






Research article

Restoring riparian wetlands for carbon and nitrogen benefits and other critical ecosystem functions

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ARTICLE INFO

Keywords:

Teal carbon
Rewetting
Hydrological reinstatement
Revegetation
Riparian wetlands
Decay

ABSTRACT

With global warming intensifying, freshwater wetland restoration is becoming an increasingly important natural climate solution. Yet, restoration efforts for climate benefits have mostly focused on peatlands due to their high carbon storage capacities. Nevertheless, restoration often results in substantial methane emissions, complicating the climate benefits of restoration. Contrastingly, the climate benefits of restoring non-peat wetlands remain largely unexplored. We investigated the short- and long-term effects of restoring riparian wetlands to reinstate critical carbon dynamics and other ecosystem functions. Using a paired experimental design, we monitored carbon dioxide (CO₂), methane (CH₄), and nitrous oxide (N₂O) fluxes before, during, and after restoration. We also monitored native wetland plant cover, surface organic carbon and nitrogen stocks, leaf litter input, organic matter decomposition, and soil moisture. In the short term (one year post-restoration), rewetting and active revegetation reduced net carbon emissions by 39 % and increased surface organic carbon and nitrogen stocks by 12 % and 43 %, respectively. Restored wetlands had higher native plant covers, with native litter experiencing less decomposition than invasive litter, likely promoting carbon preservation. Furthermore, restored wetlands retained 55 % more soil moisture after drying, with moisture levels increasing with increasing soil carbon contents. Together, these results indicate the reinstatement of critical functions like reduced carbon mineralisation, and increased nutrient retention and soil water storage. In the longer term (six years post-restoration), surface organic carbon stocks increased by 53 %, demonstrating sustained long-term benefits. Our study highlights the effectiveness of riparian wetland restoration as a natural climate solution, providing critical insights for restoration policies beyond peatlands.

1. Introduction

Freshwater wetlands play a critical role in the global carbon cycle. Globally, freshwater wetlands, such as freshwater marshes, swamps, and peatlands, cover less than 10 % of the earth's surface (Davidson et al., 2018), yet they emit 20–25 % of global methane emissions (Mitsch et al., 2013; Mitsch and Mander, 2018; Rosentreter et al., 2021). Despite these high methane emissions, freshwater wetlands have the potential to serve as important long-term carbon sinks (Lal et al., 2018; Schuster et al., 2024), with the carbon stored in freshwater wetland soils constituting one-third of the world's total soil carbon stocks (Cole et al., 2007; Kayranli et al., 2010). In addition to their carbon sequestration and storage potential, freshwater wetlands provide other critical ecosystem

functions, including nutrient cycling and remediation, drought and flood resilience, and critical habitat for native and endangered species (Gopal, 2009; Kadykalo and Findlay, 2016).

In recent centuries, a significant portion of the world's freshwater wetlands has been lost due to drainage for agriculture or soil degradation (e.g., peat extraction) or the conversion to artificial wetlands for rice and wetland cultivation. Recent estimates indicate that the global area of natural wetlands has declined by 3.4 million km² since 1700, which equals the loss of 21 % of global wetlands (Fluet-Chouinard et al., 2023). Crucially, the drainage of natural wetlands can result in the release of significant amounts of previously stored soil carbon as carbon dioxide (CO₂) and, to a lesser extent, methane (CH₄), effectively turning natural wetlands from carbon sinks into carbon sources (Lal and

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Received 8 April 2025; Received in revised form 29 May 2025; Accepted 28 June 2025

Available online 2 July 2025

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Pimentel, 2008; Lane et al., 2016; Schuster et al., 2024). Similarly, the use of fertiliser for agricultural practices can drive increased greenhouse gas emissions from degraded wetlands, including the production of nitrous oxide (N₂O) (Bonetti et al., 2022) – a greenhouse gas that is 263 times more potent at warming the climate than CO₂ on a 100-year timescale (Neubauer and Megonigal, 2015).

With global warming intensifying, the restoration of degraded wetlands is becoming increasingly important to help mitigate climate change and its impacts (Bossio et al., 2020). For example, the most common management intervention to restore degraded palustrine wetlands (e.g., peatlands, freshwater marshes, riparian wetlands) is rewetting, which involves reinstating the natural hydrological connectivity of wetlands to their original waterway (Meng et al., 2020). Specifically, the delivery of water to dried wetland areas aims to stimulate the re-establishment of native wetland vegetation (Kayranli et al., 2010; Schwieger et al., 2021). However, when restoring wetlands that have been degraded for extended periods (several years to decades), rewetting may be ineffective in returning native plant species due to the depletion of seed banks (Zedler, 2000). Given that plant biomass and leaf litter are key to re-establishing carbon sequestration and storage capacities as well as nutrient regeneration, restoration through rewetting may thus be more effective when combined with active revegetation, which involves planting seeds or tube stocks of native plant species (Spieles, 2022). Nevertheless, if and how active revegetation can improve short-term restoration outcomes remains largely unclear.

Beyond their role in climate change mitigation, freshwater wetlands provide other critical ecosystem functions. For example, riparian wetlands are at the interface of land and waterways, where they play a pivotal role in mitigating the impacts of climate change, including alleviating floods and droughts (Meli et al., 2014). Importantly, such ecosystem functions are likely intricately linked to the carbon dynamics within a wetland. Specifically, the ability of soils to take up and store water (i.e., the soil water holding capacity) generally increases with increasing soil organic carbon contents (Libohova et al., 2018). Managing degraded freshwater wetlands to maximise carbon benefits, particularly carbon sequestration and storage in the soil, may thus not only mitigate greenhouse gas emissions but also accelerate the re-establishment of other crucial ecosystem functions. Yet, the link between carbon dynamics and ecosystem functions in restored freshwater wetlands remains poorly understood.

To date, the benefits of freshwater wetland restoration for climate change mitigation and the reinstatement of other ecosystem functions have mostly been investigated in peatlands, such as bogs and fens (Loisel and Gallego-Sala, 2022; Schuster et al., 2024; Xu et al., 2019). Peatlands are the most efficient carbon sinks among freshwater wetlands due to low decomposition rates of organic matter associated with typically cooler environmental temperatures, persistent anoxic conditions, functionally limited decomposer communities, and litter and organic matter substrates that are naturally slow to decompose (Moore and Basiliko, 2006). Furthermore, peatlands are typically disconnected from other waterways, which limits the exchange of organic matter with the surrounding landscapes (Chimner and Ewel, 2005). Due to their ability to rapidly accumulate organic carbon in their soils, peatlands are thus considered high-priority systems when it comes to wetland restoration for climate change mitigation. Yet, the restoration of degraded peatlands often results in significant CH₄ emissions, which can complicate the short-term climate benefits of restoration (Schuster et al., 2024). In contrast to peatlands, non-peat wetlands are typically integrated into waterways, facilitating the exchange of nutrients and organic matter (Cunha-Santino and Bianchini Júnior, 2023). Furthermore, natural drying and wetting cycles can affect their carbon storage capacities, with some of the stored soil organic carbon being mineralised and re-emitted as CO₂ during dry periods (Smith et al., 2018). Accordingly, non-peat wetlands tend to accumulate less organic matter in their soils but fulfil other important ecosystem functions. Nevertheless, these wetland systems have received much less attention, and our understanding of the

efficacy of restoration to reinstate critical carbon dynamics is limited. For example, some studies report significant reductions in greenhouse gas emissions shortly after restoration through rewetting (Limpert et al., 2020), while others find no changes in carbon dynamics (Bonetti et al., 2021; Treby et al., 2020). Crucially, the lack of research on the efficacy of non-peat wetland restoration limits our ability to assess its role in climate change mitigation, thereby limiting the development of effective restoration policies in the freshwater wetland restoration space beyond peatlands.

In this study, we provide a comprehensive assessment of the short-term benefits of restoring degraded riparian freshwater wetlands through rewetting and active revegetation by monitoring greenhouse gas fluxes (CO₂, CH₄, and N₂O), surface organic carbon and nitrogen stocks, changes in native wetland plant cover, leaf litter input, carbon decomposition, and soil moisture. To do so, we used a paired experimental design, where each wetland site that underwent restoration (intervention sites) was paired with an unrestored wetland site with similar starting conditions (control sites). Additionally, we monitored the longer-term benefits of restoration in terms of greenhouse gas fluxes and surface organic carbon stocks in another restored riparian wetland six years post-restoration. Overall, our findings document the short- and long-term benefits of restoring non-peat ecosystems like riparian wetlands, which are key to developing impactful restoration policies amid global efforts to combat climate change.

2. Materials and methods

2.1. Study sites and experimental design

We monitored three paired riparian wetland sites as part of an Australian government-funded wetland restoration initiative in the Lower Loddon landscape in north-western Victoria, Australia (35° 57' 21.6" S, 143° 53' 01.7" E and 35° 32' 24.6" S, 143° 56' 22.1" E). Prior to restoration, all wetland sites were hydrologically disconnected from adjacent river systems, with wetlands in the area experiencing significant hydrological alterations since the early 20th century (Ramsar Convention Secretariat, 2019). The soils were predominantly clay, and the vegetation consisted of a mix of invasive and native plants, including low- to medium-stature shrubs (e.g., *Cressa australis*), herbs (e.g., *Centipeda cunninghamii*, *Polygonum aviculare*), and graminoids (e.g., *Eleocharis pallens*, *Lolium rigidum*), as well as native eucalyptus trees (*Eucalyptus largiflorens* and *Eucalyptus camaldulensis*). The region is characterised by a long-term average annual temperature and precipitation of 16.2 °C and 374 mm, respectively (Bureau of Meteorology, 2024), which is similar to the Mediterranean climate, with high temperatures and low rainfall in summer, and cooler temperatures and higher rainfall in winter.

Within each paired site, we monitored one intervention wetland that underwent restoration through rewetting and active revegetation and a corresponding control site with similar starting conditions that remained degraded according to an MBACI (multiple sites before-after control-impact) experimental design. Specifically, the intervention and control wetlands within a paired site were near each other and exhibited comparable pre-restoration vegetation structures, topographies, and hydrological conditions. Importantly, by using a paired experimental design, we could disentangle temporal and environmental effects, like temperature and precipitation, from changes that are a result of restoration. We monitored all sites once before restoration in January or March (vegetation surveys) and April 2023 (carbon dynamics) to determine baseline conditions. The three intervention wetlands were then rewetted through the addition of environmental water and revegetated through tube stock planting and direct seeding of 36 native wetland plant species in May 2023, with a second rewetting event in August 2023. To determine restoration outcomes, we monitored all sites in November 2023 while the intervention wetlands were still flooded ('during restoration'; greenhouse gas flux measurements only) and again

in March (vegetation surveys) and April 2024 (carbon dynamics) after all intervention wetlands had dried up ('after restoration').

