parameters and T is the soil temperature (°C) at 5 cm depth. Q_{10} was then calculated as:

$$Q_{10} = \exp^{10 \times b} \tag{3}$$

All data analysis and graphs were made in R version 4.2.0. Variations in the reported estimates are expressed as 95% CI.

Results

Environmental Conditions

Soil temperature at 5 cm depth ranged from −0.3 to 23.0°C and was coldest in December and warmest in August, with an overall annual mean of 10.8°C (Fig. 2A). There was no significant difference in soil temperature between near-natural and restored sites ($p = 0.3$). Groundwater levels varied between high winter and low summer levels across all sites (range: −107 to 86 cm; Fig. 2B). In near-natural grazed sites, the mean groundwater level was −26 cm (±3.6, 95% CI), while near-natural ungrazed sites had an average of −21 cm (±3.0). The restored counterparts had lower groundwater levels, with the mean at grazed sites being −39 cm (±5.1), and ungrazed sites −30 cm (±4.1). Restored sites had significantly lower mean groundwater levels and higher annual amplitude (LMM $p = 0.016$ and $p = 0.015$).

Soil bulk density showed a strong negative correlation with organic content across all sites (Spearman's ρ: −0.87, Table 1). BD was significantly higher, and organic content lower, at restored rather than near-natural sites (Mann–Whitney U test: $p < 0.001$). Particularly high organic contents and low bulk densities were found at near-natural rather than restored sites at Tryggevælde; the latter resembled the level at all sites at Omme and Odense. At the sandy sites at Omme, both $CaCO_3$ content and groundwater pH were systematically lower than at the clayish-calcareous sites at Odense and Tryggevælde. Nitrate and PO_4^{3-} concentrations in groundwater varied unsystematically among sites (Table 1).

Annual and Seasonal Greenhouse Gas Fluxes

Ecosystem processes were quantified by examining CH_4 fluxes, ecosystem respiration (R_{eco}), GPP, and NEE. Seasonal and annual values were derived by interpolating between monthly measurements.

CH_4 fluxes showed distinct seasonal patterns: near-natural sites peaked in summer, while restored sites peaked in spring (Fig. 3). At restored sites, winter and spring contributed more to annual CH_4 emissions, whereas near-natural sites were dominated by summer and fall emissions. Annual fluxes varied widely; for example, the highest annual emission was in the restored grazed Omme site (70.64 ± 135.5 g CH_4 m^{-2} yr^{-1}), 200 times that of the restored grazed site at Tryggevælde (0.14 ± 0.46 g CH_4 m^{-2} yr^{-1}), and one site (restored ungrazed, Tryggevælde) even showed a small annual uptake (−0.059 ± 0.212 g CH_4 m^{-2} yr^{-1}). Overall, near-natural ungrazed sites had the highest average emissions (33.28 ± 28.79 g CH_4 m^{-2} yr^{-1}), followed by restored grazed (28.04 ± 38.97 g CH_4 m^{-2} yr^{-1}) and near-natural grazed (25.64 ± 17.07 g CH_4 m^{-2} yr^{-1}), with restored ungrazed sites emitting less than half of near-natural ungrazed (16.46 ± 14.48 g CH_4 m^{-2} yr^{-1}). Modeling revealed no significant effects of restoration, grazing, or their interaction (LMM $p > 0.05$, Table S2).

