

Assessing the effects of restoration and conservation on gaseous carbon fluxes and climate mitigation potential across six European coastal wetlands

Miguel Cabrera-Brufau^{a,*}, Camille Minaudo^a, Katrin Attermeyer^b, Alba Camacho-Santamans^a, Rafael Carballeira^c, Benjamin Misteli^b, Jorge Montes-Pérez^a, Daniel Morant^c, Biel Obrador^a, Antonio Picazo^c, Carlos Rochera^c, Mihai Adamescu^d, Raquel Ambrosio^e, Giancarlo Bachi^f, Nina Bègue^e, Martynas Bučas^g, Lúdia Cañas Ramírez^a, Marco Carloni^f, Lamara Cavalcante^h, Constantin Cazacu^d, Giovanni Checcucci^f, J. Pedro Coelho^h, Valentin Dinu^d, Valtere Evangelista^f, Ilenia Férez Martín^a, Jonas Gintauskas^g, Relu Giuca^d, Anis Guelmami^e, Mirco Guerrazzi^f, Samuel Hilaire^e, Marija Kataržytė^g, Ana I. Lillebø^h, Raquel Lizán^c, Bruna R.F. Oliveira^h, Vitor H. Oliveira^h, Marta Pedrón^c, Jolita Petkuvienė^g, Tudor Racoviceanu^d, Michael Ronse^e, Chiara Santinelli^f, Ana I. Sousa^h, Wouter Suykerbuykⁱ, Edvinas Tiškus^g, Claudia Tropea^f, Diana Vaičiūtė^g, Silvia Valsecchi^f, Marinka van Puijenbroekⁱ, Mourine J. Yegon^b, Antonio Camacho^{c,1}, Daniel von Schiller^{a,1}

^a Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Universitat de Barcelona, Av. Diagonal 643, 08028 Barcelona, Spain

^b WasserCluster Lunz - Biologische Station, Dr. Carl Kupelwieser Promenade 5, 3293 Lunz am See, Austria

^c Institut Cavanilles de Biodiversitat i Biologia Evolutiva, Universitat de València, C/Catedratic José Beltrán 2, 46980 Paterna, Spain

^d Department of Systems Ecology and Sustainability, University of Bucharest, spl. Independentei 91 - 95, 50095 Bucharest, Romania

^e Institut de Recherche Pour la Conservation des Zones Humides Méditerranéennes, Tour du Valat, Le Sambuc, 13200 Arles, France

^f Istituto di Biofisica, Consiglio Nazionale delle Ricerche (CNR) Pisa, Via Giuseppe Moruzzi 1, 56124 Pisa, Italy

^g Marine Research Institute, Klaipėda University, Universiteto ave. 17, 92294 Klaipėda, Lithuania

^h ECOMARE, CESAM - Centre for Environmental and Marine Studies, Department of Biology, University of Aveiro, Campus de Santiago, 3810-193 Aveiro, Portugal

ⁱ Wageningen Marine Research, Wageningen University & Research, Korringaweg 7, 4401, NT, Yerseke, the Netherlands

ARTICLE INFO

Keywords:

Coastal wetlands
Ecological restoration
CO₂ fluxes
CH₄ fluxes
Climate change mitigation

ABSTRACT

Coastal wetlands play a substantial role in regulating Earth's climate through exchanges of greenhouse gases (GHGs). Current European policies promote widespread coastal wetland restoration to reverse historical losses and ongoing pressures. However, substantial uncertainty remains regarding how carbon dioxide (CO₂) and methane (CH₄) fluxes respond to restoration across different coastal wetland types and whether these responses translate into net climate mitigation in terms of CO₂ equivalents (CO₂-eq). We measured simultaneous CO₂ and CH₄ fluxes using static chambers across four seasons at multiple locations spanning preserved, altered and restored sites within six European coastal wetlands of different ecological types. By comparing GHG exchanges and resulting CO₂-eq balances across wetlands, we identified dominant biogeochemical drivers of CO₂ and CH₄ dynamics and assessed the climate mitigation potential of conservation and restoration actions. CO₂ fluxes were primarily controlled by landscape-scale vegetation cover and inundation, whereas CH₄ emissions responded to less evident changes in water quality, salinity and wetland hydrodynamics. Comparisons of CO₂-eq balances between altered and restored sites showed that seagrass replantation was associated with significant mitigation potential under both 100-year and 20-year CH₄ warming scenarios, while eutrophication reversal through improved water treatment was only significant under the 20-year scenario. In contrast, other restoration measures modified CO₂ and CH₄ fluxes in opposing directions, resulting in no significant net change in combined

* Corresponding author.

E-mail address: miguelcabrera@ub.edu (M. Cabrera-Brufau).

¹ These authors share last authorship as research heads

CO₂-eq balances. Overall, our results demonstrate that climatic responses to coastal wetland restoration are both GHG-specific and wetland-type dependent, underscoring the need for tailored restoration strategies and robust, multi-GHG monitoring to detect and accurately quantify potential climatic benefits.

1. Introduction

Coastal wetlands are relevant components of the global carbon (C) cycle and are widely recognized as blue carbon ecosystems. Despite their relatively low areal extent, they exert a disproportionate influence on the global climate by providing long-term C-sequestration and regulating atmospheric greenhouse gas (GHG) concentrations (Mitsch et al., 2013). Wetlands in good conservation status are highly productive ecosystems, where low oxygen availability limits aerobic organic matter degradation, resulting in net uptake of carbon dioxide (CO₂) and sequestration of C in sediments and biomass (Reddy et al., 2022). At the same time, wetland anoxic sediments act as hot spots for methane (CH₄) emissions, making up 20–30% of global CH₄ emissions (Saunois et al., 2016), particularly when they are degraded by alterations enriching the organic content such as eutrophication (Morant et al., 2020a, 2020b). While the magnitude of CO₂ exchanges typically exceeds that of CH₄, the higher global warming potential of the latter has the potential to overcome the effects of CO₂ uptake and might result in a net balance that favours atmospheric warming (Canadell and Monteiro, 2023). Ultimately, the net radiative forcing of coastal wetlands is largely determined by the net balance of CO₂ and CH₄ exchanges with the atmosphere.

Diverse historical and current pressures have led to important reductions of the extent and quality of global wetland ecosystems (Fluet-Chouinard et al., 2023). While areal loss quantification remains challenging, especially when assessing coastal zones with high historical development and land-reclamation practices, estimates of European coastal wetland loss exceed 65% during the last century (Airoldi and Beck, 2007). Further, the majority of remaining European standing water bodies have a poor or bad ecological status (European Environment Agency, 2024) and experience diverse natural and anthropogenic pressures (Maes et al., 2020). Although conservation policies, such as those under Ramsar (Ramsar Convention, 1971) and the EU habitats Directive, help preserve the remaining wetlands, their historical losses mean that widespread restoration is still needed. In this context, the recent EU Nature Restoration Regulation aims at reverting this widespread degradation and recovering crucial ecosystems services lost (European Union, 2024). Among the potential benefits of restoration, climate change mitigation is increasingly being used as a supporting argument. However, large uncertainties remain on the climatic mitigation capacity of coastal wetland restoration (Jones et al., 2024).

Coastal wetlands influence climate primarily through CO₂ and CH₄ exchange, governed by the balance among photosynthesis, aerobic and anaerobic respirations releasing CO₂, as well as methanogenesis (Reddy et al., 2022). While local climate and wetland type shape baseline GHG fluxes (Camacho et al., 2017), ecosystem alteration and restoration can modify these fluxes by changing key controls, including vegetation, nutrient inputs, hydrology, salinity, and sediment redox conditions (Camacho-Santamans et al., 2025; Morant et al., 2024). The biomass and type of dominant primary producers exert a large impact on the primary productivity of wetlands, as they represent the basic functional standing stock for photosynthetic CO₂ uptake. While nutrients are essential to maintain plant photosynthetic rates, excessive nutrient loads, namely nitrogen and phosphorus, can lead to eutrophication and uncontrolled proliferation of benthic algae and phytoplankton blooms (Zilius et al., 2014). This shift in primary producers results in a cascade of biogeochemical consequences, including anoxia and organic matter degradation through methanogenesis, that ultimately lead to severely enhanced CH₄ emissions (Bonaglia et al., 2025). Wetland hydrology is one of the key factors regulating ecosystem functioning, as it influences both

primary production through water availability and the balance between respiration and methanogenic degradation of organic matter through limitation of oxygen diffusion into the sediments (Cui et al., 2024; Rochera et al., 2025). However, anoxic conditions do not always result in elevated wetland CH₄ emissions, as the supply of sulphate by saline waters can severely limit methanogenesis through resource competition with more energy-efficient sulphate reduction metabolisms under the right redox conditions (Lovley and Klug, 1983; Miralles-Lorenzo et al., 2025). Emissions of CH₄ are further modulated by the existence of plant-mediated transport mechanisms, which can bypass oxidation back to CO₂ during upward diffusion through oxic sediment horizons (Ge et al., 2024).