Within each wetland site, we sampled from nine randomly allocated sampling locations across three different inundation zones (three sampling points within each zone, $n = 54$ sampling points across the six wetland sites): (i) submerged zone, which is the deepest zone of the wetland (i.e., the river channel), where inundation is greatest and aquatic vegetation can typically be found; (ii) emergent zone, which is the side of the river that is frequently inundated and predominantly characterised by emergent vegetation; and (iii) fringing zone, which is the riverbank, that is typically only intermittently inundated during flooding conditions. To ensure spatially representative sampling and reduce potential location bias, we randomly selected three well-distributed sampling blocks across the full extent of each wetland site. Within each block, we sampled from three sampling points – one from the submerged, one from the emergent, and one from the fringing zone of the wetland (i.e., three measurement points per sampling site \times three sampling sites = nine measurement points per wetland site). We then marked each sampling point with stakes and markers and recorded GPS coordinates using real-time kinematic positioning (RTK) to allow for repeated sampling over time.

We also monitored a long-term restored riparian wetland within the Lower Loddon landscape six years after it was restored through hydrological reinstatement (no revegetation) in 2017 (35° 30' 12.1" S, 143° 52' 24.8" E). This wetland site was originally monitored by Limpert et al. (2020) in 2017, who quantified soil organic carbon stocks and the short-term effects of restoration on greenhouse gas fluxes up to one month after restoration. Limpert et al. (2020) established four sampling locations within the wetland: two within the submerged zone and two within the fringing zone of the wetland, with each sampling location containing three sampling points ($n = 12$ sampling points in total; refer to their Fig. 2 for more details). We followed the authors' original sampling design to determine greenhouse gas fluxes (CO₂, CH₄, and N₂O) and surface organic carbon stocks six years after restoration. During our sampling campaign, the wetland site was dry.

2.2. Greenhouse gas flux measurements

We used 'Pondi' to quantify greenhouse gas fluxes from the different sampling locations within all wetland sites (Malerba et al., 2025). Pondi sensors consist of a gas collection chamber fitted with a Sensirion SCD40 sensor to quantify carbon dioxide (CO₂) levels (measurement range: 0–40,000 ppm), a Figaro TGS2611-E00 for methane (CH₄; measurement range: 0–10,000 ppm), and a Dynament Platinum P/N2OP/NC/4/P sensor for nitrous oxide (N₂O; measurement range: 0–1000 ppm). Each Pondi is powered by a solar panel and battery cells and uses Telstra's Cat-M1 network to transfer data to a cloud in real-time. Pondi have recently been used to monitor aquatic greenhouse gas fluxes from agricultural ponds (Odebiri et al., 2024). Full device details and specifications can be found in Malerba et al. (2025). At each sampling time point (before, during, and after restoration), we measured fluxes once (i.e., single point measurement) for 30 min at 1-min measurement intervals. For terrestrial greenhouse gas flux measurements during dry wetland conditions, we used the closed-collar chamber method with a transparent 8 L collection chamber (25 cm diameter \times 27 cm height), which accommodated the standing vegetation at all sampling points before and after restoration (predominantly low-to medium-stature grasses and native wetland plant seedlings; refer to Table S1). We used a 16 L dark floating chamber (45 cm diameter \times 15.5 cm height) for aquatic flux measurements during flooded conditions.

When determining terrestrial greenhouse gas fluxes, we first covered the transparent chamber with reflective insulation material to determine ecosystem respiration (R_e). After 30 min, we uncovered and vented all chambers, replaced them into the collars, and measured the net ecosystem exchange (NEE) under light conditions. During light measurements, we also quantified light intensity in terms of photosynthetic

active radiation (PAR; in W m⁻²) using a pyranometer (PYR) sensor that measures total solar radiation (ProCheck, USA) to account for any differences in light intensity across measurement points that could affect the NEE. PAR intensity across measurement runs (before, during, or after restoration) remained comparable in both the control and intervention wetlands (restoration \times treatment: $F_{2,86} = 0.81$, $P = 0.45$) and across inundation zones (restoration \times inundation zone: $F_{4,86} = 0.49$, $P = 0.74$). Hence, we excluded PAR measurements from the analyses. During both flux measurement runs (dark and light), we also determined CH₄ and N₂O concentrations within the chamber. CH₄ and N₂O fluxes did not differ between dark and light measurement runs (CH₄ fluxes: $F_{1,250} = 0.19$, $P = 0.66$; N₂O fluxes: $F_{1,251} = 1.06$, $P = 0.3$). We, therefore, calculated average CH₄ and N₂O fluxes across dark and light measurement runs. We calculated greenhouse gas fluxes as:

$$F = \frac{\text{slope} \times \text{volume} \times F_1 \times F_2}{F_3 \times \text{surface}}$$

where *slope* is the linear rate of change in gas concentrations over time within the chamber (ppm min⁻¹), *volume* is the chamber volume (0.008 m³ for the transparent chamber; 0.01309 m³ for the floating chamber), F_1 is the conversion factor from ppm to $\mu\text{g m}^{-3}$ for each greenhouse gas (CO₂: 1798.45; CH₄: 655.47; N₂O: 1798.56) based on the ideal gas law, which takes into account the molecular weight of each gas (CO₂: 44.009 g mol⁻¹; CH₄: 16.0425 g mol⁻¹; 44.013 N₂O: g mol⁻¹) under standardised temperature (20 °C) and pressure (1 atm) conditions, F_2 is the conversion factor from minutes to days (1,440), F_3 is the conversion factor from μg to g (1,000,000), and *surface* is the surface area of the chamber (0.049 m² for the transparent chamber; 0.128 m² for the floating chamber), which is equivalent to the soil or water surface area, from which gas fluxes were measured (Tremblay, 2005).

To calculate the net carbon fluxes from the intervention and control wetlands, we converted their average NEE (in g CO₂ m⁻² day⁻¹) and CH₄ fluxes (in g CH₄ m⁻² day⁻¹) to g C m⁻² day⁻¹ using the relative molecular weight of C in CO₂ (27.27 %) and CH₄ (75.19 %), respectively, and calculated net carbon fluxes as the sum of average NEE (in g C m⁻² day⁻¹) and CH₄ fluxes (in g C m⁻² day⁻¹).

2.3. Vegetation assessments

We performed vegetation surveys to monitor any changes in plant species abundance and composition in the intervention and control wetlands before and after restoration. To do so, we established three 10 m transects within each inundation zone (submerged, emergent, and fringing zones) and recorded all species using the line-point intercept method (Godínez-Alvarez et al., 2009), where each species that intercepted a fine metal rod passed vertically through vegetation was recorded at 20 cm intervals (50 sampling points per transect in total). We then calculated the plant cover as:

$$\text{Plant cover} = \sum_{i=1}^j \left(\frac{n_i}{50} \right) * 100$$

where n_i is the total number of hits of a given plant species i intercepted along the 10 m transect, 50 is the total number of sampling points along the transect, and j indicates the total number of unique species encountered along a transect (Wilson, 2011).

2.4. Leaf litter input and decomposition

We quantified leaf litter input into a wetland by collecting any plant leaf litter found on the ground within a 26 cm \times 26 cm (676 cm²) sampling square at each sampling point ($n = 54$). We washed and dried all leaf litter at 60 °C to constant weight before determining the dry weight (DW) and calculating mean leaf litter input in g DW m⁻².

To determine litter decomposition, we collected leaves from two

dominant native wetland species found in the study region, the common spike-rush (*Eleocharis acuta*) and the common swamp wallaby grass (*Amphibromus nervosus*). We also collected leaves from a dominant invasive grass species, ryegrass (*Lolium rigidum*), which is commonly found in degraded wetlands and pastures globally. We dried all litter samples at 60 °C to constant weight before cutting them into ~1 cm long fragments and putting them into nylon mesh tea litterbags to create two litterbag types: native leaf litter (mixture of spike-rush and wallaby grass) and invasive leaf litter (ryegrass). We also used tea bags filled with either green or rooibos tea as a standardised approach to quantify decomposition and carbon turnover (Keuskamp et al., 2013; Trevaathan-Tackett et al., 2021). Specifically, green tea is a relatively labile form of organic matter, whereas rooibos tea is more recalcitrant because of its higher lignin content (Keuskamp et al., 2013). By deploying these two types of tea in the control and intervention wetlands, we were able to determine the effects of inundation and recalcitrance on decomposition rates. Before deployment, we weighed each tea and litter bag and then buried two bags of each type at 10–15 cm soil depth at each sampling location within all wetland sites (n = 432 tea and litter bags in total). Burying the bags at this depth protects them from excessive plant ingrowth and disturbances in the soil, thereby maximising retrieval chances. We recovered a total of 375 tea and litter bags after one year (378 days after deployment), with 57 bags unrecoverable. Most of these unrecoverable bags were likely lost due to animal disturbance, which led to markers being removed or misplaced and bags either not being found (n = 16) or found dug up (n = 12). Furthermore, some bags (n = 29) were unusable due to tears in the bag, resulting in the loss of tea or litter during bag recovery. Once retrieved, we washed all bags to get rid of any soil and dried them at 60 °C to constant weight. Once dry, we removed any plant roots that had grown into the bags and determined the final tea and litter masses by weighing without the bag. To determine the proportions of mass remaining after restoration, we subtracted the average empty bag weight (average weight of 100 empty tea litterbags) from the initial weight (tea or litter + bag) and divided the net tea or litter weight after restoration by the net tea or litter weight before restoration.

2.5. Surface organic carbon and nitrogen stocks

To determine surface organic carbon and nitrogen stocks, we took 10 cm syringe soil cores at the before- and after-restoration time points that we sectioned at 0–1 cm, 1–2 cm, 2–3 cm, 3–5 cm, and 5–10 cm (n = 270 sections). We focused on the upper soil layers of the wetlands since changes in soil organic carbon stocks are mostly expected to happen in the topsoil layers, particularly in the short term (<20 cm soil depth; Xu et al., 2019). To capture fine-scale variation in surface soil dynamics, we used finer stratification in the upper 3 cm (0–1, 1–2, and 2–3 cm), where organic matter inputs and microbial processing are typically concentrated. In the deeper soil sections (3–5 and 5–10 cm), we used coarser layers to balance analytical resolution with sample processing feasibility, while still capturing early signals of change in deeper soil. All sections were dried to constant weight at 60 °C. We then used the dry weight to calculate soil bulk density and homogenised each section with a stainless-steel mortar and pestle (Retsch RM 200, Germany). We sent all sections to the Queensland University of Technology in Queensland, Australia, for elemental carbon and nitrogen content analyses (LECO 928 Series Macro Determinator, USA).