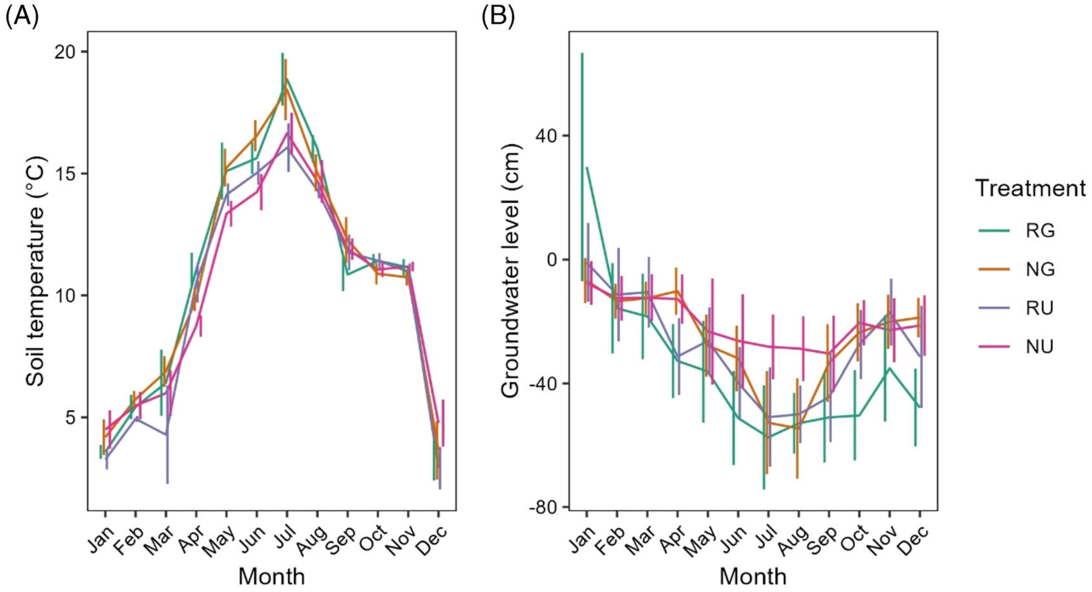

Figure 2. Seasonal variation of soil temperature (A) and groundwater level (B) grouped by treatment (mean ±95% CI). NG, near-natural grazed; NU, near-natural ungrazed; RG, restored grazed; RU, restored ungrazed.