While the general biogeochemical controls of wetland CO₂ and CH₄ exchanges are relatively well understood, large uncertainty remains on how these interact under practical cases of ecological restoration, leading to poorly constrained climatic mitigation potential (Griscom et al., 2017). Wetland restoration generally enhances CO₂ uptake outweighing increases in CH₄ emissions and resulting in net climate benefits (He et al., 2024). However, existing literature is dominated by studies focused on inland systems (peatlands) and on just a few coastal wetland types (mangroves, saltmarshes), which do not capture coastal wetland diversity accurately (Misteli et al., 2025a, 2025b; Taillardat et al., 2020). Other synthesis efforts on coastal wetland restoration focus exceedingly on C sequestration (i.e., Blue Carbon), overlooking the large role of CH₄ emissions on the net climatic outcome of wetland restoration (Bertolini and da Mosto, 2021). In addition, while valuable for identifying broad patterns, global syntheses often aggregate the high diversity of wetland types, alteration histories and restoration strategies into a limited number of categories (O'Connor et al., 2020), thereby obscuring relevant contextual factors and limiting process-based effective transferable knowledge for management. Overall, current evidence is still scarce on how coastal wetland restoration influences GHG fluxes (Macreadie et al., 2019; Misteli et al., 2025a, 2025b) and coordinated, multi-site assessments are needed to reveal common controls that are robust across wetland types and restoration pathways.

In order to better understand the climate mitigation potential of restoring and conserving European coastal wetlands, this study examines concomitant CO₂ and CH₄ exchanges and their combined carbon dioxide equivalent (CO₂-eq) climatic effect across six diverse European case pilot coastal wetlands: saltmarshes, seagrass meadows, freshwater and brackish marshes, riverine lakes and freshwater coastal lagoons. By explicitly embracing the diversity of coastal wetland types, conservation status, and restoration pathways represented across Europe, we aim to move beyond site-specific assessments and identify common patterns and drivers governing GHG flux responses to alteration and restoration. Using standardized static chamber measurements conducted during four seasonal sampling campaigns, we compare instantaneous GHG exchanges across wetland sites representative of preserved, altered, and restored status. Our objectives are to (i) systematically identify the main biogeochemical drivers controlling CO₂ and CH₄ fluxes in the main European coastal wetland types, and (ii) quantify the extent to which restoration and conservation modify their net climatic effect, expressed as daily CO₂-eq fluxes. We hypothesize that (i) the drivers and sensitivity of GHG fluxes to the conservation status differ between CO₂ and CH₄, reflecting their distinct production and consumption pathways, and that (ii) the net climatic response to restoration depends on both the type of anthropogenic alteration and the wetland type considered. At the same time, we expect that consistent cross-system patterns will emerge, allowing the identification of shared controls on GHG fluxes despite the heterogeneity of wetland types and restoration contexts examined.

2. Methods

2.1. Study areas

Six case pilots were strategically selected to cover a wide range of European coastal wetland types, thereby providing a representative sample of the ecosystem and climatic diversity across the continent, covering major European coastlines (Atlantic, Mediterranean, Black Sea, Baltic Sea). The selected case pilots were (Fig. 1, Fig. S1): South-West Dutch Delta (DU, intertidal salt marshes, Netherlands), Ria de Aveiro (RI, intertidal seagrass beds, Portugal), Camargue (CA, freshwater marshes and ponds, France), the Valencian wetland Marjal dels Moros (VA, brackish marshes, Spain), Danube Delta (DA, freshwater lakes and ponds with reed beds, Romania) and Curonian Lagoon (CU, freshwater lagoon with reed and submerged vegetation, Lithuania). Within each case pilot, sites representing three conservation statuses were selected in duplicate: preserved, altered, and restored. Preserved sites served as reference systems with unaltered structure and function, whereas altered and restored sites reflected wetland-specific dominant anthropogenic pressures and corresponding restoration measures. Accordingly, the “restored” category represents context-dependent interventions linked to the ecological functioning and alteration history of each wetland system rather than a standardized restoration approach across case pilots. Sites within each pilot wetland were geographically close, ensuring comparable climatic conditions and allowing differences in biogeochemical functioning to be attributed to the conservation status. Site characteristics are summarized in Table 1, with further details provided in supplementary materials and in Oliveira et al. (2026).

2.2. Sampling design

A standardized sampling protocol using static chamber GHG flux measurements was applied across all case pilot wetlands (Minaudo et al., 2023). All 36 sites were sampled once per season, between October 2023 and August 2024. In each site, the areal proportion of three land cover strata classes was estimated in advance using aerial photography and remote sensing images, then confirmed visually upon arrival: (i) open

Table 1
Summary descriptions of studied wetland type, main alterations and restoration activities for each of the six case pilots.

Case pilot	Wetland type	Alteration	Restoration
South-West Dutch Delta (DU)	Intertidal salt marshes	Erosion-protection coastal infrastructures	Removal of barriers and passive saltmarsh recovery
Ria de Aveiro (RI)	Intertidal <i>Zostera noltii</i> seagrass meadows	Bait-digging, trampling, vegetation loss	Active re-vegetation (transplantation)
Camargue (CA)	Freshwater marshes and ponds	Land-use change and artificial hydrological regime	Habitat reconstruction (Soil, hydrology, morphology, vegetation)
Marjal dels Moros (VA)	Brackish marshes	Desalination, hydromorphological and soil degradation, invasive species	Habitat reconstruction (Soil, hydrology, morphology, vegetation)
Danube Delta (DA)	Freshwater lakes and ponds with reed beds	Land-use change (crops and livestock)	Habitat reconstruction (hydrology, morphology, vegetation)
Curonian Lagoon (CU)	Freshwater littoral with submerged vegetation and reed beds	Water quality (eutrophication)	Passive restoration through the reduction of nutrient load and hydrological changes.

water areas (i.e., without emergent vegetation and with >10 cm of water depth), (ii) vegetated areas (i.e., covered by emergent vegetation (helophytes, and, for Ria de Aveiro, seagrasses), regardless of water presence), and (iii) bare areas (i.e., covered by soil or sediment exposed to the atmosphere at the sampling time). Strata representing <10% of the site area at the time of the visit were excluded from sampling. Each remaining stratum was sampled with a minimum of 3 static chamber



Fig. 1. Map showing the location of the six case pilots. Map lines do not necessarily depict accepted national boundaries. Representative pictures can be found in Fig. S1.

deployments, with additional deployments allocated proportionally to stratum areal cover and randomly distributed within each of them. On each sampling day, an average of 15 ± 2 (mean $\pm$ SD) chamber deployments per site were performed, depending on logistical constraints.

All chamber deployments included a dark incubation to minimize heating effects (Lorke et al., 2015). In vegetated areas, an additional transparent incubation was performed to assess the effects of photosynthesis on GHG fluxes. Concentrations of CO₂, CH₄, and H₂O were measured by recirculating chamber headspace through portable gas analyzers (Li-COR 7810, Picarro G4301, GLA132-GGA). Incubation start and end times were recorded manually and, whenever possible, via instrument software. Two different custom-built static chambers were used depending on the strata. Open water fluxes were measured using a floating opaque semi-spherical chamber ($V = 14.4$ L, $A = 1134$ cm², Fig. S2) with 10–15 min incubations to capture diffusive and ebullitive fluxes. Bare and vegetated areas were sampled using a modular transparent cylindrical plexiglass chamber with 3–5 min incubations; collars were inserted 1–3 cm into the sediment and dark conditions were ensured by covering the chamber with an opaque blanket. Chamber volume ($V = 4.6$ to 69 L, $A = 460$ cm², Fig. S2), was adjusted to vegetation height to optimize sensitivity. In flooded vegetated areas, and to avoid mobilization of sediment CH₄, the chamber was maintained on the water surface either using a flotation ring (Fig. S2) or holding it by hand. Effective chamber volume was calculated for each deployment based on chamber height above the water and sediment surface.

2.3. Flux calculation

2.3.1. Instantaneous flux estimates

All data treatment, including flux calculations and statistical analyses, was performed in R version 4.5.0 (R Core Team, 2025). Incubation time periods were mapped onto the raw gas concentration time series and start-end times adjusted to exclude instrument and manipulation artefacts after individual visual inspection of each incubation. Ebullitive patterns of CH₄ timeseries were identified but not excluded. A total of 52 CO₂ (1.7%) and 56 CH₄ (1.8%) time series were discarded due to severe artefacts or documented manipulation errors. For the remaining 2990 CO₂ and 2986 CH₄ time series, instantaneous fluxes were estimated independently for each gas species using three approaches: (i) a two-point method, where the flux was calculated from the net concentration change throughout the incubation using the average (10 s) initial and final concentrations; (ii) a linear model (LM); and (iii) a non-linear (HM) (Hutchinson and Mosier, 1981) regression model. LM and HM models were obtained using the goFlux R package v2.0.0 (Rheault et al., 2024). Areal molar fluxes were calculated for each of the three approaches via the ideal gas law using chamber geometry, and site-specific temperature and atmospheric pressure recorded by the nearest meteorological station. For each gas time series, a best-flux estimate was selected from the three available models following sequential objective criteria (see **supplementary materials**). The resulting dataset, containing 2990 CO₂ and 2986 CH₄ instantaneous fluxes from 2106 static chamber deployments, is deposited at LifeWatch ERIC (Cabrera-Brufau et al., 2025). The unprocessed GHG concentration time-series dataset is deposited at Zenodo (Cabrera-Brufau et al., 2026) and code for reproduction of the instantaneous flux dataset is available through the GitHub repository (Cabrera-Brufau and Minaudo, 2026).