2.6. Soil moisture content

We used a HOBO EC-5 soil moisture sensor combined with a HOBO USB Micro Station Data Logger (Onset, USA) set to a 5-s logging interval to quantify soil moisture contents at the before- and after-restoration sampling points (n = 54). We measured soil moisture for 2 min and then calculated the average soil moisture content.

2.7. Statistical analyses

We used linear mixed-effects models to test for the effects of restoration time point (before, during, and after restoration), treatment (intervention and unrestored control wetlands), inundation zone (submerged, emergent, and fringing zones), and their interactions on greenhouse gas fluxes, surface organic carbon and nitrogen stocks, leaf litter input, and plant cover. To test for the effects of restoration time point, treatment, inundation zone, surface organic carbon stocks, and their interactions on soil moisture contents, we used beta regressions to account for moisture data being confined within 0 and 1 (or 0 % and 100 %). We included sampling plot ID (nine unique measurement plots within each wetland site) nested within site ID (three paired sites, each comprised of a restored intervention and a paired unrestored control wetland site) as random intercepts in all models to account for repeated measures. When testing for the effects of restoration time point, treatment, inundation zone, and sampling depth (0–1 cm, 1–2 cm, 2–3 cm, 3–5 cm, or 5–10 cm) on surface organic carbon and nitrogen stocks, we included soil core slice ID nested within sampling plot ID and site ID as random effects to account for the non-independence of depth sampling points within each sampling plot. To determine the effects of tea or litter type (invasive or native leaf litter; green or rooibos tea), treatment, and inundation zone on tea and leaf litter decomposition (proportion mass remaining), we used a linear mixed-effects model with sampling plot ID nested within site ID as random intercepts. When standardised residuals showed unequal variances, we included treatment- and/or restoration time point-specific variance coefficients in the model (function varIdent) to account for heteroskedasticity.

We used linear mixed effects models to test for the effects of restoration time point (before, 1 month after, and 6 years after restoration), inundation zone (submerged or fringing zone), and their interaction on greenhouse gas fluxes and surface organic carbon stocks in the long-term restored wetland. In all models, we included sampling location (two within the submerged zone, two within the fringing zone) as a random intercept to account for repeated measures. When testing for the effects of restoration time point, inundation zone, and sampling depth (0–5 cm or 5–10 cm) on surface organic carbon stocks, we also included soil core slice ID nested within sampling plot ID and sampling location as a random effect. When standardised residuals showed unequal variances, we included inundation zone- and/or restoration time point-specific variance coefficients in the model (function varIdent).

We tested for spatial autocorrelation in model residuals using Moran's I, based on a k-nearest-neighbour structure (k = 3) applied to spatial coordinates collected via RTK-GPS. We conducted separate tests for each wetland site and for each response variable (ecosystem respiration, NEE, methane fluxes, net carbon fluxes, plant cover, leaf litter input, tea and litter decomposition, surface organic carbon and nitrogen stocks, and soil moisture content), using the R package 'spdep' v.1.3–11 (Bivand and Wong, 2018). Overall, we detected no significant spatial autocorrelation in model residuals for most sites and variables. Two wetland sites showed marginally significant autocorrelation for different response variables (plant cover at site 4: Moran's I = 0.13, P = 0.04; soil moisture at site 1: Moran's I = 0.19, P = 0.03). However, in both cases, the effect sizes were small, and the observed values of Moran's I indicated only weak spatial structure, indicating that spatial non-independence was adequately addressed by the nested random-effects structure used in all linear mixed-effects models (refer to Tables S2 and S3).

We used the R package 'nlme' v.3.1–166 for linear mixed effects models (Pinheiro et al., 2024) and 'glmmTMB' for beta regressions (Brooks et al., 2017). If we found significant interactions, we used the R package 'emmeans' v.1.10.4 (Lenth, 2024) to conduct tukey-adjusted post hoc tests. We performed all analyses in R v.4.4.1 (R Core Team, 2013) and used the package 'ggplot2' v.3.5.1 for data visualisation and plotting (Wickham, 2016).

3. Results

3.1. Greenhouse gas fluxes

In the intervention wetlands, CO₂ emissions (ecosystem respiration, R_e) decreased, on average, by 35 % and 40 % during and after restoration, respectively. Specifically, CO₂ fluxes decreased from 8.29 g CO₂ m⁻² day⁻¹ before restoration to 5.41 g CO₂ m⁻² day⁻¹ during and 4.99 g CO₂ m⁻² day⁻¹ after restoration (restoration time point × treatment: $F_{2,73} = 5.62, P = 0.005$; Fig. 1a; Table S4). Similarly, the net ecosystem exchange (NEE, that considers CO₂ emissions and CO₂ uptake through photosynthesis) decreased, on average, by 43 % after restoration (from 3.19 g CO₂ m⁻² day⁻¹ to 1.83 g CO₂ m⁻² day⁻¹; $F_{2,97} = 3.19, P = 0.04$; Fig. 1b). In the unrestored control wetlands, average CO₂ emissions and the NEE increased by 46 % (from 3.05 to 4.44 g CO₂ m⁻² day⁻¹) and 129 % (from 2.07 to 4.75 g CO₂ m⁻² day⁻¹), respectively, during restoration but returned to baseline emissions at the after-restoration time point (Fig. 1a and b).

Methane fluxes in both the intervention and control wetlands did not significantly differ among restoration time points (restoration time point × treatment: $F_{2,98} = 1.94, P = 0.15$; restoration time point: $F_{2,98} = 2.02, P = 0.14$; Fig. 1c; Table S4). We could not detect any N₂O fluxes.

Considering the NEE and CH₄ fluxes, average net carbon fluxes from the intervention wetlands decreased, on average, by 21 % and 39 %

during and after restoration, respectively. Specifically, average carbon fluxes from the intervention wetlands were 1.03 g C m⁻² day⁻¹ before restoration, 0.81 g C m⁻² day⁻¹ during restoration, and 0.62 g C m⁻² day⁻¹ after restoration (Fig. 1d). Contrastingly, average net carbon emissions from the control wetlands increased by 126 % and 169 % at the during-restoration time point (1.29 g C m⁻² day⁻¹) compared to the before- (0.57 g C m⁻² day⁻¹) and after-restoration time points (0.48 g C m⁻² day⁻¹), respectively (restoration time point × treatment: $F_{2,95} = 3.87, P = 0.02$; Fig. 1d; Table S4).

3.2. Wetland plant cover

The total plant cover increased significantly after restoration in the intervention wetlands, but the effect varied across inundation zones (restoration time point × treatment × inundation zone: $F_{2,102} = 3.67, P = 0.03$; Table S5). Specifically, the average plant cover increased by 702 % (from 8.79 to 70.6) and 346 % (from 16.62 to 74.2) in the submerged and emergent wetland zones after restoration, but did not significantly change in the fringing zone. Contrastingly, the total plant cover in the control wetlands remained comparable between the before- and after-restoration time points (Fig. 2a; refer to Table S1 for a list of plant species).

The overall increase in total plant covers in the intervention wetlands was driven by changes in native wetland plant covers, which increased

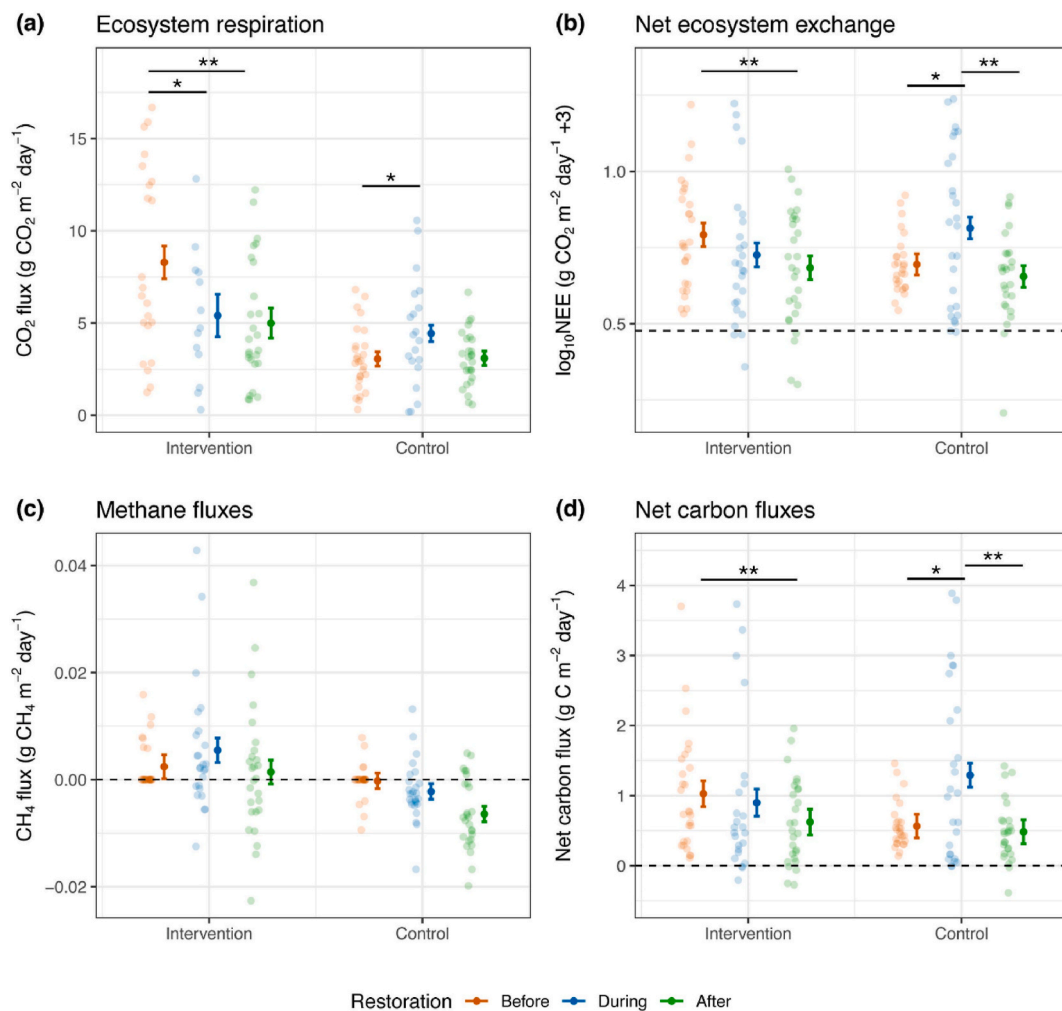


Fig. 1. (a) Ecosystem respiration (R_e; in g CO₂ m⁻² day⁻¹), (b) the net ecosystem exchange (NEE; in g CO₂ m⁻² day⁻¹), (c) methane fluxes (CH₄; in g CH₄ m⁻² day⁻¹), and (d) net carbon fluxes (in g C m⁻² day⁻¹) from the intervention (restored) and control (unrestored) wetlands before (in orange), during (in blue), and one year after restoration (in green). Opaque points are the predicted means and error bars indicate standard errors from the statistically significant linear mixed effects models; semi-transparent points are the raw data; asterisks indicate significant differences.