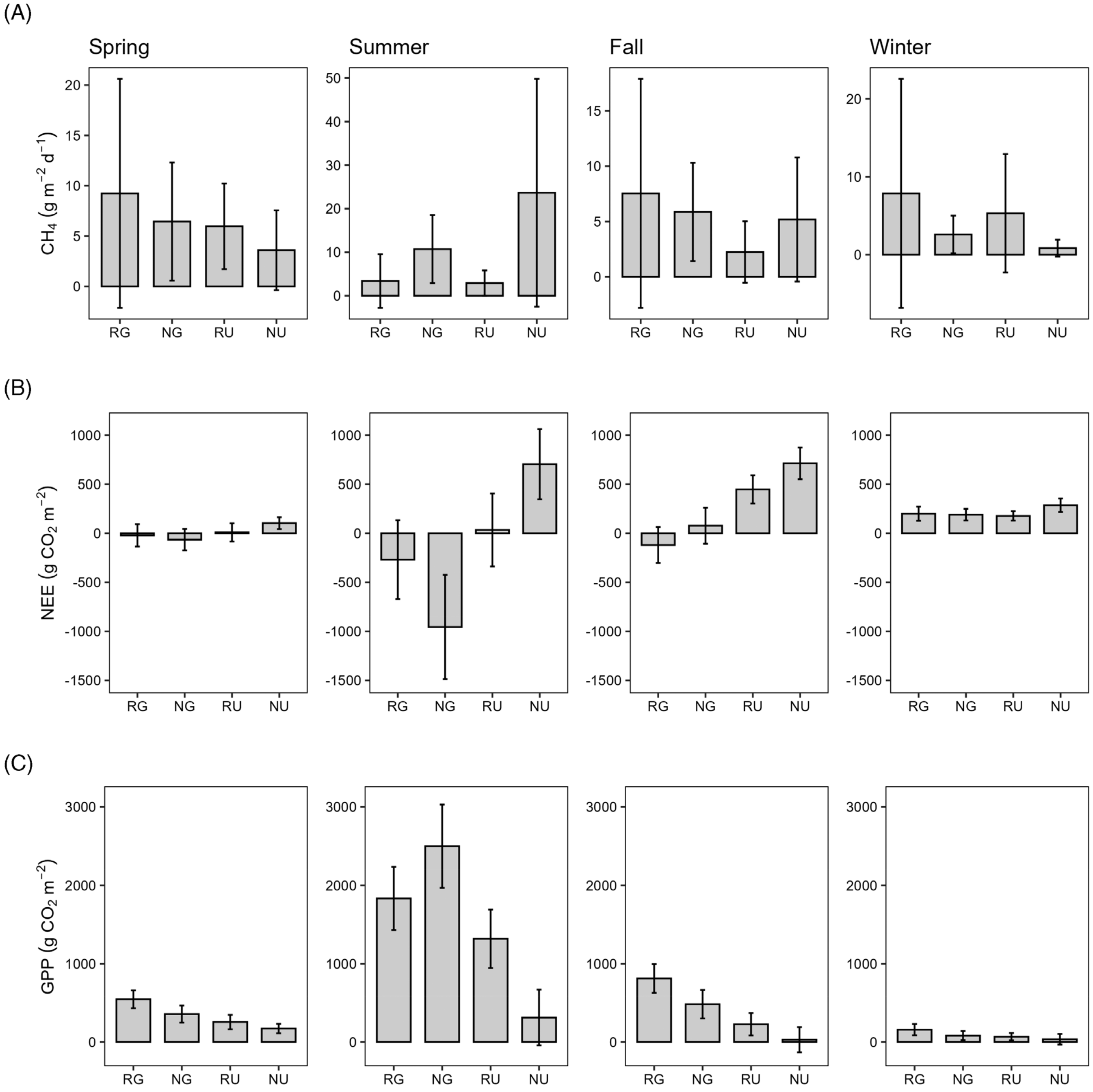

Figure 3. Diffusive CH_4 fluxes (A), net ecosystem exchange (NEE, B) and gross primary production (GPP, C) for bryophyte and herb level, that is, excluding effects of woody plants in ungrazed sites, partitioned by season (means ±95% confidence intervals). Winter is December–February, spring is March–May, summer is June–August, and fall is September–November. Data from the four types of wetlands investigated; near-natural grazed (NG), near-natural ungrazed (NU), restored grazed (RG), and restored ungrazed (RU). Each wetland type was represented by one site in each of three river valleys (each site with six plots) and monitored by monthly measurements over a full year (for individual fluxes at the site-level, see Fig. S2).

There was no significant effect of grazing or restoration on ecosystem respiration (LMM $p > 0.05$; Table S5). Ecosystem respiration was slightly higher in the grazed sites and, within each disturbance regime, restored sites tended to have a higher R_{eco} than near-natural ones (restored grazed; 3142 ± 466 g CO_2 m^{-2} yr^{-1}, near-natural grazed; 2671 ± 706, restore ungrazed; 2528 ± 402 and near-natural ungrazed; 2354 ± 462). Rates varied across sites, with restored grazed, Omme, at the highest (4130 g CO_2 m^{-2} yr^{-1}), more than double that of near-natural ungrazed, Omme, at the lowest (1821 g CO_2/m^2).

Gross primary production (GPP) was highest in near-natural grazed sites and similar in restored grazed sites (3353 ± 537 and

3425 ± 511 g CO_2 m^{-2} yr^{-1}, respectively). By far the lowest GPP was found in the shrub-dominated near-natural unmanaged sites (549 ± 302 g CO_2 m^{-2} yr^{-1}), where the GPP of aboveground woody plants was not included because of the chamber methodology. Restored ungrazed sites had the second-lowest GPP (1870 ± 601 g CO_2 m^{-2} yr^{-1}). Thus, grazed sites had a significantly higher GPP compared to ungrazed sites (LMM $p < 0.001$; Table S5). This difference remained significant when the scrub-dominated near-natural unmanaged sites were excluded from the model ($p < 0.001$; Table S6). Among ungrazed sites, restored sites had higher GPP ($p = 0.024$); whereas, for grazed sites, there was no significant difference between near-natural and restored ($p = 0.88$). Additionally, within both near-natural and restored sites, ungrazed sites had lower GPP ($p < 0.001$ and $p = 0.015$).

We observed large seasonal differences in NEE (Fig. 3). In summer, grazed sites had net carbon uptake while ungrazed sites released carbon. Spring fluxes were low, fall fluxes were high—especially in ungrazed sites—and winter fluxes were uniformly positive. Annually, grazed sites exhibited net CO_2 uptake (near-natural: −754 ± 661; restored: −211 ± 451 g CO_2 m^{-2} yr^{-1}) compared to net CO_2 release in ungrazed sites (near-natural: 1805 ± 574; restored: 660 ± 501). Overall, grazed sites had significantly lower NEE (LMM $p = 0.007$ and $p = 0.017$ with NU excluded, Tables S2 & S6), with no effect from restoration or its interaction with grazing. Pairwise comparisons revealed significant differences between grazed and ungrazed near-natural sites ($p = 0.007$), but not between the two restored types ($p = 0.21$).

Environmental Drivers of GHG Fluxes

Individually measured CH_4 fluxes varied extensively between low uptake (−0.0026) and high release (5.77 g CH_4 m^{-2} day^{-1}), with a median of 0.0018 g CH_4 m^{-2} day^{-1} and a substantially higher mean, 0.079 g CH_4 m^{-2} day^{-1}, reflecting a highly skewed data distribution. Groundwater level and soil temperature were both significant positive predictors of CH_4 flux (LMM $p < 0.001$, Table S3; Fig. 4) and showed significant interaction ($p = 0.025$). The interaction suggests that the effect of higher groundwater levels was stronger at warmer temperatures and vice versa. Disturbance regime and restoration status were not significant ($p = 0.066$ and 0.072), but the two interacted significantly ($p = 0.03$), indicating that grazing tended to increase CH_4 emissions in restored sites and decrease them at near-natural sites (Fig. 4). However, none of the pairwise comparisons were significant. When plotting individual fluxes with corresponding groundwater levels, we found a steep increase in the running median at approximately −40 cm (Fig. 4). However, when we plotted annual values together with annual mean groundwater levels, we found elevated emissions starting at a groundwater level of approximately −20 cm (Fig. S3).