2.3.2. Data filtering and pooling of non-vegetated strata

To ensure comparability across case pilots and conservation statuses, deployments conducted outside site boundaries or after substantial manipulation (e.g., vegetation removal) were discarded (54 deployments). In the two tidally influenced case pilots (Ria de Aveiro and Dutch delta), deployments during rising and receding tides were also discarded (93 deployments), due to the transient nature of peak-fluxes under these conditions (Lin et al., 2024) and the difficulty of attributing them to the conservation status of the location where they were

obtained. Therefore, all subsequent analyses for these case pilots refer only to low-tide conditions. Overall, 147 of the 2106 deployments with valid fluxes (7%) were excluded from further analysis. Additionally, to ensure strata representativity across statuses and seasons within each case pilot, the three sampled strata were pooled into two classes based on the presence or absence of emergent vegetation (vegetated vs. non-vegetated), enabling robust assessment of strata-specific status effects.

2.3.3. Daily temporal integration and calculation of CO₂ equivalent flux

Instantaneous fluxes were temporarily integrated into a single net daily flux for each chamber deployment, accounting for stratum-specific incubation availability. For vegetated strata, net daily fluxes were calculated by scaling transparent and dark instantaneous fluxes to the respective daytime and nighttime fractions at each site and date, based on official sunrise and sunset times calculated with the *sunalc* R package (Thieurmél and Elmarhraoui, 2022). For non-vegetated strata, net daily fluxes were derived either directly from a single dark instantaneous measurement (1087 chambers, 94.7%) or, when both dark and transparent incubations were available due to visible micro-phytobenthos (61 chambers, 5.3%), using the same temporal scaling approach applied to vegetated strata. Daily combined climatic effects as CO₂ equivalent (CO₂-eq) flux were calculated for each chamber deployment using the daily CO₂ and CH₄ fluxes and applying the global warming potential (GWP) factors for CH₄ mass flux of either 27 or 79.7 for 100-year or 20-year time horizons, respectively (IPCC, 2023). In total, 1917 CO₂, 1916 CH₄, and 1887 CO₂-eq daily fluxes were obtained. Fluxes are reported as daily molar CO₂ and CH₄ fluxes per unit area and time, or as daily CO₂-eq mass fluxes per unit area and time (Neubauer, 2021).

2.4. Statistical treatment

To assess the effects of the conservation status on GHG fluxes, generalized linear mixed effects models (GLMM) were independently built for daily CO₂ and CH₄ fluxes for each case pilot. Flux data was transformed using the *bestNormalize* package (Peterson, 2021), selecting the transformation that maximized normality for each dataset. In addition to the default transformation options, a pseudo-log transformation from the *scales* package (Wickham et al., 2025) was included, allowing continuous treatment of positive and negative fluxes while transitioning to linear scaling near zero. Daily flux was modelled as a function of conservation status, season, vegetation presence, and their interactions as fixed effects, while site was included as a random intercept to account for repeated seasonal sampling and site-specific variability. Gaussian-distribution models were preferentially used; t-family models were used when gaussian model assumptions were not met. For Ria de Aveiro, vegetation presence was excluded from the fixed-effects structure due to the absence of non-vegetated areas in restored sites. Models were fitted using the *glmmTMB* package (McGillcuddy et al., 2025) and validated using DHARMA diagnostics (Hartig, 2024).

Estimated marginal means (EMMs) were obtained using the *emmeans* package (Lenth, 2025). For models including vegetation presence, EMMs were weighted according to the seasonal proportional cover of vegetated and non-vegetated areas, while maintaining equal weighting across seasons for annual estimates. For Ria de Aveiro, equal seasonal weights were applied. A paired parametric bootstrap approach was implemented independently for each case pilot to improve the robustness of model-derived estimates. The paired structure additionally allowed uncertainty from CO₂ and CH₄ models to be propagated into combined climate metrics (CO₂-eq). Using the fitted CO₂ and CH₄ models, 5000 paired bootstrap iterations were generated by simulating new response values while preserving the original sampling design, predictor structure, and correspondence between gases. For each bootstrap iteration, EMMs were recalculated for both gases, yielding paired model-scale distributions for all relevant predictor combinations (i.e., status, status within season and status within vegetated and non-

vegetated conditions).

To quantify the magnitude of CO₂ and CH₄ fluxes at each predictor level, bootstrap EMM distributions for each gas were back-transformed to the original molar flux scale, from which mean estimates, standard errors (SE), and 95% confidence intervals (CI95) were calculated. To quantify flux differences between predictor levels, pairwise contrasts were calculated from these back-transformed distributions and mean, SE, and CI95 values were calculated. The significance of these comparisons was assessed on model scale by recalculating the pairwise contrasts from the bootstrap EMM distributions. Empirical two-sided *p*-values were derived directly from bootstrap contrast distributions. *P*-values were adjusted for multiple comparisons using the Holm correction method.

To estimate combined climate forcing, paired bootstrap distributions of back-transformed CO₂ and CH₄ fluxes were converted into CO₂-eq fluxes using both 100-year and 20-year global warming potential scaling factors for CH₄. For each bootstrap iteration, paired CO₂ and scaled CH₄ estimates were summed, preserving the correspondence between gases across simulations and generating paired distributions of CO₂-eq exchanges. From these paired real-scale CO₂-eq distributions, EMMs and pairwise contrasts were calculated, together with their associated SE and CI95. Empirical *p*-values for CO₂-eq contrasts were derived directly from the bootstrap contrast distributions and adjusted with Holm correction. Thus, while significance testing for CO₂ and CH₄ contrasts was performed on their respective model scales, the significance of combined CO₂-eq contrasts was assessed on the real scale.

All figures were produced with ggplot2 package (Wickham, 2016). A significance threshold of $\alpha = 0.05$ was applied for all statistical tests. Different letters (Compact Letter Display, CLD) were assigned to significantly different EMMs groups in figures using the multcompView package (Graves et al., 2024). The scripts used for statistical analyses and figure generation are archived at Zenodo (<https://doi.org/10.5281/zenodo.21129514>).

2.5. Methodological considerations

Several limitations affect the representativeness of the GHG flux estimates presented. Static chamber measurements are prone to closing/opening artefacts and non-linear patterns (Maier et al., 2022). These were mitigated through careful handling, timeseries screening, and standardized flux selection, ensuring transparent processing and minimizing subjective biases (Minaudo et al., 2026). While our approach allowed estimation of CH₄ fluxes in the presence of ebullitive dynamics, it is important to recognize that ebullition is a stochastic emission pathway over the short temporal scales of chamber deployments and is generally better constrained by methods integrating fluxes over longer periods, such as bubble traps (Wik et al., 2013). Nevertheless, this source of variability was partially mitigated through the high replication of chamber measurements, which is often logistically challenging for bubble-trap approaches. Spatially, the highly localized nature of chamber measurements may result in substantial variability of wetland-level average fluxes. This was accounted for by the stratified sampling design, ensuring good representation of relevant strata while allowing for the detection of strata-specific effects. Nevertheless, while the employment of modular chambers allowed for coverage of most strata, their dimensions precluded the sampling of large (>1.5 m) vegetation stands, likely resulting in underestimations of CO₂ uptake for reed dominated sites. Temporally, sampling was limited to one low-tide event per season and relied on opaque chambers instead of direct night-time measurements. Consequently, the seasonal patterns reported here should not be interpreted as robust representations of true climatic seasonality, as they reflect both seasonal and short-term meteorological variability. Similarly, the integration of daily fluxes from paired dark and transparent chamber measurements does not fully capture diel variability in GHG exchange and may introduce biases associated with differences between dark chamber conditions and true night-time

ecosystem functioning. Finally, our measurements were restricted to surface-atmosphere GHG exchanges and therefore do not account for potential lateral GHG transport through surface-water or groundwater pathways (Sadat-Noori et al., 2025), which may represent important additional components of whole-system GHG budgets (Schutte et al., 2020). Accordingly, the approach was not intended to generate fully scalable site-level GHG budgets, but to enable consistent comparisons across conservation statuses to assess how wetland-specific alteration and restoration pathways influence GHG exchanges and potential climate mitigation signals.

3. Results

3.1. Fluxes across preserved wetlands

Daily net fluxes at preserved sites varied among case pilot wetlands and GHG species (Fig. 2). Preserved sites generally exhibited daily CO₂ fluxes (mmol CO₂ m⁻² d⁻¹) centred around zero but with substantial variability (Fig. 2a). Atlantic tidal sites DU (median = -23.6, IQR = -214 to 17.1) and RI (median = -32.6, IQR = -56 to -18.2), showed net CO₂ uptake, with DU presenting one of the largest flux variabilities. Mediterranean sites exhibited similarly high variability, with CA showing the highest CO₂ flux (median = 15.7, IQR = -57.2 to 86) and VA having CO₂ fluxes closest to net zero (median = 2.0, IQR = -30.3 to 67.2). Eastern sites showed similar CO₂ flux profiles, with intermediate median fluxes and relatively low variability for DA (median = 6.1, IQR = -4.9 to 24.4) and slightly higher fluxes for CU (median = 9.2, IQR = -0.8 to 36.4).