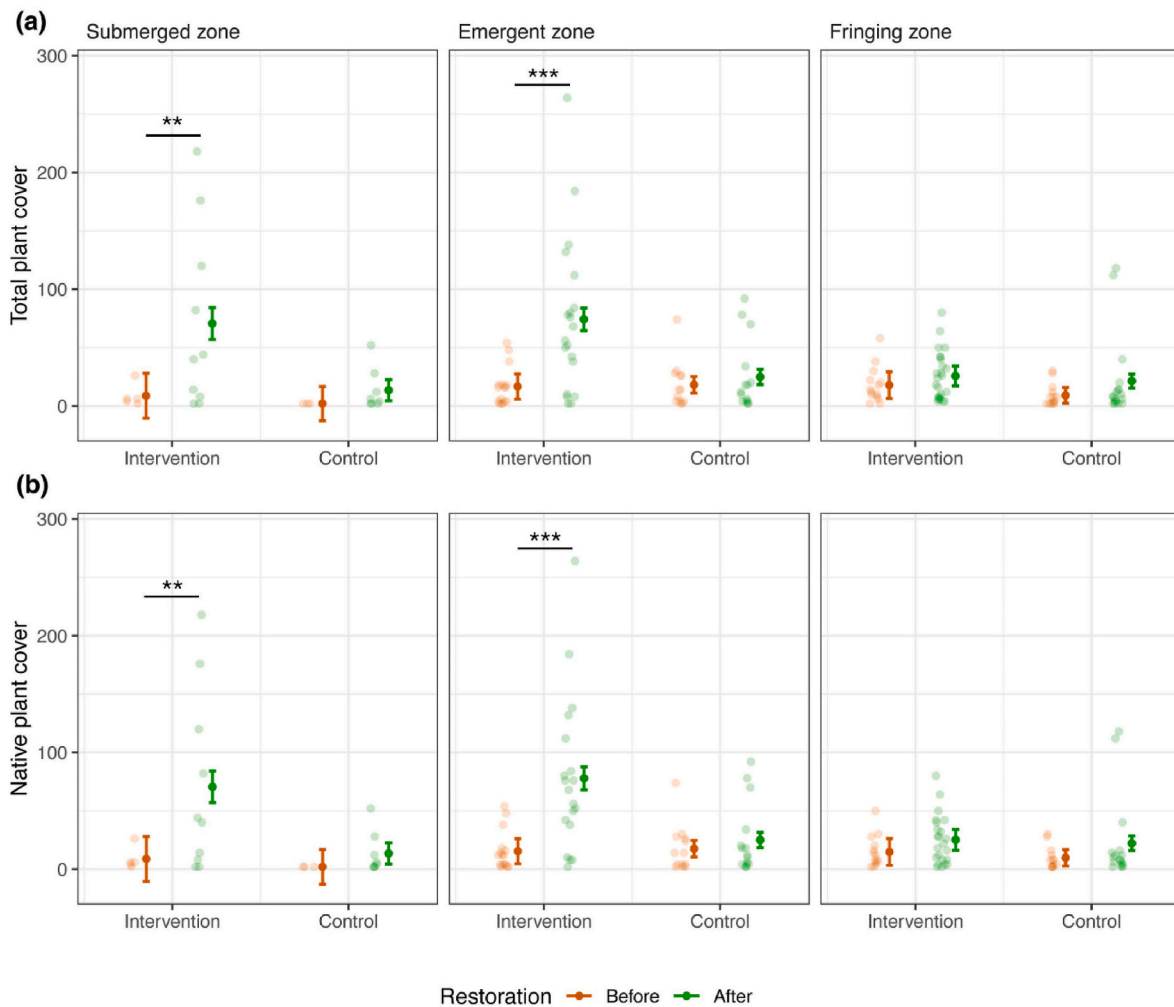


Fig. 2. (a) Total and (b) native plant covers within the different inundation zones (submerged, emergent, and fringing zone) in the intervention and control wetlands before (orange) and after restoration (green). Opaque points are the predicted means and error bars indicate standard errors from the statistically significant linear mixed effects model; semi-transparent points are the raw data; asterisks indicate significant differences.

by 703 % (from 8.79 to 70.6) and 406 % (from 15.38 to 77.89) in the submerged and emergent wetland zones after restoration but not in the fringing zone (restoration time point \times treatment \times inundation zone: $F_{2,97} = 3.59$, $P = 0.03$; Fig. 2b). Invasive plant covers did not significantly change across the restoration period at all wetland sites ($F_{1,8} = 0.33$, $P = 0.58$; Table S5).

3.3. Leaf litter input and decomposition

Leaf litter input increased after restoration, but the effect tended to differ across intervention and control wetlands (restoration time point \times treatment: $F_{1,50} = 3.77$, $P = 0.06$; Table S6). Specifically, the leaf litter input into the intervention wetlands increased by 211 % after restoration (from 54.53 to 149.15 g DW m⁻²; Fig. 3a). Conversely, leaf litter input into the control wetlands remained comparable between the before- and after-restoration time points (Fig. 3a).

In terms of tea and leaf litter decomposition, the proportion of mass remaining was significantly lower for the green tea and invasive leaf litter types compared to the rooibos tea and native leaf litter ($F_{3,318} = 376.73$, $P < 0.0001$), indicating greater mass losses in the green tea and invasive leaf litter bags (Fig. 3b and S1). Furthermore, the proportions of remaining tea and leaf litter masses for both the invasive and native tea and leaf litter types were significantly lower in the submerged and emergent zones compared to the fringing zone ($F_{2,50} = 3.34$, $P = 0.04$; Fig. S2; Table S6).

3.4. Surface organic carbon and nitrogen stocks

Surface organic carbon and nitrogen stocks (top 10 cm) in the intervention wetlands increased, on average, by 12 % (from 24.02 to 26.89 Mg C ha⁻¹; restoration time point \times treatment: $F_{1,44} = 4.57$, $P = 0.04$) and 43 % (from 1.6 to 2.28 Mg N ha⁻¹; restoration time point \times treatment: $F_{1,44} = 5.23$, $P = 0.03$; Table S7), respectively, after restoration (Fig. 4a and b). Contrastingly, surface organic carbon stocks in the control wetlands were, on average, 10 % lower at the after-restoration time point (from 28.39 to 25.49 Mg C ha⁻¹; Fig. 4a). Surface nitrogen stocks did not significantly differ between restoration time points in the control wetlands (Fig. 4b).

The effects of restoration on surface organic carbon and nitrogen stocks differed among soil sampling depths (restoration time point \times treatment \times sampling depth; organic carbon stocks: $F_{4,220} = 3$, $P = 0.02$; nitrogen stocks: $F_{4,228} = 2.49$, $P = 0.04$; Table S8). Specifically, surface organic carbon stocks in the intervention wetlands increased, on average, by 27 % in the middle soil layers between 1 and 5 cm soil depth after restoration (Fig. S3a). Contrastingly, surface nitrogen stocks increased, on average, by 82 % in the deeper soil layers (2–10 cm) but not in the uppermost layers (0–1 cm and 1–2 cm; Fig. S3b). In the control wetlands, surface organic carbon stocks decreased, on average, by 35 % in the deeper soil layer (5–10 cm), whereas surface nitrogen stocks did not significantly differ across soil depths before and after restoration (Fig. S3a and b).

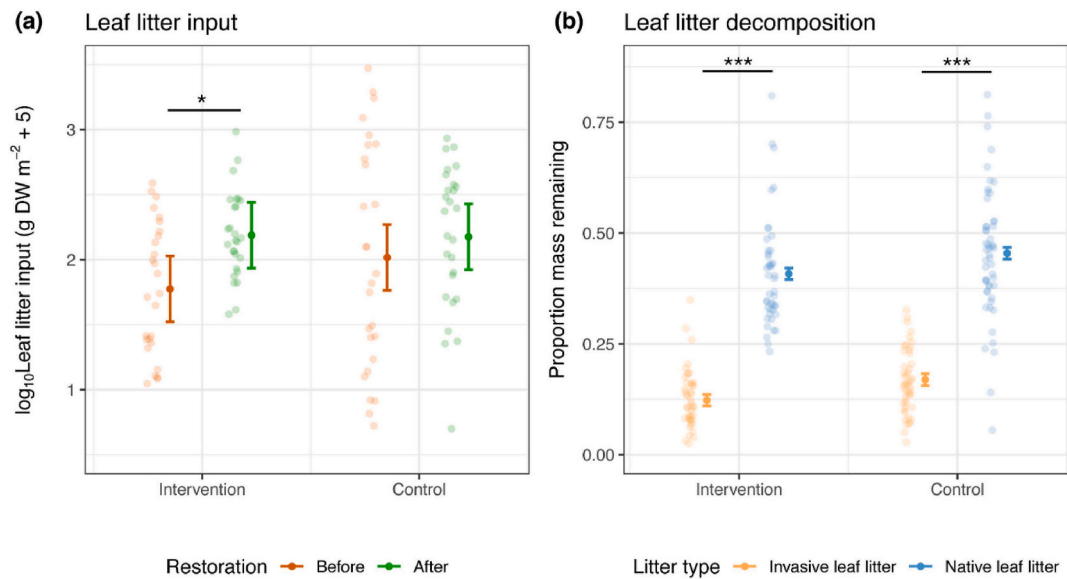


Fig. 3. (a) Leaf litter input (in g DW m⁻²) in the intervention and control wetlands before (orange) and after (green) restoration and (b) proportions of invasive (in light orange) and native leaf litter masses (in light blue) remaining after restoration in the intervention and control wetlands. Opaque points are the predicted means and error bars indicate standard errors from the statistically significant linear mixed effects models; semi-transparent points are the raw data; asterisks indicate significant differences.