Ecosystem respiration ranged between 0.02 and 41.7 g CO_2 m^{-2} day^{-1}, with a mean of 7.9 g CO_2 m^{-2} day^{-1} (median 5.5). Groundwater level was a significant negative predictor of R_{eco} ($p < 0.001$); that is, R_{eco} was lower with a groundwater table closer to the terrain (Fig. 5). Soil temperature was a significant positive predictor ($p < 0.001$), but there was no significant interaction between the two. Restoration and grazing did not have a significant effect on respiration (Table S3). Across all treatments and groundwater levels, the temperature stimulation of R_{eco} corresponded to a Q_{10} of 3.0 between 3.0 and 16.0°C.

GPP varied between 0.003 and 25.0 g CO_2 m^{-2} day^{-1}, with a mean of 3.7 g CO_2 m^{-2} day^{-1} (median: 1.79). Modeling showed that an increase in soil temperature and grazing significantly increased GPP (LMM $p < 0.001$ and $p = 0.017$), while it decreased with higher groundwater levels ($p = 0.039$; Fig. 6). Further, pairwise comparisons showed a significant difference with lower GPP in ungrazed compared to grazed near-natural sites ($p = 0.01$), while grazing did not significantly affect GPP in restored sites ($p = 0.19$). There were no indications of interaction neither between restoration status and grazing nor between water level and temperature (Table S3, <0.05).

Discussion

We measured GHG fluxes from wetland sites with various restoration statuses (restored and near-natural) and disturbance regimes (grazed and ungrazed) at monthly intervals for a full year in three river valleys representing different dominant soil types in the catchments. Our aim was to investigate the extent to which ecosystem functioning with respect to carbon cycling had recovered 12–17 years after restoration. Additionally, we wanted to evaluate how different disturbance regimes and environmental conditions in restored and near-natural wetlands affected carbon cycling. Overall, we found no significant carbon cycling differences between near-natural and restored sites.

Previous research has reported that hydrological properties are not necessarily restored following wetland restoration (Kreyling et al. 2021). In agreement, we found that the mean annual groundwater levels were lower and the amplitude higher at restored sites. Moreover, bulk density was higher and organic content lower at restored sites. This indicates that restoration has not fully raised the groundwater table to pre-restoration levels—perhaps due to insufficient raising of the streambeds or soil compaction and subsidence because of previous draining and agriculture. Decomposition of organic material during drainage increases bulk density, decreases porosity and hydraulic conductivity, and results in higher groundwater table fluctuations (Kreyling et al. 2021). CH_4 emissions have been shown to be higher during continuous than intermittent inundation (Sha et al. 2011; Boonman et al. 2024). Although we did not find a statistically significant difference, probably due to a large degree of site-specificity and high temporal variation, the average CH_4 emissions from restored sites were numerically lower than near-natural ones, 12–17 years after rewetting. The restoration age of the sites in the present study is similar to (or older than) the one Kalhori et al. (2024) observed transitioning from carbon source to sink in a multi-year study of a rewetted peatland site.

The large, site-specific differences in CH_4, R_{eco}, and NEE balances, included as random effects in our models, explained a substantial part of the observed variation. Our study design aimed at generalizing across site types (restoration status and disturbance regime) and the observed large and overlapping