Net daily CH₄ fluxes (mmol CH₄ m⁻² d⁻¹) were generally positive across all preserved sites, with higher median emissions associated with greater variability and strongly skewed distributions (Fig. 2b). Atlantic tidal wetlands showed the lowest CH₄ emissions, with similar values at DU (median = 1.5×10^{-3} , IQR = -4.2×10^{-3} to 1.6×10^{-2}) and RI (median = 8.0×10^{-3} , IQR = 4.3×10^{-3} to 1.2×10^{-2}). Mediterranean preserved sites exhibited intermediate CH₄ emissions, with CA (median = 1.7×10^{-2} , IQR = 1.9×10^{-3} to 1.5×10^{-1}) showing lower median fluxes than VA (median = 3.4×10^{-2} , IQR = 3.4×10^{-3} to 1.3×10^{-1}) but comparable variability. Eastern preserved sites showed the highest emissions, with DA (median = 1.1, IQR = 0.7 to 9.9) displaying the highest CH₄ fluxes and extreme skewness, while CU (median = 0.8, IQR = 0.4 to 1.7) had lower and less variable CH₄ fluxes.

The contrasting CO₂ and CH₄ flux profiles at preserved sites resulted in CO₂-eq distributions reflecting the dominant contributor to climatic forcing in each case pilot under both 100-year and 20-year GWP scaling factors for CH₄ (Fig. 2c). CO₂ generally dominated the 100-year CO₂-eq balance, with CH₄ contributing minor proportions (mean $\pm$ SD) in Atlantic ($2 \pm 5\%$ in both DU and RI) and Mediterranean wetlands ($7 \pm 19\%$ in CA, $7 \pm 17\%$ in VA), but substantially larger shares in eastern wetlands ($49 \pm 32\%$ in DA, $34 \pm 27\%$ in CU). Regarding 100-year GWP CO₂-eq fluxes (g CO₂ eq. m⁻² d⁻¹), values were lowest in the Atlantic tidal wetlands RI (median = -1.5, IQR = -2.5 to -0.9) and DU (median = -1.0, IQR = -9.1 to 0.8), intermediate in the Mediterranean wetlands CA (median = 0.8, IQR = -1.2 to 4.2) and VA (median = 0.3, IQR = -1.0 to 3.1), and highest in the eastern wetlands DA (median = 1.0, IQR = 0.2 to 3.8) and CU (median = 0.9, IQR = 0.3 to 2.3). The relative contributions of CH₄ to the CO₂-eq balances increased markedly under the 20-year GWP scenario, particularly in freshwater eastern wetlands, reaching $65 \pm 30\%$ in DA and $52 \pm 28\%$ in CU. Mediterranean wetlands showed intermediate CH₄ contributions ($12 \pm 23\%$ for both CA and VA), whereas Atlantic wetlands remained comparatively low despite increased variability ($3 \pm 10\%$ for DU and $3 \pm 9\%$ for RI). Under the 20-year GWP scenario, tidal wetlands showed only minor changes in CO₂-eq fluxes (RI: median = -1.5, IQR = -2.5 to -0.9; DU: median = -0.9, IQR = -9.1 to 0.8). Mediterranean systems showed moderate increases (CA: median = 1.1, IQR = -0.4 to 4.7; VA: median = 0.4, IQR = -0.9 to 3.2), while the largest increases under the 20-year GWP scenario

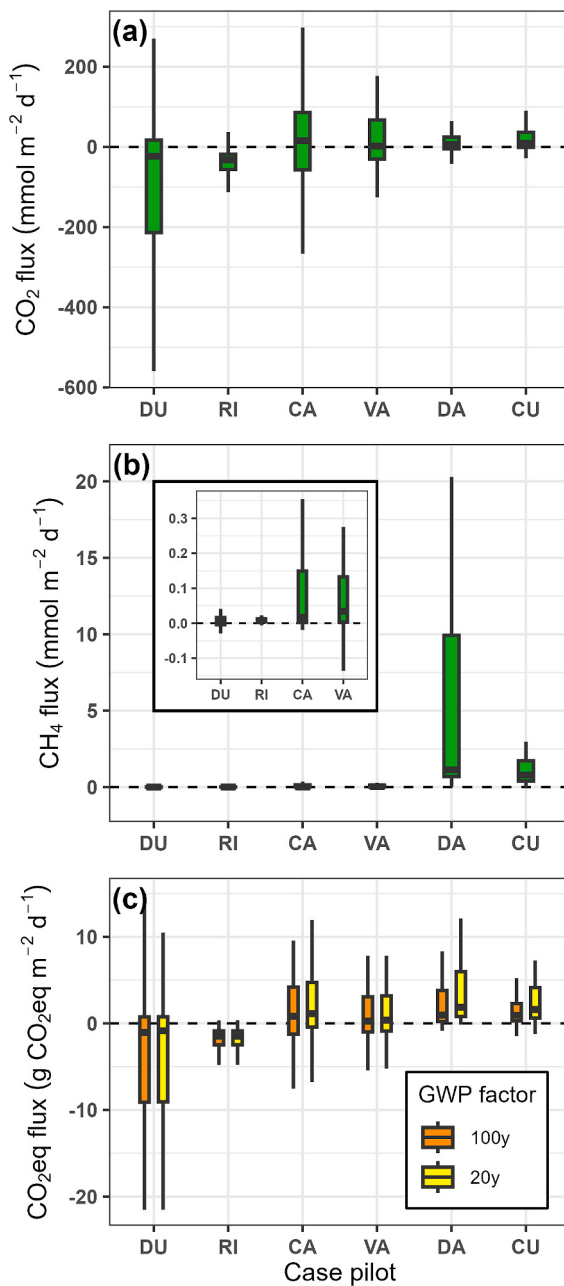


Fig. 2. Greenhouse gas fluxes across preserved case pilot wetlands of (a) CO₂, (b) CH₄, and (c) combined CO₂-eq under 100-year and 20-year GWP scenarios. Boxplots show the median, interquartile range (IQR), and whiskers extending to 1.5xIQR; data outside these ranges are not displayed for clarity. Inset in (b) shows a zoomed-in view of CH₄ flux data for DU, RI, CA, and VA to better visualize differences; y-axis scale differs from the main panel.

occurred in eastern wetlands, including DA (median = 1.9, IQR = 0.8 to 6.0) and CU (median = 1.6, IQR = 0.6 to 4.1).

3.2. Effect of conservation status on CO₂ fluxes

Daily CO₂ fluxes (mmol m⁻² d⁻¹) showed wetland-specific patterns related to the conservation status (Fig. 3). Significant status effects were detected in three case pilot wetlands (RI, DA, CU) (Table S1), with clear differences between preserved, altered, and restored sites (Table S3). In RI and DA, altered sites exhibited significantly higher CO₂ fluxes than preserved ($p \leq 0.002$) and restored ($p < 0.001$) sites, which showed similar low fluxes ($p = 0.71$) in RI while restored sites of DA showed