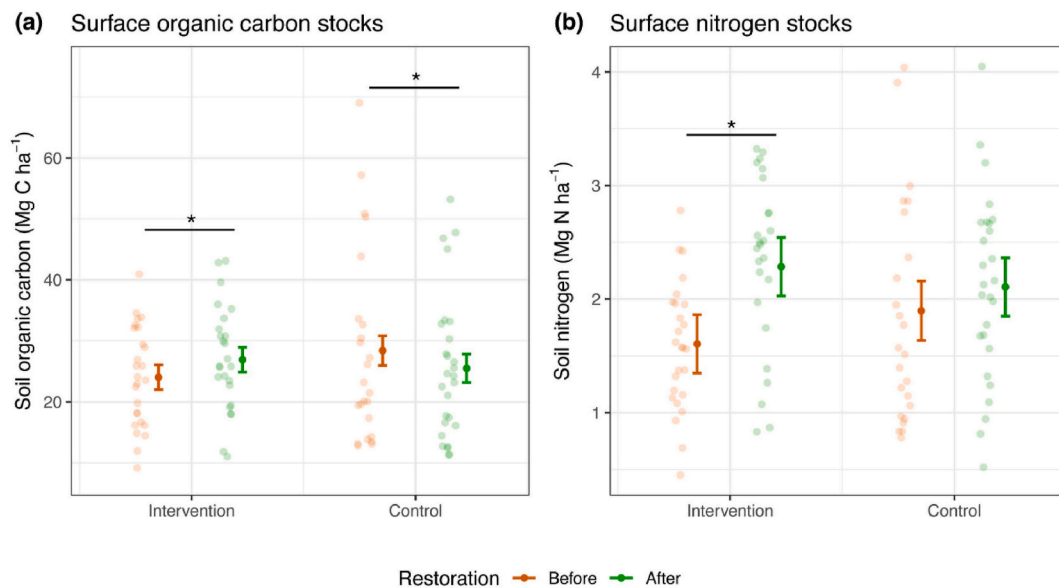


Fig. 4. (a) Surface organic carbon stocks (in Mg C ha⁻¹) and (b) surface nitrogen stocks (in Mg N ha⁻¹) in the intervention and control wetlands before (orange) and after (green) restoration. Opaque points are the predicted means and error bars indicate standard errors from the statistically significant linear mixed effects models; semi-transparent points are the raw data; asterisks indicate significant differences.

3.5. Soil moisture content

Soil moisture content differed significantly between the before- and after-restoration time points, but the effect varied between control and intervention wetlands (restoration time point \times treatment: $\chi^2 = 4.13$, $P = 0.04$; Table S9). Specifically, soil moisture content in the intervention wetlands increased, on average, by 55 % following restoration (from 2.28 % to 3.53 %), whereas soil moisture levels in the control wetlands remained comparable between the before- and after-restoration time points (Fig. 5). Overall, soil moisture levels were linked to a wetland's soil organic carbon content (restoration time point \times surface organic carbon stocks: $\chi^2 = 3.23$, $P = 0.07$), with soil moisture tending to increase with increasing surface organic carbon stocks at the after-

restoration time point (Fig. 6).

3.6. Long-term restored wetland site

Limpert et al. (2020) reported that restoration decreased CO₂ emissions (R_e), on average, by 60 % one month after restoration in both the submerged (from 6.08 to 2.42 g CO₂ m⁻² day⁻¹) and fringing inundation zones (from 7.39 to 1.78 g CO₂ m⁻² day⁻¹). After six years, we found that CO₂ emissions from the fringing zone remained similarly low (1.25 g CO₂ m⁻² day⁻¹) compared to emissions one month after restoration but were, on average, 62 % higher from the submerged inundation zone (9.83 g CO₂ m⁻² day⁻¹; restoration time point \times inundation zone: $F_{2,33} = 10.67$, $P < 0.001$; Fig. 7a; Table S10).

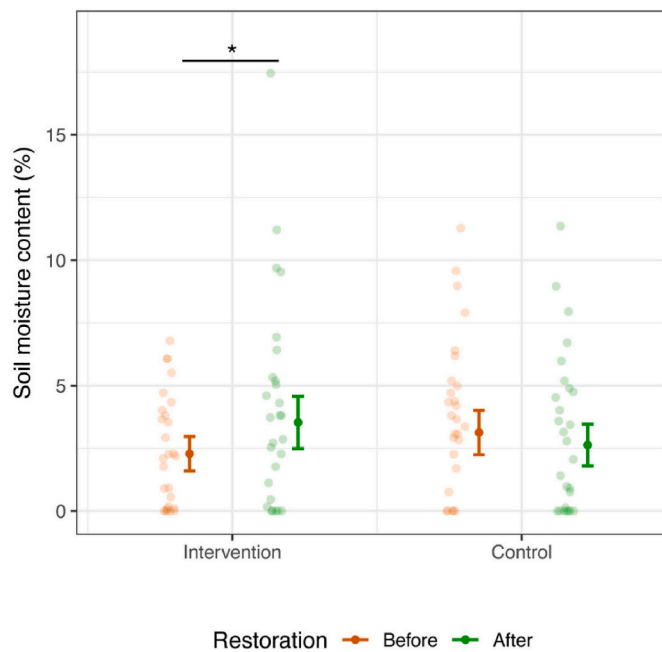


Fig. 5. Soil moisture content (in %) in the intervention and control wetlands before (orange) and after restoration (green). Opaque points are the predicted means and error bars indicate standard errors from the statistically significant linear mixed effects model; semi-transparent points are the raw data; asterisks indicate significant differences.

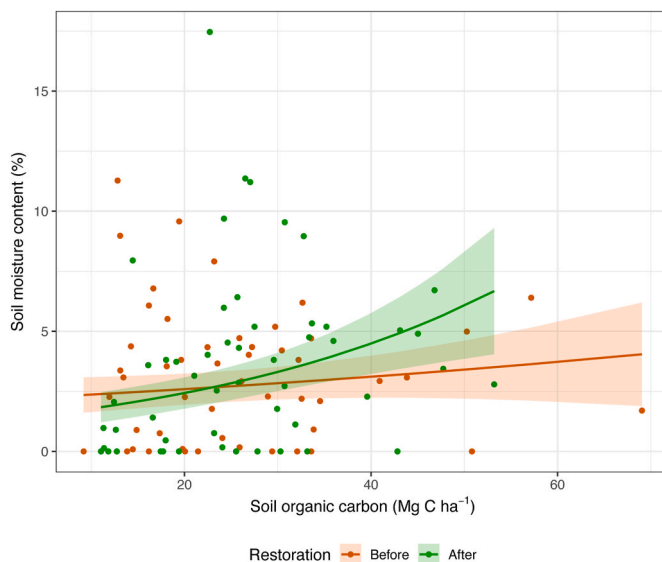


Fig. 6. Relationship between soil moisture content (in %) and surface organic carbon stocks (in Mg C ha^{-1}) at the before- (orange) and after-restoration (green) time points. Points are the raw data; the lines indicate the statistically significant effect following the best-fitting mixed effect model $\pm 95\%$ confidence intervals.

The net ecosystem exchange (NEE) did not significantly differ between the submerged and fringing inundation zones six years after restoration ($F_{1,2} = 2.13$, $P = 0.28$; Fig. 7b). Note that Limpert et al. (2020) did not measure NEE during their monitoring campaign. Therefore, we cannot make any inferences about changes in NEE since the wetland was restored. Contrastingly, average methane fluxes from both inundation zones increased from $-0.006 \text{ g CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ before restoration and $-0.004 \text{ g CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ one month after restoration to $0.005 \text{ g CH}_4 \text{ m}^{-2} \text{ day}^{-1}$ six years after restoration ($F_{2,34} = 3.93$, $P = 0.03$;

Fig. 7c). Considering the NEE and CH_4 fluxes, average net carbon fluxes from the long-term restored wetland were $0.96 \text{ g C m}^{-2} \text{ day}^{-1}$ across both inundation zones ($F_{1,2} = 2.04$, $P = 0.29$; Fig. 7d). We could not detect any N_2O fluxes.

Surface organic carbon stocks increased, on average, by 53 % six years after restoration (from 16.74 to $25.57 \text{ Mg C ha}^{-1}$) within both the submerged and fringing inundation zones ($F_{1,14} = 7.65$, $P = 0.02$; Fig. 8; Table S11). However, the effect of restoration on surface organic carbon stocks differed across soil sampling depths and inundation zones (restoration time point \times inundation zone \times sampling depth: $F_{1,12} = 5.91$, $P = 0.03$; Table S12). Specifically, surface organic carbon stocks within the fringing zone increased, on average, by 68 % and 90 % in the upper (0–5 cm) and deeper (5–10 cm) soil layers, respectively, whereas within the submerged zone, surface organic carbon stocks increased, on average, by 99 % in the upper soil layer (0–5 cm), but did not significantly change in the deeper soil layer (5–10 cm; Fig. S4).

4. Discussion

With global warming intensifying, the restoration of degraded freshwater wetlands to mitigate climate change and its impacts is becoming increasingly important (Bossio et al., 2020). We found that restoring degraded riparian wetlands through rewetting and active revegetation reduced net carbon emissions ($\text{CO}_2 + \text{CH}_4$ fluxes) by 39 % and increased surface organic carbon and nitrogen stocks by 12 % and 43 %, respectively, within one year of restoration. Contrastingly, net carbon emissions from the unrestored control wetlands increased by 169 % during our measurement period, with average surface organic carbon stocks decreasing by 10 %. In the restored wetlands, the native wetland plant cover increased significantly after restoration, with leaf litter from two dominant native wetland species showing lower decomposition levels than leaf litter derived from an invasive lawn species, indicating the potential to promote higher carbon preservation in the soil. Furthermore, the soils of the restored wetland sites retained more moisture during the dry period, whereas the degraded control wetlands were drier compared to before restoration took place. We also monitored the carbon dynamics in a long-term restored riparian wetland and found that surface organic carbon stocks increased by 53 % six years after restoration, demonstrating sustained long-term benefits of wetland restoration.

We found that CO_2 emissions decreased by 40 % in the short-term restored wetland sites, whereas CO_2 fluxes increased by 46 % in the unrestored control sites. The reinstatement of hydrological dynamics within the intervention wetlands creates anoxic conditions in the wetland sediments, which limits the aerobic mineralisation of carbon and, consequently, decreases CO_2 production (Mitsch et al., 2013). Even when the intervention wetlands returned to dry conditions after restoration, they retained higher soil moistures and lower levels of CO_2 production. Importantly, in the long-term restored wetland, the reduction in CO_2 fluxes observed one month after restoration (refer to Limpert et al., 2020) was sustained six years post-restoration, at least in the fringing zone. Contrastingly, increased CO_2 fluxes in the submerged zone after restoration were likely driven by the dark respiration of wetland vegetation, which is supported by a relatively low NEE, indicating high gross primary productivity in the long-term restored wetland (GPP, given that $\text{GPP} = \text{R}_e - \text{NEE}$). In the unrestored control wetlands, higher CO_2 emissions were likely a result of increased rainfall levels while restoration took place (Australian spring) – a phenomenon known as the “Birch effect” or rainfall pulse response (Jiang et al., 2021). These findings underscore the importance of sustained hydrological restoration, since prolonged water coverage is critical for creating anoxic soil conditions that limit microbial carbon mineralisation and enhance long-term carbon sequestration (Kayranli et al., 2010). Overall, our findings demonstrate the efficacy of riparian wetland restoration in reducing CO_2 emissions. However, annual flux estimates are needed to determine if and when such wetland systems turn into net carbon sinks.