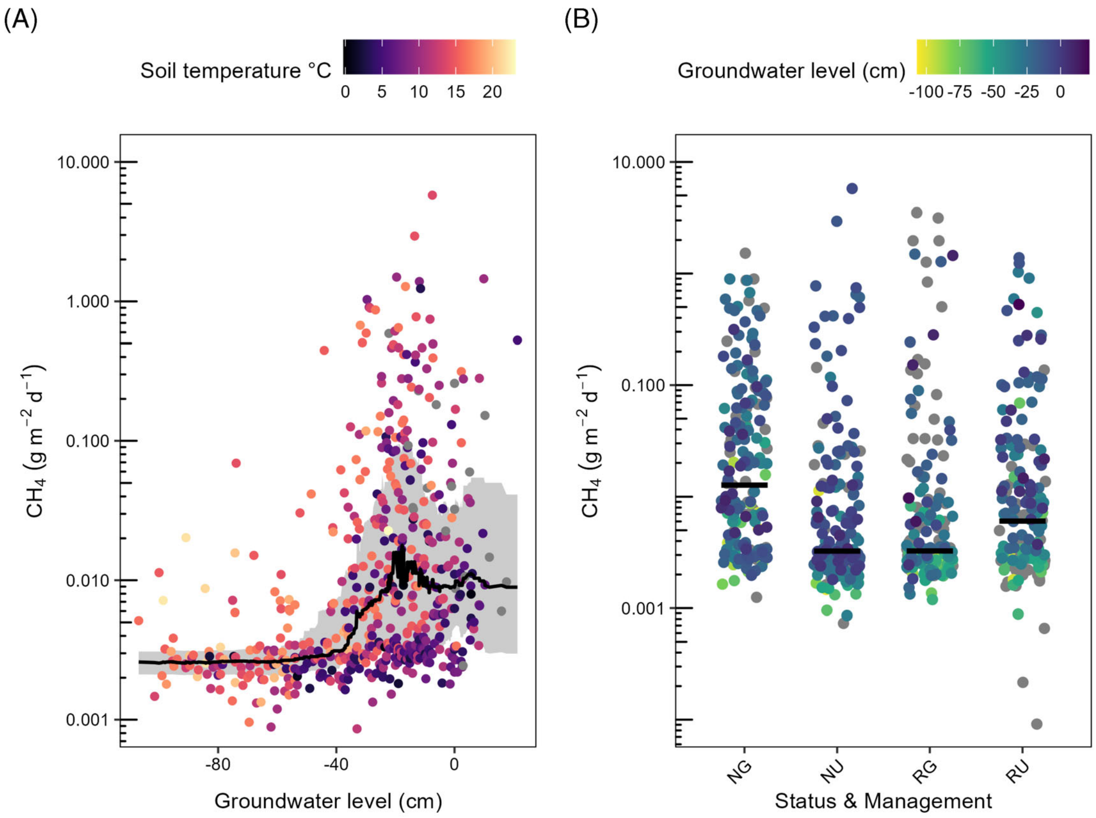

Figure 4. Methane emission from the four types of wetlands investigated; near-natural grazed (NG), near-natural ungrazed (NU), restored grazed (RG), and restored ungrazed (RU). Each wetland type was represented by one site in each of three river valleys (each site with six plots) and monitored by monthly measurements over a full year (for site-level data, see Fig. S2). (A) Emissions as a function of groundwater level with the colors signifying the soil temperature gradient. The black line is the running median and the gray ribbon represents the 25–75th running percentiles based on 100 running observations. (B) Emissions as a function of restoration status and disturbance regime, with the black bars representing the medians and the colors signifying the groundwater level gradient. Gray points indicate missing soil temperature (A) or groundwater level data (B). To transform negative fluxes, a constant (0.0027) was added, allowing visualization on a logarithmic *y*-axis.

variation within both near-natural and restored sites indicated that the restored sites fell within the range of natural fluctuations in GHG release. Finding small potential differences between carbon cycling in restored and near-natural sites would require mesocosm experiments or field studies with an even higher number of sites included.

The observed CH_4 emission rates were comparable to those found in other studies in similar ecosystems (Audet et al. 2013; Abdalla et al. 2016). Annual emissions of CH_4 in restored sites were well below the Intergovernmental Panel on Climate Change default emission factor for nutrient-rich rewetted organic soils (32.4 g CH_4 m^{-2} yr^{-1}, Hiraishi et al. 2014). However, we might have underestimated the CH_4 flux as we did not include the ebullitive (bubble) part of the fluxes. Our manual, chamber-based measurements conducted in a short time frame do not enable accurate estimation of ebullitive fluxes, which are typically erratic in time and require much higher temporal resolution for reliable estimates (Ramirez et al. 2017). While ebullition can play a role in fen-like ecosystems, such as the ones studied, it has also been shown to be very low when the water saturated zone is below −10 cm, which was typically the case in the summer period where we, as well as others, observed the highest fluxes (Stanley et al. 2019). Incorporating bubble traps, automated operating chambers, or eddy covariance towers could have ruled out the potential underestimation of the total CH_4 emission (Stanley et al. 2019; Kalhori et al. 2024). Thus, our annual budgets, calculated using linear interpolation between monthly measurements, represent somewhat crude estimates of yearly fluxes, but the method allows for comparison between the analyzed site types, which was the main aim of the study.

The grazed sites, both restored and near-natural, were carbon sinks, especially the near-natural sites. In contrast, ungrazed sites were carbon sources whose emissions had a net warming effect. However, we did not include the CO_2 and CH_4 release from the grazing livestock (Felber et al. 2016). Moreover, our chamber-based method does not capture the influence of trees and shrubs, which were mainly restricted to the near-natural ungrazed sites, on net carbon incorporation and CH_4 exchange.