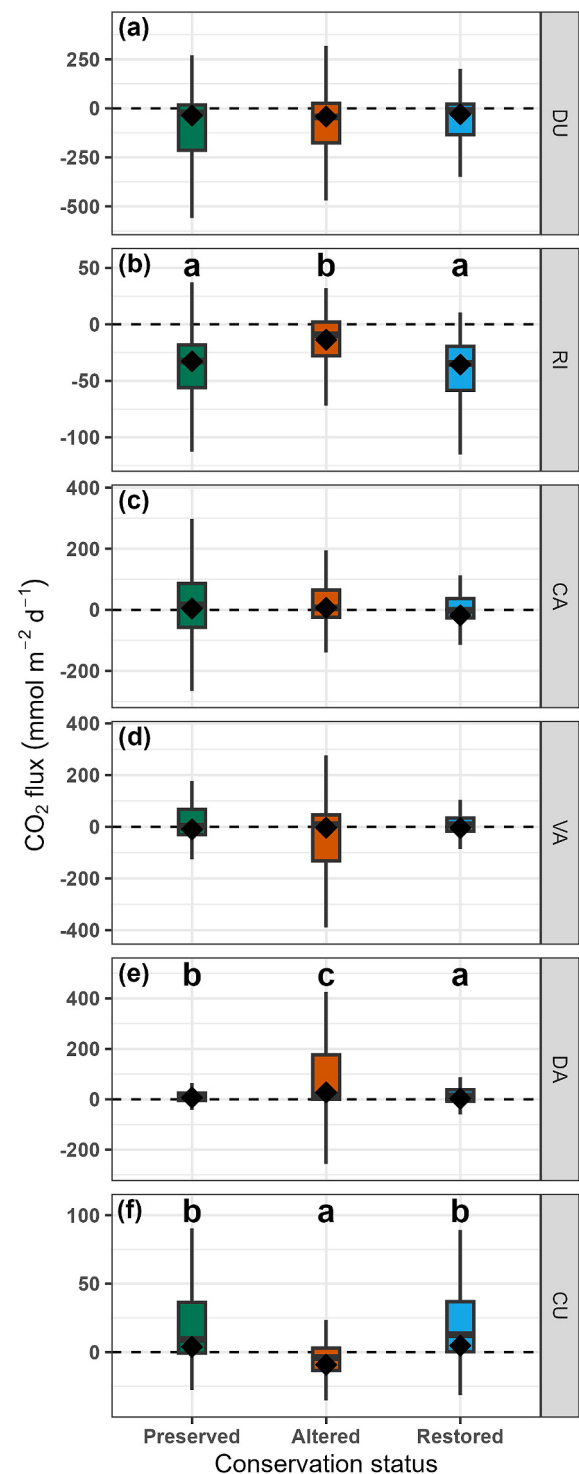


Fig. 3. CO₂ fluxes (mmol m⁻² d⁻¹) according to conservation status for each case pilot. Boxplots show the median, interquartile range (IQR), and whiskers extending to 1.5xIQR; data outside these ranges are not displayed for clarity. Diamonds represent estimated marginal means (EMMs) derived from parametric bootstrap distributions. Different letters indicate significant differences among EMMs based on empirical pairwise contrasts ($p < 0.05$; Table S3).

slightly lower fluxes than preserved ones ($p = 0.042$). In contrast, CU displayed lower CO₂ fluxes in altered sites compared to preserved ($p < 0.001$) and restored ($p < 0.001$) sites. No statistically significant status effects were observed in DU, CA, or VA, where CO₂ fluxes were comparable across conservation statuses ($p \geq 0.39$). Beyond status, CO₂

fluxes were consistently influenced by seasonality and vegetation presence, often interacting with the conservation status, even when status alone was not significant (Table S1, Figs. S3 and S6). The three case pilot wetlands with significant conservation status effects on CO₂ fluxes (RI, DA, and CU) showed only minor increases from marginal to conditional R² values (Table S1), suggesting limited additional variance explained by the random site effect.

3.3. Effect of conservation status on CH₄ fluxes

CH₄ fluxes (mmol m⁻² d⁻¹) showed clearer and more frequent statistically significant responses to conservation status across case pilot wetlands (Fig. 4). Significant status effects were detected in all case pilot wetlands except DU (Table S1), where CH₄ fluxes did not differ among preserved, altered and restored sites (Table S3). In RI, preserved and restored sites exhibited slightly higher CH₄ fluxes than altered sites ($p = 0.006$, and $p < 0.001$, respectively). In the Mediterranean wetlands (CA and VA), altered sites showed higher CH₄ emissions than preserved sites ($p \leq 0.022$), with restored sites of CA showing fluxes similar to preserved sites ($p = 0.26$) and lower than altered ones ($p = 0.029$), while restored sites of VA showed intermediate fluxes not different from altered or preserved sites ($p > 0.35$). In DA, restored sites had higher CH₄ fluxes than altered sites ($p = 0.041$), while preserved sites were intermediate. In CU, altered sites exhibited substantially higher CH₄ emissions than both preserved and restored sites ($p < 0.001$), which showed similarly low fluxes. As for CO₂, CH₄ flux variability was strongly influenced by seasonality across all case pilots and by vegetation presence in most cases, with frequent interactions between the conservation status, season, and vegetation presence (Table S1, Figs. S4 and S7). In contrast to CO₂ models, CH₄ models generally showed substantially higher conditional than marginal R² values (Table S1), indicating that site-level variability contributed importantly to model explanatory power, particularly in DA ($R^2_m = 0.50$, $R^2_c = 0.68$).

3.4. Effect of conservation status on CO₂-eq fluxes

The influence of conservation status on combined CO₂-eq fluxes (Fig. 5) was assessed using pairwise comparisons of bootstrap CO₂-eq distributions under both 100-year and 20-year CH₄ GWP scaling factors (Table S3). In general, differences in CO₂-eq fluxes among conservation statuses were less consistent than those observed for CO₂ and CH₄ individually and depended on the selected GWP time horizon. The clearest status-related differences were observed for the RI case pilot wetland, where restored and preserved sites consistently showed lower CO₂-eq fluxes than altered sites ($p \leq 0.002$), while not differing from each other ($p > 0.71$) under both 100-year and 20-year GWP scenarios. The only other wetland showing significant differences in CO₂-eq fluxes among conservation statuses was CU, although these differences were only detected under the 20-year GWP scenario. In CU, restored and preserved sites showed lower CO₂-eq fluxes than altered sites ($p \leq 0.006$), while remaining similar to each other ($p = 0.82$). Although the central distributions of CO₂-eq fluxes appeared to follow status-specific patterns in some wetlands (e.g., CA or DA), no statistically significant differences among conservation statuses were detected in these systems (Table S3). As observed for the individual CO₂ and CH₄ flux components, CO₂-eq fluxes also exhibited substantial variability that appeared associated with seasonality and vegetation presence (Figs. S5 and S8), although these effects were not directly quantified for combined CO₂-eq metrics.

4. Discussion

4.1. Biogeochemical drivers of gaseous C exchange in European coastal wetlands

Across the wetlands examined, the effects of conservation status on

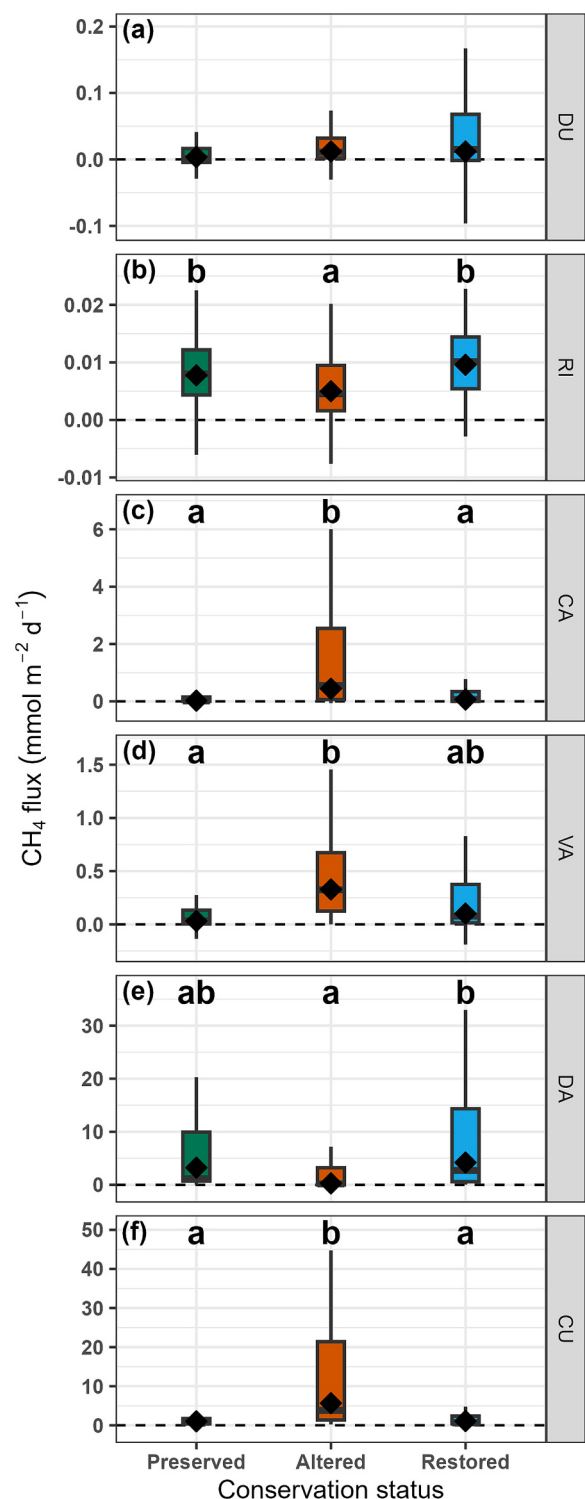


Fig. 4. CH₄ fluxes (mmol m⁻² d⁻¹) according to conservation status for each case pilot. Boxplots show the median, interquartile range (IQR), and whiskers extending to 1.5xIQR; data outside these ranges are not displayed for clarity. Diamonds represent estimated marginal means (EMMs) derived from parametric bootstrap distributions. Different letters indicate significant differences among EMMs based on empirical pairwise contrasts ($p < 0.05$; Table S3).