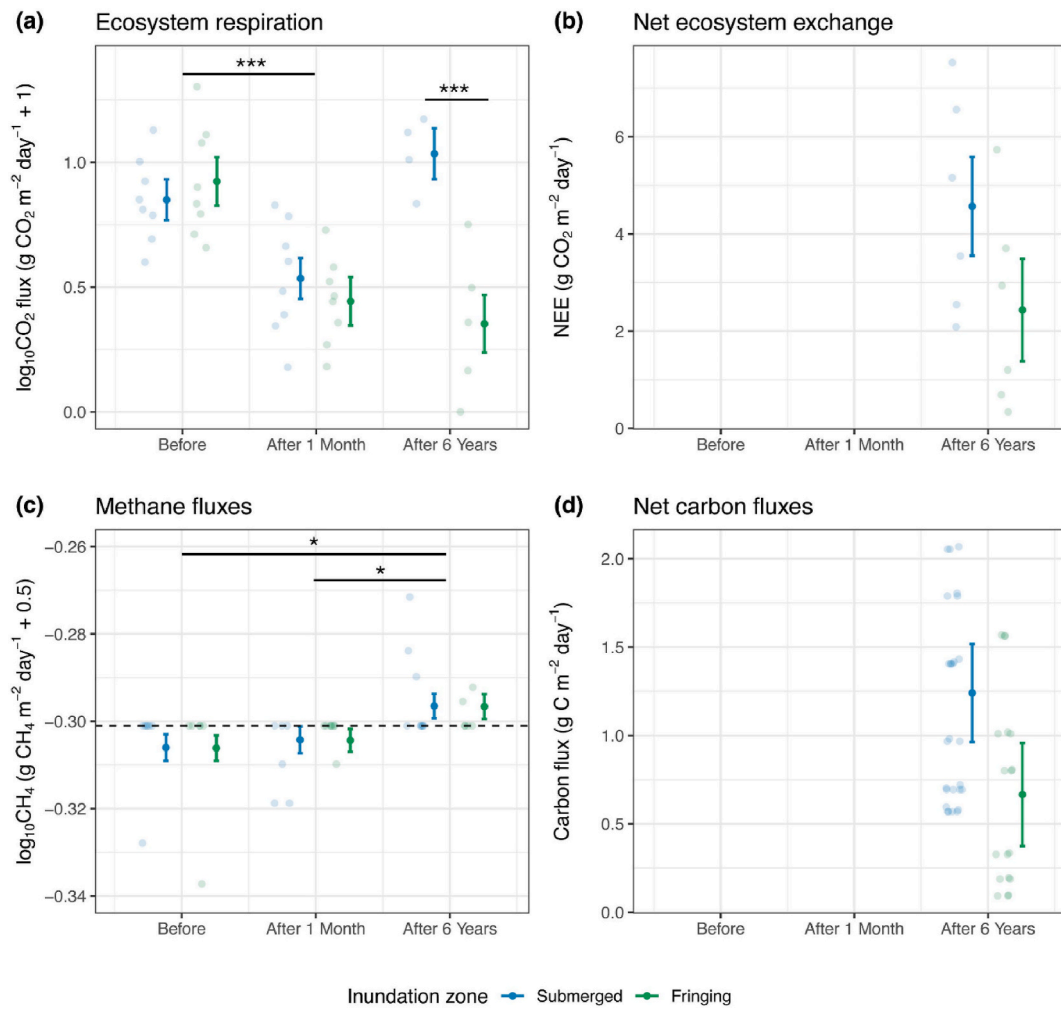


Fig. 7. (a) Ecosystem respiration (R_e ; in $\text{g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$), (b) the net ecosystem exchange (NEE; in $\text{g CO}_2 \text{ m}^{-2} \text{ day}^{-1}$), (c) methane fluxes (CH_4 ; in $\text{g CH}_4 \text{ m}^{-2} \text{ day}^{-1}$), and (d) net carbon fluxes (in $\text{g C m}^{-2} \text{ day}^{-1}$) from the submerged (in blue) and fringing (in green) inundation zones within the long-term restored wetland before, one month and six years after restoration. Opaque points are the predicted means and error bars indicate standard errors from the statistically significant linear mixed effects models; semi-transparent points are the raw data; asterisks indicate significant differences. Dashed lines indicate the zero line.

CH_4 and N_2O fluxes did not significantly increase following restoration. In some instances, wetland restoration can produce notable CH_4 and N_2O emissions, which can offset any greenhouse gas emission reductions and thus complicate the short-term climate benefits of wetland restoration (Malerba et al., 2022; Schuster et al., 2024). However, there are several ways through which CH_4 and N_2O fluxes can be mitigated. For example, CH_4 production can be alleviated through competition between methanogens and iron-reducing microbes, which can limit the availability of hydrogen and acetate for methanogenesis (Jerman et al., 2009). Such interactions are particularly relevant in wetlands that undergo frequent wetting and drying cycles, like riparian wetlands, which can re-oxidise reduced iron (Küsel et al., 2008). Furthermore, the presence of vascular plants can hamper CH_4 emissions by promoting CH_4 oxidation in plant stems and in the soils at the rhizosphere. Similarly, floating vegetation can trap CH_4 bubbles before they reach the water surface, thereby facilitating microbial CH_4 oxidation within the water column (Bastviken et al., 2023; Dušek et al., 2023; Wang et al., 2024). Notably, we observed negative CH_4 fluxes in some restored and unrestored wetlands, likely indicating net methane uptake via methanotrophy (Kayranli et al., 2010). Net CH_4 uptake typically occurs in dry, aerated soils, particularly near oxic-anoxic interfaces or in unsaturated surface layers, where CH_4 uptake exceeds production (Dalal et al., 2008). Nevertheless, even flooded freshwater wetlands can exhibit net CH_4 uptake under specific conditions when microbial oxidation is highly

efficient (Kolb and Horn, 2012). Plants also compete with soil microbes for nutrients like nitrate (Hodge et al., 2000; Kuzyakov and Xu, 2013), effectively reducing denitrification and the production of N_2O (He et al., 2016). The prompt re-establishment of native wetland vegetation, which can be facilitated through active revegetation, may thus be crucial to help regulate the release of CH_4 and N_2O after restoration. Nevertheless, more research is needed to determine the prevalence of competitive dynamics and plant-mediated mechanisms to regulate greenhouse gas fluxes in restored riparian wetlands.

Contrary to the short-term restored wetlands, we found that CH_4 emissions increased significantly in the long-term restored riparian wetland six years post-restoration. Over time, increased CH_4 emissions may be due to increased soil carbon availability, a key substrate for methanogenesis (Moreno-Mateos et al., 2012). Alternatively, reduced competition between methanogens and iron-reducing microbes due to iron depletion can also lead to increased CH_4 production (Keshta et al., 2023). Nevertheless, even if CH_4 emissions increase over time, greater CO_2 sequestration rates associated with higher plant productivity should supersede these CH_4 emissions, resulting in net carbon uptake (Schuster et al., 2024; Whiting and Chanton, 2001). However, more longitudinal greenhouse gas flux assessments are needed to capture any daily and seasonal variability in emissions to more accurately determine the long-term effects of restoration on CH_4 dynamics in freshwater wetlands.

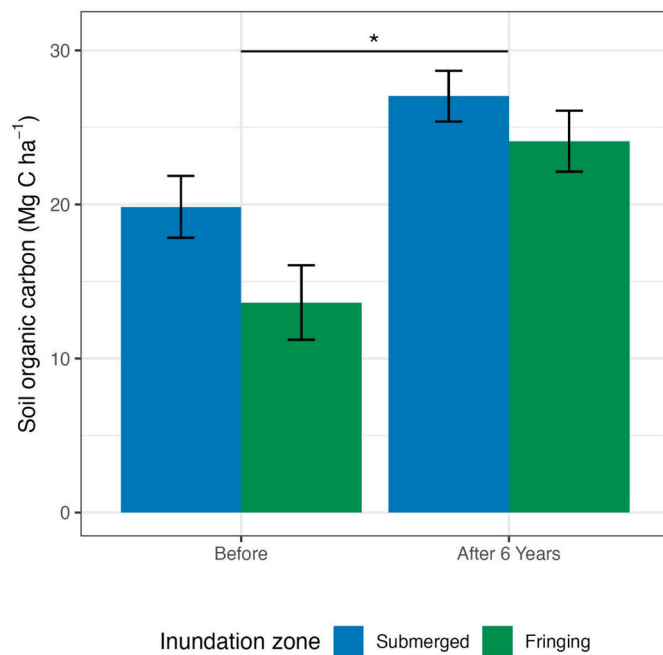


Fig. 8. Surface organic carbon stocks (in Mg C ha^{-1}) in the submerged (in blue) and fringing inundation zones (in green) within the long-term restored wetland before and six years after restoration. Bars show the predicted means and error bars indicate standard errors from the statistically significant linear mixed effects model; the asterisk indicates significant differences.

We found that surface organic carbon stocks significantly increased after restoration. Combined with anoxic conditions prevailing in inundated wetland soils, these higher carbon stocks are likely a result of the increased leaf litter input associated with increased plant productivity and the type of leaf litter found within the restored wetlands. Specifically, we found that the native leaf litter derived from two dominant native wetland plant species and buried in the wetland soils experienced less decomposition than the invasive leaf litter derived from annual lawn plant species typically found in degraded wetlands. These findings indicate that the native leaf litter was more recalcitrant than the invasive litter, which results in higher plant carbon availability for preservation in the soil (Schlesinger, 1977). Similarly, the more recalcitrant standardised rooibos tea experienced slower decomposition than the labile green tea, with decomposition dynamics being comparable to other Australian freshwater wetland studies (Trevathan-Tackett et al., 2021). Our findings highlight the role of recalcitrant native vegetation in replenishing soil organic carbon stocks after restoration. Freshwater wetland restoration through rewetting combined with active revegetation may thus be crucial to promptly re-establish critical carbon dynamics within restored wetlands and guarantee the short-term success of restoration for climate change mitigation.