Few studies explore the GHG effects of temperate riparian scrubs dominated by *Salix* and *Alnus*. An exception, Mitsch et al. (1991), reports an annual net productivity of 1280 g of biomass corresponding to 2347 g CO_2 m^{-2} yr^{-1} on a periodically

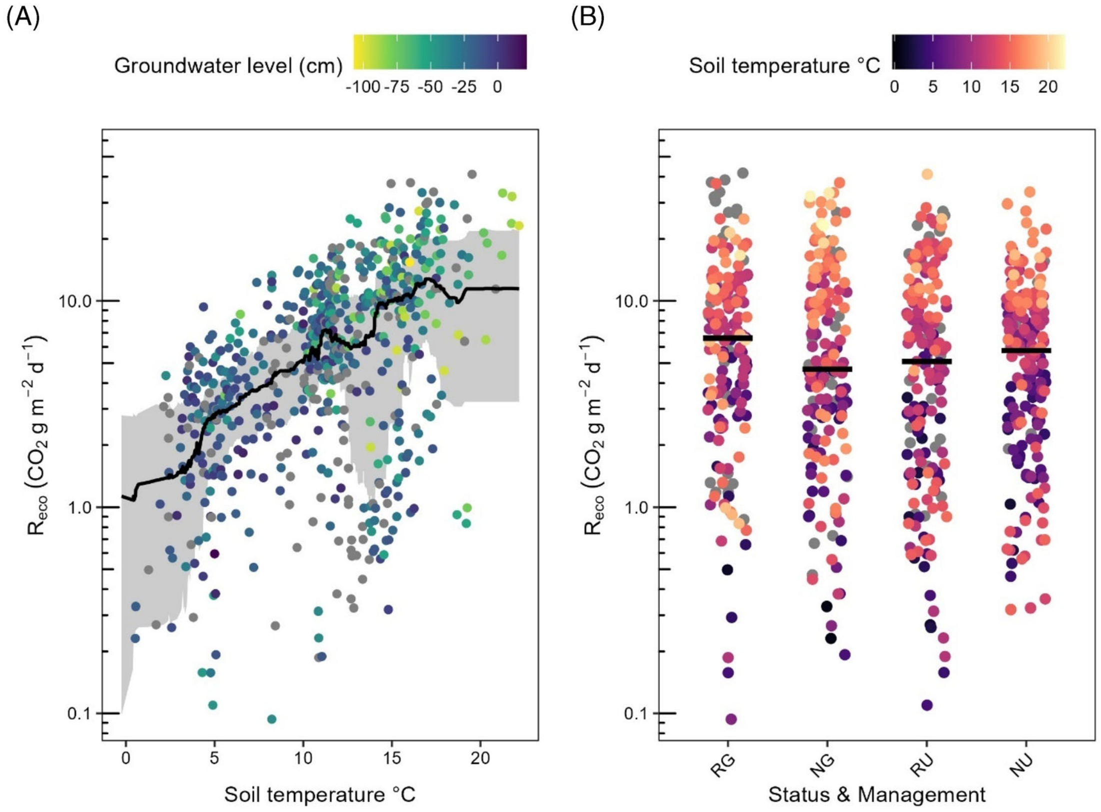

Figure 5. Ecosystem respiration from the four types of wetlands investigated: near-natural grazed (NG), near-natural ungrazed (NU), restored grazed (RG), and restored ungrazed (RU). Each wetland type was represented by one site in each of three river valleys (each site with six plots) and monitored by monthly measurements over a full year (for site-level data, see Fig. S2). (A) Respiration as a function of soil temperature, with the colors signifying the groundwater level gradient. The black line is the running median, and the gray ribbon represents the 25–75th running percentiles based on 100 running observations. (B) Respiration as a function of restoration status and disturbance regime, with the black bars representing the medians and the colors signifying the soil temperature gradient.

flooded forested riparian wetland in western Kentucky. This result suggests that, with an observed average annual NEE of 1805 g CO_2/m^2, our near-natural ungrazed sites, which were shrub-dominated, might have a net carbon uptake, like their grazed counterparts. Net productivity is possibly lower in temperate Denmark, compared to subtropical Kentucky; however, Mitch et al.'s methodology does not account for the growth of root biomass, which further increases carbon sequestration. Further, trees growing in temperate wetlands such as alder, ash, and birch have been shown to emit CH_4 from the base of their stems (Bastviken et al. 2023), but recent evidence also suggests a substantial uptake by bark-dwelling methanotrophs higher up (Gauci et al. 2024) leaving the net role of trees somewhat unresolved. Clearly, these crude considerations are not sufficient for solid conclusions, and there is an urgent need for estimates of net ecosystem CO_2 and CH_4 exchange in northern wet scrubs, which could be achieved, for example, by using eddy covariance towers.