CO₂ and CH₄ fluxes varied among the studied wetland types, their specific alterations and associated restoration measures. CO₂ fluxes showed variations significantly associated with the conservation status in only three of six case pilots, whereas CH₄ fluxes were more responsive, with significant effects in five of six case pilots. Wherever status

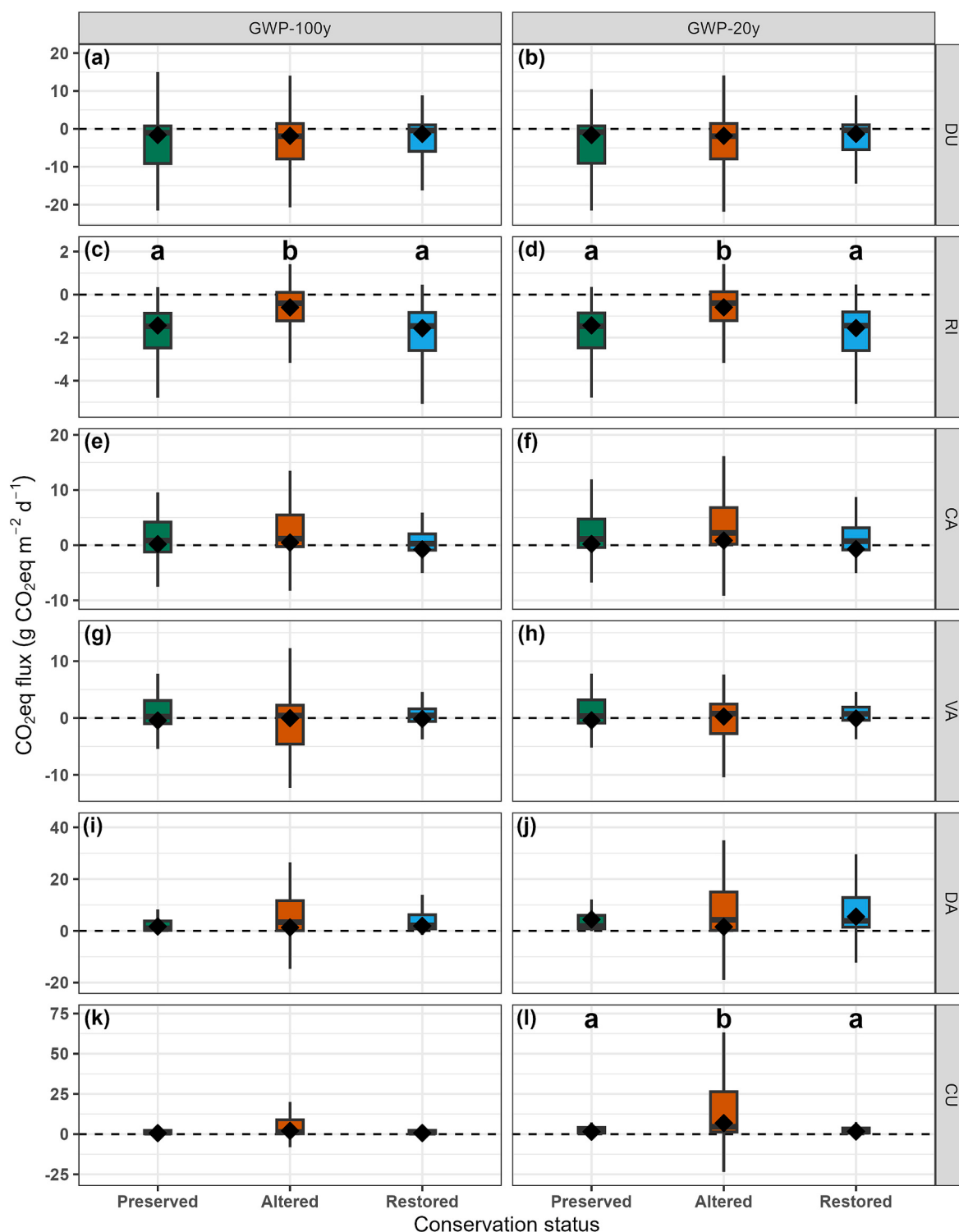


Fig. 5. CO₂-eq flux (g CO₂ eq. m⁻² d⁻¹) according to conservation status for each case pilot under 100-year and 20-year GWP scenarios. Boxplots show the median, interquartile range (IQR), and whiskers extending to 1.5xIQR; data outside these ranges are not displayed for clarity. Diamonds represent estimated marginal means (EMMs) derived from paired parametric bootstrap distributions of CO₂ and CH₄ models after application of the corresponding GWP factors. Different letters indicate significant differences among EMMs based on empirical pairwise contrasts ($p < 0.05$; Table S3).

effects were detected for CO₂, they were consistently opposite in direction to those of CH₄, reflecting contrasting conditions that control the underlying processes regulating CO₂ and CH₄ exchanges in the different wetlands considered, with enhancement of aerobic conditions increasing CO₂ release, while actions favoring anaerobic conditions (e. g., rewetting) increased CH₄ emissions. Despite this variability, mostly

depending on the specific features of each wetland type and the conservation status of sites, some common mechanisms were evident across wetland types.

The diversity of wetland types and ecological conditions examined allowed identification of key drivers of CO₂ and CH₄ exchanges, strongly modulated by seasonality. CO₂ fluxes were primarily controlled by

vegetation cover and sediment oxygen availability, which regulated the balance between photosynthetic uptake and respiration-mediated release of CO₂. Emissions of CH₄ were mostly related to hydrology-driven oxygen availability in the sediment, salinity conditions, and presence of reed-type vegetation, while labile organic matter supply was important in some systems. CO₂ exchange responded mostly to alteration and restoration actions that severely modified the landscape of the wetlands, either through substantial loss or gain in abundance of primary producers or through profound changes in inundation patterns related to land-use change. CH₄ emissions were more sensitive to less evident hydrological changes, either through variations in water quality and salinity or through hydrodynamics modifying the extent and timing of wetlands flooding and water table depths. This sensitivity is strongly seasonal and temperature-driven, an effect that becomes increasingly evident at lower latitudes. Global changes that extend warm periods could potentially extend the duration of the observed seasonal CH₄ emission peaks in summer (Camacho et al., 2017; Morant et al., 2024); thus, accounting for seasonal variability is essential to accurately assess restoration outcomes, or the consequences of their absence.

Emergent vegetation presence exerted strong and consistent impact on CO₂ fluxes across all wetland types where it was evaluated, with vegetated areas generally acting as net CO₂ sinks (Table S1, Fig. S6). This evidences that, although strongly regulated by seasonality and local climatic conditions, vegetation standing stock is a primary driver of ecosystem-level primary production through photosynthetic uptake of CO₂ (Reddy et al., 2022). While our statistical framework could not explicitly include this effect for the seagrass meadows of Ria de Aveiro, the expected stronger CO₂ uptake by *Zostera noltii* meadows with respect to bare mudflats becomes evident when considering the strong differences in vegetated coverage between the sites of different conservation status sampled. RI altered sites suffered from erosion, bait-digging and trampling (Table 1), which reduced their *Z. noltii* coverage to an average of 8%. Instead, preserved sites as well as restored sites after seagrass planting showed much higher average *Z. noltii* coverages (61% and 96%, respectively), which is the likely explanation behind the significantly enhanced CO₂ uptake shown by these sites (Fig. 3b).

Plant community composition is also sometimes shown to influence overall CO₂ uptake rates in wetlands (Ward et al., 2009). Several of the wetlands studied suffered from alterations that involved modified vegetation communities such as presence of invasive species and loss of native vegetation and land use change (Table 1). Generally, the CO₂ exchange profile in vegetated areas of different conservation status did not reveal significant differences (Fig. S6), indicating that environmental alterations related to shifts in plant community composition had little impact on CO₂ exchange in the studied wetlands. While vegetation composition is a good indicator of the overall ecological integrity of wetland systems, the potential biogeochemical effects of these types of shifts (Davidson et al., 2018) were not of sufficient magnitude to be detected in our study. Although the vegetated areas of the Danube Delta wetlands did show significant differences that might be associated with differences in primary productivity of reed stands and agricultural crop species (Fig. S6), these coincided with permanently inundated substrates and agricultural soils, respectively. Thus, the observed differences likely arise from two main factors: differences in vegetation primary production efficiency and lower aerobic respiration rates due to oxygen limitation in submerged sediments and the water column compared with well-aerated agricultural soils (Bianchi et al., 2021). This interpretation is supported by the higher CO₂ emissions measured in non-vegetated areas of altered sites relative to preserved and restored sites in the Danube Delta (Fig. S6). These two non-exclusive mechanisms likely resulted in the status-level differences in CO₂ fluxes observed in the Danube Delta (Fig. 3e). Finally, the abundance of other primary producers (phytoplankton) appears to be the dominant driver responsible for the CO₂ exchange profiles observed in the Curonian Lagoon (Fig. 3f). In this wetland, nutrient load was the main alteration factor related to conservation status and ecosystem interventions

(Table 1), leading to eutrophication and associated massive phytoplankton blooms in altered sites (Vaičiūtė et al., 2021; Zilius et al., 2014), as indicated by water chlorophyll-*a* concentrations (Table S4). Thus, enhanced CO₂ uptake and reduced respiration under anoxic conditions driven by organic C accumulation by phytoplankton in open water areas (Fig. S6) seem to be the main drivers behind the general status-level differences in CO₂ exchange profiles of the Curonian Lagoon (Fig. 3f).