The short-term restored wetlands had significantly higher surface nitrogen stocks and retained higher soil moisture during the dry period, both of which can be linked to the reinstatement of critical ecosystem functions. For example, increased surface nitrogen stocks may indicate higher levels of nitrogen cycling and retention, which is critical for nutrient removal and water purification (Johnston, 1991; Land et al., 2016). Additionally, higher soil nitrogen levels can support plant growth and diversity, which, in turn, can help regulate floods and reduce soil erosion (Wheeler, 2005). Higher water retention also facilitates certain decomposition processes, such as abiotic leaching, that reintroduce soluble nutrients and organic matter from leaf litter into the soil for plants and animals to use (Fennessy et al., 2023). Accordingly, abiotic leaching likely drove the increased mass loss in all tea and litter types in the intervention compared to the control wetlands (Trevathan-Tackett

et al., 2021), while anaerobic conditions are expected to facilitate slower decay rates and carbon preservation in the longer term (Zhang et al., 2020). Higher water retention in the soil during dry periods further indicates increased water storage capacities of wetland soils, which is critical for drought resilience (Ferreira et al., 2023). Importantly, soil moisture retention increased with increasing surface organic carbon stocks, indicating that the reinstatement of these ecosystem functions was likely linked to the rapid re-establishment of carbon dynamics, including increased carbon sequestration and storage in productive, anoxic soil (Libohova et al., 2018). Our findings thus suggest that restoration through rewetting and active revegetation can effectively restore critical carbon and nitrogen dynamics and associated ecosystem functions shortly after restoration.

Our findings align with other studies that investigated the benefits of restoring riparian wetlands for carbon and nitrogen benefits. For instance, Audet et al. (2013) reported a 37 % reduction in CO_2 emissions one year after rewetting a degraded riparian wetland, with no changes in N_2O fluxes. Similarly, CH_4 fluxes remained stable overall, apart from a permanently inundated area within the restored wetland that exhibited elevated CH_4 emissions during the summer months. Other studies also found no significant increases in CH_4 emissions from ephemeral wetlands after rewetting (Schuster et al., 2024), indicating that water table fluctuations and/or the presence of vascular wetland plants may mitigate short-term CH_4 emissions (Cui et al., 2024; Kayranli et al., 2010). Our observed increases in surface organic carbon and nitrogen stocks are also consistent with those reported by other studies (An et al., 2021; Xu et al., 2019), underscoring the potential of freshwater wetland restoration to rapidly reinstate critical biogeochemical functions. Overall, our study contributes to the growing body of evidence that the restoration of ephemeral wetlands, like riparian wetlands, can lead to immediate reductions in CO_2 emissions and enhancements in soil carbon and nitrogen stocks. Nevertheless, longer-term biogeochemical dynamics warrant further investigation to optimise restoration strategies for climate change mitigation.

To investigate the short-term effects of wetland restoration, we employed a paired experimental design, where each restored wetland was paired with an unrestored control wetland to disentangle the effects of restoration from other environmental or temporal effects on wetland dynamics (Mitsch and Gosselink, 2015; Schuster et al., 2024). However, to quantify the long-term restoration effects on wetland organic carbon stocks and greenhouse gas fluxes, we adopted the original experimental design by Limpert et al. (2020) and sampled from one restored wetland site only, without including any control wetlands. While this approach provides rare insights into restored wetland dynamics over multiple years, the lack of control sites means that the observed changes in organic carbon stocks and greenhouse gas flux dynamics cannot be exclusively attributed to restoration efforts and may also reflect natural processes unrelated to local management. It is thus important to use long-term paired experimental designs to isolate restoration effects from broader environmental dynamics. Future studies assessing wetland restoration success should prioritise such paired designs to ensure robust and reliable conclusions.

5. Conclusions

We showed that restoring degraded riparian wetlands through rewetting and revegetation significantly reduced CO_2 emissions, whereas CH_4 and N_2O emissions did not significantly increase within one year of restoration. We also found that surface organic carbon stocks, native plant cover, and plant litter production increased after restoration. An increase in the number and abundance of native plant species that produce more recalcitrant and decomposition-resistant leaf litter, combined with anoxic conditions prevailing in the soil, likely promoted increased carbon preservation in the restored wetlands. These findings highlight the efficacy of riparian wetland restoration through rewetting and active revegetation as a natural climate solution to cut

carbon emissions and increase soil carbon storage. We further showed that restored wetlands had higher surface nitrogen stocks and retained higher soil moisture during the dry period, which indicates the reinstatement of critical ecosystem functions like nutrient and organic matter retention and increased water storage capacities, which are directly linked to climate change resilience. Importantly, our findings highlight the effectiveness of freshwater wetland restoration for climate benefits beyond peatland ecosystems and will help inform future policies on implementing management actions to mitigate climate change and its impacts. Future studies should include annual greenhouse gas balances to inform about the potential of restoration to turn degraded non-peat wetlands into carbon sinks.

CRedit authorship contribution statement

Lukas Schuster: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Stacey Trevathan-Tackett:** Writing – review & editing, Investigation, Data curation, Conceptualization. **Paul Carnell:** Writing – review & editing, Funding acquisition, Conceptualization. **Kay Morris:** Writing – review & editing, Data curation, Conceptualization. **Bryan Mole:** Writing – review & editing, Data curation, Conceptualization. **Martino E. Malerba:** Writing – review & editing, Supervision, Funding acquisition, Data curation, 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.

Acknowledgements

We thank Rachel Kelly, Rocio Araya, Josh Glen, Dr Sutthana Plodomboon, Ms Karnjanaporn Sornchai, and the numerous interns and volunteers who helped with fieldwork and sample processing. We also thank Ashley Sparrow for providing valuable comments and suggestions on the manuscript. We are grateful to Damien Cook, Jacqui Slings, Talia Jenkins, and the Wetland Revival Trust for facilitating this research and to landowners who allowed us to work on their lands. This work was supported by the Future Drought Fund: Drought Resilient Soils and Landscapes Grant Program (project ID: 4-H8FXRTH) and Deakin University's Blue Sky Fund. M.E.M. and S.T.T. were supported by ARC DECRA Fellowships (project IDs: DE220100752 for M.E.M. and DE210101029 for S.T.T.).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jenvman.2025.126433>.

Data availability

All data is available on Figshare (doi.org/10.6084/m9.figshare.29435528).

References

An, Y., Gao, Y., Liu, X., Tong, S., Liu, B., Song, T., Qi, Q., 2021. Soil organic carbon and nitrogen variations with vegetation succession in passively restored freshwater wetlands. *Wetlands* 41, 1–10.

Audet, J., Elsgaard, L., Kjaergaard, C., Larsen, S.E., Hoffmann, C.C., 2013. Greenhouse gas emissions from a Danish riparian wetland before and after restoration. *Ecol. Eng.* 57, 170–182.

Bastviken, D., Treat, C.C., Pangala, S.R., Gauci, V., Enrich-Prast, A., Karlson, M., Gålfalk, M., Romano, M.B., Sawakuchi, H.O., 2023. The importance of plants for methane emission at the ecosystem scale. *Aquat. Bot.* 184, 103596.

Bivand, R.S., Wong, D.W., 2018. Comparing implementations of global and local indicators of spatial association. *Test* 27, 716–748.

Bonetti, G., Limpert, K.E., Brodersen, K.E., Trevathan-Tackett, S.M., Carnell, P.E., Macreadie, P.I., 2022. The combined effect of short-term hydrological and N-fertilization manipulation of wetlands on CO₂, CH₄, and N₂O emissions. *Environ. Pollut.* 294, 118637.

Bonetti, G., Trevathan-Tackett, S.M., Carnell, P.E., Treby, S., Macreadie, P.I., 2021. Local vegetation and hydroperiod influence spatial and temporal patterns of carbon and microbe response to wetland rehabilitation. *Appl. Soil Ecol.* 163.

Bossio, D., Cook-Patton, S., Ellis, P., Fargione, J., Sanderman, J., Smith, P., Wood, S., Zomer, R., Von Unger, M., Emmer, I., 2020. The role of soil carbon in natural climate solutions. *Nat. Sustain.* 3, 391–398.

Brooks, M.E., Kristensen, K., Van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Mächler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *R J.* 9, 378–400.

Bureau of Meteorology, 2024. Climate Statistics for Australian Locations. Retrieved 4 Sep 2024 from http://www.bom.gov.au/climate/averages/tables/cw_080023.shtml.

Chimner, R.A., Ewel, K.C., 2005. A tropical freshwater wetland: II. Production, decomposition, and peat formation. *Wetl. Ecol. Manag.* 13, 671–684.

Cole, J.J., Prairie, Y.T., Caraco, N.F., McDowell, W.H., Tranvik, L.J., Striegl, R.G., Duarte, C.M., Kortelainen, P., Downing, J.A., Middelburg, J.J., 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. *Ecosyst.* 10, 172–185.

Cui, S., Liu, P., Guo, H., Nielsen, C.K., Pullens, J.W.M., Chen, Q., Pugliese, L., Wu, S., 2024. Wetland hydrological dynamics and methane emissions. *Commun. Earth Environ.* 5.

Cunha-Santino, M.B.d., Bianchini Júnior, I., 2023. Reviewing the organic matter processing by wetlands. *Acta Limnol. Brasil.* 35.

Dalal, R., Allen, D., Livesley, S., Richards, G., 2008. Magnitude and biophysical regulators of methane emission and consumption in the Australian agricultural, forest, and submerged landscapes: a review. *Plant Soil* 309, 43–76.

Davidson, N.C., Fluet-Chouinard, E., Finlayson, C.M., 2018. Global extent and distribution of wetlands: trends and issues. *Mar. Freshwat. Res.* 69.

Dusek, J., Faußer, A., Stellner, S., Kazda, M., 2023. Stems of *Phragmites australis* are buffering methane and carbon dioxide emissions. *Sci. Total Environ.* 882, 163493.

Fennessy, M.S., Moon, J.B., Max Finlayson, C., 2023. Linking wetland ecological processes with the delivery of ecosystem services. In: Gell, P.A., Davidson, N.C., Finlayson, C.M. (Eds.), *Ramsar Wetlands*. Elsevier, pp. 153–178.

Ferreira, C.S.S., Kasanin-Grubin, M., Solomun, M.K., Sushkova, S., Minkina, T., Zhao, W., Kalantari, Z., 2023. Wetlands as nature-based solutions for water management in different environments. *Curr. Opin. Environ. Sci. Health* 33.

Fluet-Chouinard, E., Stocker, B.D., Zhang, Z., Malhotra, A., Melton, J.R., Poulter, B., Kaplan, J.O., Goldewijk, K.K., Siebert, S., Minayeva, T., 2023. Extensive global wetland loss over the past three centuries. *Nature* 614, 281–286.

Godínez-Alvarez, H., Herrick, J., Mattocks, M., Toledo, D., Van Zee, J., 2009. Comparison of three vegetation monitoring methods: their relative utility for ecological assessment and monitoring. *Ecol. Indic.* 9, 1001–1008.

Gopal, B., 2009. Biodiversity in wetlands. In: Maltby, E., Barker, T. (Eds.), *The Wetlands Handbook*. Blackwell Publishing Ltd, Oxford, UK, pp. 65–95.