In the studied restored ungrazed sites, the cover of woody plants was low, and sites were still significant carbon sources, emitting over 600 g CO_2 m^{-2} yr^{-1}. The annual GHG balance of a riparian wetland in Denmark wetland 2 years after rewetting showed that the site was a carbon source of similar magnitude, emitting 807 g CO_2 m^{-2} yr^{-1} (Kandel et al. 2019). The authors attributed this mainly to the management approach of cutting and leaving the cut thatch to mulch. Our study supports the notion that post-restoration management with grazing can turn restored wetlands into carbon sinks. In agreement with findings by Ward et al. (2007), grazing increased photosynthetic assimilation more than it increased R_{eco}, which was not significantly higher in restored sites. To summarize, our results show that management through grazing increased carbon uptake in the restored sites, while ungrazed restored sites acted as carbon sources. Thus, grazing with livestock seems to be a feasible land management strategy in restored wetlands for mitigating GHG release and this has also been shown to improve plant biodiversity (Baumane et al. 2025). While our data indicated that management without grazing seems not to be a suitable GHG mitigation strategy within the analyzed time frame, long-term vegetation succession leading to wooded conditions might promote GHG mitigation and biodiversity (Brunbjerg et al. 2022). Potential promotion of GHG mitigation in shrub-dominated near-natural wetlands, could not be documented in this present study due to the focus on carbon exchange of the soil and herb layers, and not the exchange of woody plants.

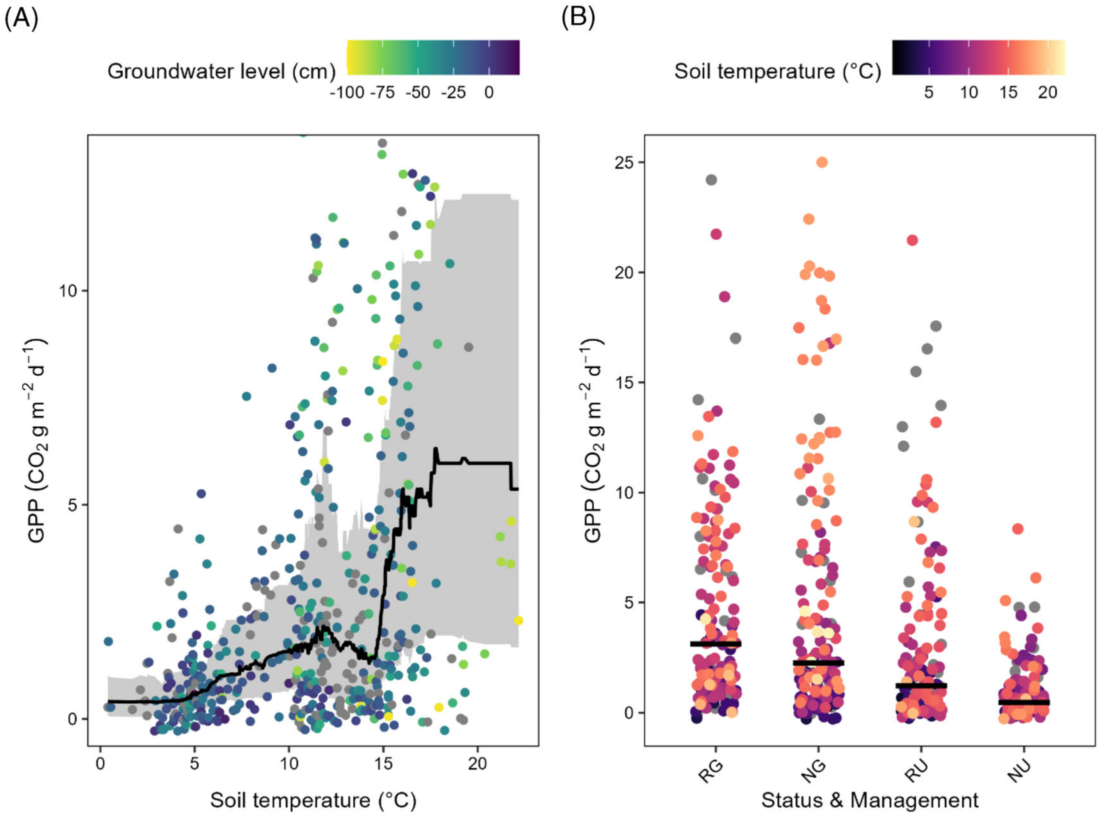

Figure 6. Gross primary production (GPP shown as negative values) from the four types of wetlands investigated: near-natural grazed (NG), near-natural ungrazed (NU), restored grazed (RG), and restored ungrazed (RU). Each wetland type was represented by one site in each of three river valleys (each site with six plots) and monitored by monthly measurements over a full year (for site-level data, see Fig. S2). (A) GPP as a function of soil temperature with the colors signifying the groundwater level gradient; the black line is the running median and the gray ribbon represents the 25–75th running percentiles based on 100 running observations. A total of 12 points between 16 and 25 g CO_2 m^{-2} day^{-1} were omitted for clarity. (B) GPP as a function of restoration status and disturbance regime; the black bars represent the medians and the colors signify the soil temperature gradient.