Hydrology emerged as a dominant control on CH₄ exchanges across the wetlands studied, with site inundation proportion (quantified as the percentage of chambers deployed in flooded areas) showing a clear positive relationship with CH₄ emissions across systems (Fig. S9). Permanently flooded sediments promote anoxic conditions that favor methanogenesis (Camacho-Santamans et al., 2025; Rochera et al., 2025) while restricting aerobic respiration and thus CO₂ releases. This mechanism is exemplified by the general inter-wetland type variability observed for CH₄ (Fig. 2), where well-preserved freshwater systems characterized by permanently flooded conditions and limited salinity constraints on methanogenesis (Camacho et al., 2017; Miralles-Lorenzo et al., 2025; Morant et al., 2024), such as Danube Delta lakes and the Curonian Lagoon, presented by far the largest emission profiles of CH₄. A similar pattern was observed for the freshwater marshes of Camargue, where wetland hydrology was a main determinant of the conservation status (Table 1) and CH₄ emissions (Fig. 4c). The hydrodynamics of altered CA sites favored flooded conditions, as reflected by 73% of chamber deployments in these sites occurring in inundated areas with respect to 48% for preserved sites. Accordingly, altered sites presented overall higher CH₄ emissions (Fig. 4c, Table S3), particularly during the summer season (Fig. S4), coinciding with the highest discrepancy in flooded area proportion between altered and preserved sites (82% vs. 40%) and high temperatures that likely limited oxygen availability and enhanced microbial activity in submerged sediments (Cui et al., 2024). Modified hydrology was also an important factor regulating CH₄ emissions in the brackish Mediterranean marshes of Marjal dels Moros, where similar differences in inundation proportion (65% vs 26%) were likely contributing to the higher CH₄ emissions observed in altered sites, with respect to preserved ones (Fig. 4d). This strong hydrological control likely also explains why CH₄ models generally had larger differences between marginal and conditional R² values than CO₂ models (Table S1). Because fine-scale inundation variability was not explicitly represented in the fixed-effects structure, part of the hydrological variability regulating CH₄ production was likely absorbed by the random site effect, increasing its relative explanatory contribution. This pattern was particularly evident in the Danube Delta wetlands, where altered sites encompassed strongly contrasting hydrological conditions (Supplementary Methods).

Nevertheless, CH₄ emissions were not only influenced by hydrology-driven oxygen availability of the sediments but also by salinity (electrical water conductivity), which showed a clear negative relationship with CH₄ emissions across wetlands (Fig. S10). Through the provision of sulfate as a more energetically favorable electron acceptor than CO₂, seawater intrusion regulates the dominance of sulfate-reducing over methanogenic microbes (Koebsch et al., 2019; Miralles-Lorenzo et al., 2025). This mechanism helps to explain the gradient in CH₄ emissions observed along the progressively more saline altered, restored and preserved sites of Marjal dels Moros (Fig. 4d, Table S4). Additionally, this salinity-driven methanogenesis limitation in tidal wetlands such as DU saltmarshes and RI *Z. noltii* meadows is likely responsible for their extremely low CH₄ emissions with respect to the other coastal wetlands examined (Fig. 2).

While anoxia and salinity help to regulate the dominant catabolic metabolism in sediments, the supply of different organic matter substrates is one of the principal factors regulating the overall rates of organic C degradation, and CH₄ emissions (Rissanen et al., 2023). Across the wetlands examined, the effect of labile organic matter supply in regulating CH₄ production can help to explain small but significantly

higher CH₄ emissions of preserved and restored *Z. noltii* meadows with respect to bare altered sites of RI (Fig. 4b), as seagrasses produce and release methylated compounds that represent an attractive substrate for methanogens (Schorn et al., 2022). Of more relevance is the pattern observed in the Curonian Lagoon wetland, where enhanced phytoplankton growth fueled by increased nutrient loads (Table S4) resulted in an accumulation of labile organic matter in the sediments of altered sites (Remeikaitė-Nikienė et al., 2016). Rapid degradation of phytoplankton-derived organic-C leads to anoxic conditions which, together with the freshwater character of the sites (Zilius et al., 2014), resulted in an ideal environment for methanogenesis, helping to explain the stark differences in CH₄ overall emissions between the altered and preserved and restored sites of this wetland (Fig. 4f). Additionally, although these increased emissions of CU eutrophic sites were consistently detected in both open-water and vegetated areas, the magnitude of CH₄ emissions was much higher in reed-covered zones of CU, which is a common pattern observed across many of the wetlands examined (Fig. S7). The consistently higher CH₄ emissions observed in vegetated zones likely result from vegetation-facilitated transfer of CH₄ from sediments to the atmosphere, bypassing oxidation in sediments and the water column (Ge et al., 2024). Ebullitive CH₄ transfer likely also contributed to the high variability observed in CH₄ fluxes, particularly in freshwater wetlands with high overall CH₄ emissions such as the Danube delta and Curonian Lagoon. Ebullition accelerates CH₄ transport to the atmosphere, limiting oxidation during water-column transit, but is also inherently variable over short temporal scales. Although ebullition was not independently quantified in this study, visual evidence of ebullitive dynamics was more prevalent in wetlands with higher CH₄ emissions, suggesting that this mechanism likely contributed to the elevated CH₄ fluxes and variability observed in these systems.

Importantly, the restoration actions examined across case pilots were not equivalent interventions applied across comparable systems, but rather context-specific responses to different forms of wetland alteration. Thus, comparisons of GHG fluxes among conservation statuses were made within each case pilot, rather than across them. Nevertheless, two non-exclusive mechanisms emerged as primary drivers of changes in GHG exchange across wetlands: shifts in areal habitat composition and changes in process rates within habitats. Major alterations and restoration actions can modify wetland structure to the point where entire habitats such as vegetated or open water areas are lost along with their biogeochemical functioning. The loss and replantation of seagrass beds in Ria de Aveiro or the land-use changes involving draining and rewetting of the Danube Delta wetlands are extreme examples of this mechanism. Conversely, subtler interventions that do not visually alter the ecosystem landscape can nonetheless shift underlying processes and result in significant impacts on biogeochemical process rates. The degradation and subsequent recovery of water quality in the Curonian Lagoon through regulation of nutrient-loads is a good example of this mechanism: while the composition of open water and reed beds habitats remained the same between altered and restored sites, their habitat-specific rates of CO₂ and CH₄ production and atmospheric exchange were significantly different (Figs. S6, S7). While the above examples represent extremes of these two mechanisms, it is important to recognize the existence of a continuum between them. It is also important to acknowledge that no single habitat-specific “reference” rate exists for any natural process. In this context, seasonal variability regulates GHG fluxes through two pathways: temperature and physiological shifts alter habitat-specific process rates, while seasonal flooding dynamically redistributes the relative extent of open water, vegetated areas, and bare sediments within wetlands.

The contrasting sensitivities and drivers of CO₂ and CH₄ often led to opposite flux responses to the same environmental interventions, making CO₂-eq outcomes dependent on wetland-specific gas dominance. Three general response groups emerged. In tidal wetlands (Dutch Delta and Ria de Aveiro), constant seawater supply suppressed CH₄ emissions to the point that this gas only represented an average 6% and 4% of CO₂-

eq exchanges (20-year GWP), respectively. In these wetlands, only vegetation-related interventions resulted in a significant impact on their climatic functionality, with changes in CO₂ fluxes outbalancing all detected variations in CH₄ emissions (regardless of GWP scaling). In seasonally inundated Mediterranean marshes (Camargue and Marjals dels Moros), CH₄ played a moderate role in their CO₂-eq fluxes (25% and 19%, respectively; 20-year GWP). In these wetlands, high CO₂ flux variability obscured detected changes in CH₄ emissions, leading to no significant differences in CO₂-eq fluxes (for both 100-year and 20-year GWP). In permanently flooded freshwater wetlands (Danube lakes and Curonian Lagoon), CH₄ represented a higher average proportion of the wetland GHG balance in terms of CO₂-eq (56% and 62%, respectively; 20-year GWP). In these wetlands, ecosystem interventions had clear but opposite effects for CO₂ and CH₄ exchanges, which only resulted in changes of combined CO₂-eq fluxes when CO₂ responses were of relatively low magnitude and outbalanced by strong CH₄ changes scaled with a 20-year GWP factor.

4.2. Climate change mitigation potential of coastal European wetland restoration and conservation

This study offers valuable insights into the potential of European coastal wetland restoration as a climate mitigation tool through the exemplary results obtained from six diverse pilot wetlands. Comparison of CO₂, CH₄ and CO₂-eq exchange balances between altered and restored sites provide a quantitative estimate of the mitigation potential of restoration across different wetland types (Table S3).