He, H., Jansson, P.-E., Svensson, M., Meyer, A., Klemetsson, L., Kasimir, Å., 2016. Factors controlling nitrous oxide emission from a spruce forest ecosystem on drained organic soil, derived using the CoupModel. *Ecol. Model.* 321, 46–63.

Hodge, A., Robinson, D., Fitter, A., 2000. Are microorganisms more effective than plants at competing for nitrogen? *Trends Plant Sci.* 5, 304–308.

Jerman, V., Metje, M., Mandić-Mulec, I., Frenzel, P., 2009. Wetland restoration and methanogenesis: the activity of microbial populations and competition for substrates at different temperatures. *Biogeosciences* 6, 1127–1138.

Jiang, Z., Bian, H., Xu, L., Li, M., He, N., 2021. Pulse effect of precipitation: spatial patterns and mechanisms of soil carbon emissions. *Front. Ecol. Evol.* 9.

Johnston, C.A., 1991. Sediment and nutrient retention by freshwater wetlands: effects on surface water quality. *Crit. Rev. Environ. Sci. Technol.* 21, 491–565.

Kadykalo, A.N., Findlay, C.S., 2016. The flow regulation services of wetlands. *Ecosyst. Serv.* 20, 91–103.

Kayranli, B., Scholz, M., Mustafa, A., Hedmark, Å., 2010. Carbon storage and fluxes within freshwater wetlands: a critical review. *Wetlands* 30, 111–124.

Keshta, A.E., Yarwood, S.A., Baldwin, A.H., 2023. Methane emissions are highly variable across wetland habitats in natural and restored tidal freshwater wetlands. *Wetlands* 43.

Keuskamp, J.A., Dingemans, B.J.J., Lehtinen, T., Sarneel, J.M., Hefting, M.M., Muller-Landau, H., 2013. Tea bag index: a novel approach to collect uniform decomposition data across ecosystems. *Methods Ecol. Evol.* 4, 1070–1075.

Kolb, S., Horn, M.A., 2012. Microbial CH₄ and N₂O consumption in acidic wetlands. *Front. Microbiol.* 3, 78.

Küsel, K., Blöthe, M., Schulz, D., Reiche, M., Drake, H.L., 2008. Microbial reduction of iron and porewater biogeochemistry in acidic peatlands. *Biogeosciences* 5, 1537–1549.

Kuzyakov, Y., Xu, X., 2013. Competition between roots and microorganisms for nitrogen: mechanisms and ecological relevance. *New Phytol.* 198, 656–669.

Lal, R., Pimentel, D., 2008. Soil erosion: a carbon sink or source? *Science* 319, 1040–1042.

Lal, R., Smith, P., Jungkunst, H.F., Mitsch, W.J., Lehmann, J., Nair, P.R., McBratney, A.B., de Moraes Sá, J.C., Schneider, J., Zinn, Y.L., 2018. The carbon sequestration potential of terrestrial ecosystems. *J. Soil Water Conserv.* 73, 145A–152A.

- Land, M., Granéli, W., Grimvall, A., Hoffmann, C.C., Mitsch, W.J., Tonderski, K.S., Verhoeven, J.T.A., 2016. How effective are created or restored freshwater wetlands for nitrogen and phosphorus removal? A systematic review. *Environ. Evid.* 5.
- Lane, R.R., Mack, S.K., Day, J.W., DeLaune, R.D., Madison, M.J., Precht, P.R., 2016. Fate of soil organic carbon during wetland loss. *Wetlands* 36, 1167–1181.
- Lenth, R., 2024. Emmeans: estimated marginal means, aka least-squares means. R package, version 1.10.4.
- Libohova, Z., Seybold, C., Wysocki, D., Wills, S., Schoeneberger, P., Williams, C., Lindbo, D., Stott, D., Owens, P.R., 2018. Reevaluating the effects of soil organic matter and other properties on available water-holding capacity using the national cooperative soil survey characterization database. *J. Soil Water Conserv.* 73, 411–421.
- Limpert, K.E., Carnell, P.E., Trevathan-Tackett, S.M., Macreadie, P.I., 2020. Reducing emissions from degraded floodplain wetlands. *Front. Environ. Sci.* 8.
- Loisel, J., Gallego-Sala, A., 2022. Ecological resilience of restored peatlands to climate change. *Commun. Earth Environ.* 3.
- Malerba, M.E., Edwards, B., Schuster, L., Odebiri, O., Glen, J., Kelly, R., Phan, P., Grinham, A., Macreadie, P.I., 2025. Pondi – a low-cost logger for long-term monitoring of methane, carbon dioxide, and Nitrous Oxide in Aquatic and Terrestrial Systems. EGUSphere.
- Malerba, M.E., Friess, D.A., Peacock, M., Grinham, A., Taillardat, P., Rosentreter, J.A., Webb, J., Iram, N., Al-Haj, A.N., Macreadie, P.I., 2022. Methane and nitrous oxide emissions complicate the climate benefits of teal and blue carbon wetlands. *One Earth* 5, 1336–1341.
- Meli, P., Rey Benayas, J.M., Balvanera, P., Martínez Ramos, M., 2014. Restoration enhances wetland biodiversity and ecosystem service supply, but results are context-dependent: a meta-analysis. *PLoS One* 9.
- Meng, B., Liu, J.L., Bao, K., Sun, B., 2020. Methodologies and management framework for restoration of wetland hydrologic connectivity: a synthesis. *Integr. Environ. Assess. Manag.* 16, 438–451.
- Mitsch, W.J., Bernal, B., Nahlik, A.M., Mander, Ü., Zhang, L., Anderson, C.J., Jørgensen, S.E., Brix, H., 2013. Wetlands, carbon, and climate change. *Landsc. Ecol.* 28, 583–597.
- Mitsch, W.J., Gosselink, J.G., 2015. *Wetlands*. John Wiley & Sons.
- Mitsch, W.J., Mander, Ü., 2018. Wetlands and carbon revisited. *Ecol. Eng.* 114, 1–6.
- Moore, T., Basiliko, N., 2006. Decomposition in boreal peatlands. In: Wieder, R.K., Vitt, D.H. (Eds.), *Boreal Peatland Ecosystems*. Springer, Berlin, Heidelberg, pp. 125–143.
- Moreno-Mateos, D., Power, M.E., Comin, F.A., Yockteng, R., 2012. Structural and functional loss in restored wetland ecosystems. *PLoS Biol.* 10, e1001247.
- Neubauer, S.C., Megonigal, J.P., 2015. Moving beyond global warming potentials to quantify the climatic role of ecosystems. *Ecosyst.* 18, 1000–1013.
- Odebiri, O., Archbold, J., Glen, J., Macreadie, P.I., Malerba, M.E., 2024. Excluding livestock access to farm dams reduces methane emissions and boosts water quality. *Sci. Total Environ.* 951.
- Pinheiro, J., Bates, D., R Core Team, 2024. nlme: linear and nonlinear mixed effects models. R package version 3, pp. 1–166.
- R Core Team, 2013. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ramsar Convention Secretariat, 2019. Information Sheet on Ramsar Wetlands (RIS): Kerang Wetlands.
- Rosentreter, J.A., Borges, A.V., Deemer, B.R., Holgerson, M.A., Liu, S., Song, C., Melack, J., Raymond, P.A., Duarte, C.M., Allen, G.H., 2021. Half of global methane emissions come from highly variable aquatic ecosystem sources. *Nat. Geosci.* 14, 225–230.
- Schlesinger, W.H., 1977. *Biogeochemistry: an Analysis of Global Change*, second ed. Academic Press, San Diego, California.
- Schuster, L., Taillardat, P., Macreadie, P.I., Malerba, M.E., 2024. Freshwater wetland restoration and conservation are long-term natural climate solutions. *Sci. Total Environ.* 922, 171218.
- Schwieger, S., Kreyling, J., Couwenberg, J., Smiljanić, M., Weigel, R., Wilmking, M., Blume-Werry, G., 2021. Wetter is better: rewetting of minerotrophic peatlands increases plant production and moves them towards carbon sinks in a dry year. *Ecosyst.* 24, 1093–1109.
- Smith, K.A., Ball, T., Conen, F., Dobbie, K.E., Massheder, J., Rey, A., 2018. Exchange of greenhouse gases between soil and atmosphere: interactions of soil physical factors and biological processes. *Eur. J. Soil Sci.* 69, 10–20.
- Spieles, D.J., 2022. Wetland construction, restoration, and integration: a comparative review. *Land* 11, 554.
- Treby, S., Carnell, P.E., Trevathan-Tackett, S.M., Bonetti, G., Macreadie, P.I., 2020. Assessing passive rehabilitation for carbon gains in rain-filled agricultural wetlands. *J. Environ. Manage.* 256, 109971.
- Tremblay, A., 2005. Greenhouse Gas emissions-fluxes and Processes: Hydroelectric Reservoirs and Natural Environments. Springer Science & Business Media.
- Trevathan-Tackett, S.M., Kepfer-Rojas, S., Engelen, A.H., York, P.H., Ola, A., Li, J., Kelleway, J.J., Jinks, K.I., Jackson, E.L., Adame, M.F., Pendall, E., Lovelock, C.E., Connolly, R.M., Watson, A., Visby, I., Trethowan, A., Taylor, B., Roberts, T.N.B., Petch, J., Farrington, L., Djukic, I., Macreadie, P.I., 2021. Ecosystem type drives tea litter decomposition and associated prokaryotic microbiome communities in freshwater and coastal wetlands at a continental scale. *Sci. Total Environ.* 782.
- Wang, F., Zhang, S., Hu, X., Lv, X., Liu, M., Ma, Y., Manirakiza, B., 2024. Floating plants reduced methane fluxes from wetlands by creating a habitat conducive to methane oxidation. *J. Environ. Sci.* 135, 149–160.
- Wheeler, B.D., 2005. Water and Plants in Freshwater Wetlands, Eco-hydrology. Routledge, pp. 127–180.
- Whiting, G.J., Chanton, J.P., 2001. Greenhouse carbon balance of wetlands: methane emission versus carbon sequestration. *Tellus B* 53, 521–528.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer.
- Wilson, J.B., 2011. Cover plus: ways of measuring plant canopies and the terms used for them. *J. Veg. Sci.* 22, 197–206.
- Xu, S., Liu, X., Li, X., Tian, C., 2019. Soil organic carbon changes following wetland restoration: a global meta-analysis. *Geoderma* 353, 89–96.
- Zedler, J.B., 2000. Progress in wetland restoration ecology. *Trends Ecol. Evol.* 15, 402–407.
- Zhang, S., Yu, Z., Lin, J., Zhu, B., 2020. Responses of soil carbon decomposition to drying-rewetting cycles: a meta-analysis. *Geoderma* 361.