Our modeling shows that groundwater level and temperature strongly influenced CH_4 fluxes; they interacted significantly, suggesting that the stimulation of CH_4 fluxes by high soil temperature was stronger when the groundwater level was high; thus, the anoxic soil layers are close to the soil surface. Our findings support the general notion that groundwater level and soil temperature are the main determinants of CH_4 emissions in wetlands (Yvon-Durocher et al. 2014; Tiemeyer et al. 2020). An important implication is that lower groundwater levels during the warmer part of the year should decrease CH_4 emissions. Indeed, we find that restored sites, which have a higher yearly groundwater amplitude and tend to become drier in summer, have their highest CH_4 emissions in spring, while near-natural sites peak in summer. The novel hydrology of restored wetlands seems to affect the seasonal CH_4 dynamics without necessarily changing their annual magnitudes much.

We observed a drastic increase in CH_4 fluxes as groundwater levels passed approximately −40 cm belowground, according to the running median of individual CH_4 fluxes. Other studies have identified approximately −20 cm as a threshold for increased emissions, but this threshold was based on mean annual groundwater levels (Couwenberg et al. 2011; Tiemeyer et al. 2020) and not on parallel measurements of CH_4 fluxes and actual groundwater levels throughout the year.

Ecosystem respiration (R_{eco}) and GPP were both significantly affected by groundwater level and soil temperature. A higher groundwater level decreased R_{eco} and decreased GPP. Groundwater level is well-established as a decomposition control due to the inefficient and partial degradation of organic matter under anoxic conditions. Although the annual groundwater level was significantly lower in restored sites, this was not reflected in the annual R_{eco} values, which seemed to be unaffected by restoration. Seemingly, even if the natural hydrology is not fully restored, it seems to be sufficient to support net carbon sequestration in grazed sites. The soil temperature was the strongest apparent controller regardless of management approach, according to our models. Across sites, seasons, and groundwater levels, we estimate a Q_{10} of 3.0, which is in line with previous findings (Moore & Dalva 1993; Li et al. 2021).

Although the restoration of riparian wetlands had not fully reestablished a natural hydrology, which was observed to have severe negative effects on the recovery of wetland biodiversity (Baumane et al. 2025), we found that restored and near-natural sites had similar carbon cycling. This suggests that ecosystem function, with regard to carbon cycling, was generally restored more completely than hydrologic recovery. Extending the study to multiple years with different climatic conditions could help verify this finding.

Further, our results show some indication that grazing by livestock affected ecosystem functioning by increasing GPP in grazed compared to ungrazed sites. Consequently, grazed sites acted as carbon sinks, while ungrazed sites were carbon sources.

Our chamber-based measurements did not capture grazing cattle contribution to the carbon balance or the primary production of taller shrubs and trees dominating the near-natural ungrazed sites. These contributions would likely reduce the observed differences between grazed sites and near-natural ungrazed sites. Future studies using methodological setups that allow for a separation of fluxes from woody vegetation (eddy covariance towers), grazing animals (global positioning system tagging) and herb layer fluxes (chambers) are needed to assess the magnitude of the GHG emissions in the restored wetlands emerging in the coming decades, which is a necessary first step toward constraining these emissions.

Acknowledgments

This work was supported by a grant to K.S.-J. from the Independent Research Fund Denmark (0217-00112B). The M-GPC-918 Los Gatos GHG analyzer was financed through a grant from the Carlsberg Foundation (CF21-0166). We thank J. S. Sø for assistance in creating an alternative CO_2 sensor system and D. Stuligross for proofreading the manuscript.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Overview of study sites.
Table S2. Model results of annual GHG fluxes.
Table S3. Output from environmental models.
Table S4. Output from environmental CH_4 model on the full dataset.
Table S5. Output from annual models of gross primary production (GPP) and ecosystem respiration (R_{eco}).
Table S6. Output from models excluding NU (near-natural ungrazed) sites of annual gross primary production (annual GPP) and annual net ecosystem exchange (annual NEE) as well as gross primary production (GPP).
Figure S1. Heat map showing the proportion of flagged (i.e. excluded) fluxes of NEE and R_{eco} (A) and GPP (B) arranged by site and campaign month.
Figure S2. Scatterplot with individual fluxes of CO_2 (A) and CH_4 (B) for all sites.
Figure S3. Yearly mean methane emissions (g CH_4 m^{-2} yr^{-1}) as a function of yearly average groundwater level.

Coordinating Editor: Virginia Matzek

Received: 24 March, 2025; First decision: 16 May, 2025; Revised: 12 August, 2025; Accepted: 13 August, 2025