Although the central distributions of daily net fluxes showed apparent reductions in GHG fluxes following restoration in several pilot wetlands (Figs. 3, 4, 5), driven by significant effects of the conservation status (Table S1), high data variability precluded the detection of statistically significant mean flux reductions in some cases (Table S3). Across the pilot wetlands, statistically significant mitigation of CO₂ fluxes was only detected for the restoration of Ria de Aveiro seagrass meadows and Danube Delta freshwater lakes, likely driven by increased net primary production of seagrass relative to bare sediment areas and reduced organic C decomposition rates in freshwater lakes compared with agricultural land use, respectively. For CH₄ fluxes, statistically significant mitigation was only observed following water quality improvement in the Curonian Lagoon, while restoration of natural hydrodynamics in Camargue achieved marginal CH₄ reductions that approached statistical significance. When CO₂ and CH₄ were combined as CO₂-eq, significant mitigation potential was only detected for seagrass replantation in Ria de Aveiro under both 100-year and 20-year CH₄ warming scenarios and for re-oligotrophication in the Curonian Lagoon under the 20-year scenario. These different outcomes emphasize that the climate change mitigation effects of wetland restoration mediated by changes in GHG fluxes cannot be generalized across intervention types or ecosystems. Restoration actions target different system-specific degradation pathways and therefore can influence distinct biogeochemical controls on GHG exchange, resulting in climatic effects that are strongly dependent on ecosystem context.

The magnitude of potential mitigated emissions associated with the restoration interventions examined across the pilot wetlands, quantified as significant reductions in GHG fluxes using altered conditions as baseline (Table S3) and reported here as mean ± SE [CI95 range], were generally within the range reported for other nature-based solutions. Restoration of RI seagrass meadows reduced fluxes by -353 ± 108 [-567 to -145] g CO₂-eq m⁻² y⁻¹ considering only CO₂ fluxes, with minimal change when CH₄ fluxes were incorporated (-351 ± 108 [-565 to -144] g CO₂-eq m⁻² y⁻¹; 20-year GWP). These reductions are comparable to the -73 and -154 g CO₂-eq m⁻² y⁻¹ reported by Oreska et al. (2020) for 12- and 15-year seagrass restoration projects, and fall within the range of the global average net sink estimated for seagrass systems by Rosentreter et al. (2023) of -592 ± 309 g CO₂-eq m⁻² y⁻¹ (mean ± SE), including CO₂ and CH₄ fluxes (100-year GWP).

Restoration of CU substantially reduced CH₄ emissions, corresponding to mitigation potentials of -719 ± 319 [-1485 to -230] and -2124 ± 942 [-4381 to -679] g CO₂-eq m⁻² y⁻¹ under 100-year and 20-year GWP scenarios, respectively. However, these reductions were partially offset by increased CO₂ fluxes, such that significant mitigation of combined CO₂-eq fluxes was only detected under the 20-year GWP scenario (-1900 ± 942 [-4176 to -447] g CO₂-eq m⁻² y⁻¹). This pattern contrasts with that of peatland rewetting described by Darusman et al. (2023), where reductions in CO₂ emissions of -522 ± 131 [-781 to -226] were partially offset by increased GWP20-CH₄ emissions of 349 ± 29 [262 to 407] g CO₂-eq m⁻² y⁻¹. Nevertheless, the mitigation potential estimated for CU falls within the ranges reported by Bernal et al. (2018) for other ecosystem interventions over a 20-year period, including planted forests (-4070 to -450), agroforestry (-1560 to -1080), and mangrove restoration (-2310 to -670) g CO₂-eq m⁻² y⁻¹. Finally, restoration of freshwater marshes in CA did not significantly affect CO₂ fluxes (Table S1), but did significantly reduce CH₄ emissions, (Table S3). When considered independently, these CH₄ reductions corresponded to a maximum mitigation potential of -175 ± 122 [-496 to -20] g CO₂-eq m⁻² y⁻¹ under the 20-year GWP scenario. The contrasting outcomes between 100-year and 20-year CH₄ warming scenarios highlight how the perceived climatic effectiveness of wetland restoration depends strongly on the temporal framework used to evaluate CO₂-eq exchanges. Thus, careful consideration of these scenarios should be made when assessing the climate mitigation potential associated with wetland restoration.

The results show mitigation potential for restoration of some types of degraded coastal European wetlands; however, the cumulative nature of GHG emissions must be considered. Even in cases where restoration completely reverts the biogeochemical functioning of a degraded wetland back to pristine conditions, the net effect must account for the time during which the wetland presented increased emissions incurring in a “recovery debt” (Moreno-Mateos et al., 2017). While the limited potential impact of restoration might appear discouraging, the same temporal consideration highlights the elevated and persistent costs of inaction and the necessity to avoid degradation of coastal wetlands in the first place. Differences in GHG profiles between preserved and degraded conditions revealed clear trends that demonstrate the climate change mitigation potential of maintaining coastal European wetlands in good conservation status (Table S3). Potentially avoided emissions through conservation were often of similar or greater magnitude than those estimated for restoration of RI and CU wetlands, while achieving statistical significance in more cases. For example, in Mediterranean marsh systems where conservation status did not significantly affect CO₂ fluxes (CA and VA), avoided CH₄ emissions through conservation exceeded those estimated for restoration and corresponded to mitigation potentials of up to -193 ± 121 [-511 to -46] and -139 ± 107 [-418 to -21] g CO₂-eq m⁻² y⁻¹, respectively, under a 20-year GWP scenario. These patterns reveal fundamental differences in the functioning of well preserved and restored ecosystems.

Restoration projects guided by ecological restoration theory typically focus on alleviating pressures through passive restoration and reconstructing ecosystem structures to accelerate inherent functional recovery via active restoration (Palmer et al., 2016). However, even when restoration is well implemented, functional recovery often lags structural recovery due to slow reestablishment of natural biotic networks underpinning biogeochemical processes (Moreno-Mateos et al., 2012). Additionally, hysteretic dynamics in the face of ecosystem degradation and recovery may lead to trajectories favoring unintended alternative degraded states (Suding et al., 2004). Overall, the risks inherent to wetland restoration, recovery pathways and generally slow biogeochemical functional recovery emphasize the importance of preserving natural wetlands in a good conservation status.

Despite the differences shown above, conservation and restoration are complementary tools for climate mitigation and should not be viewed as alternative management strategies. Additionally, the climate

change mitigation signals (GHG abatement) discussed here should be interpreted within the scope of the methodological approach employed, which quantified surface-atmosphere GHG exchanges over limited temporal windows and did not account for potential lateral GHG transport pathways (see Section 2.5). It is important to recognize that our current assessment of restoration-associated climate mitigation potential does not account for other biogeochemically relevant benefits, such as expansion of wetland extent or potential reductions of nitrous oxide (N₂O) emissions (Kasak et al., 2021; Leo et al., 2019), and represents only a snapshot of the functional recovery process likely to improve over time (Moreno-Mateos et al., 2017). Thus, the lack of statistically significant reductions in areal CO₂ and CH₄ exchanges reported in Table S3 should not be interpreted as evidence that wetland restoration lacks climate mitigation benefits. Moreover, none of the restoration strategies implemented across the different wetlands examined targeted GHG mitigation as an explicit primary objective (Oliveira et al., 2026). Therefore, the detected effects on GHG exchanges can be considered as an additional co-benefit of restoration alongside improvements in other ecosystem services such as biodiversity, water quality and flood risk mitigation (Meli et al., 2014; Singh et al., 2019; Wu et al., 2023). Ultimately, although the results show that restoration caused significant increases in emissions of either CO₂ or CH₄ in some wetlands, these were always accompanied by similar or greater changes in the opposite direction for the other GHG species studied. Therefore, when considering the combined CO₂-eq exchange patterns associated with restoration of degraded wetlands, the only significant effects detected were net reductions, indicating a net climatic cooling effect (Table S3).

This study highlights the diverse biogeochemical controls on GHG regulation across European coastal wetlands under different conservation statuses. These functional and site-specific differences must be explicitly considered in restoration and management planning to avoid trade-offs with other ecosystem services (Pörtner et al., 2021). Restoration strategies should therefore incorporate targeted, long-term monitoring to track wetland recovery and detect structural or functional deviations that require corrective action.

Wetlands have been heavily impacted by land-use change due to the historical undervaluation of their ecosystem services, often favoring higher-value uses despite substantial ecological losses (Zorrilla-Miras et al., 2014). This underscores the need to explore financing mechanisms that recognize the economic value of wetland ecosystem services, particularly their potential for climate mitigation. However, wetland climate mitigation capacity arises from complex, system-specific interactions among multiple GHGs, characterized by high spatial and temporal variability. Financing schemes should therefore be linked to comprehensive, long-term monitoring of all GHG fluxes relevant to the climatic functioning of each wetland system to avoid incomplete accounting and over-crediting risks prevalent in current carbon offset markets (Romm et al., 2025). Monitoring schemes should thus be guided by the understanding of each wetland's biogeochemical functioning while making use of standardized methodologies for fair monitoring, reporting and verification (Misteli et al., 2025a, 2025b). Given the strong seasonal variability observed across all wetlands examined, single annual measurements would likely be insufficient to characterize GHG dynamics robustly. However, in systems overwhelmingly dominated by CO₂ exchanges such as the RI seagrass meadows, monitoring resources could be prioritized toward measuring CO₂ over CH₄ fluxes and, if system functioning is sufficiently well understood, even toward proxies such as vegetation extent or biomass. Ultimately, for coastal wetland restoration to be an effective nature-based climate solution, projects must demonstrate additionality, feasibility, and permanence, and provide enough evidence to accurately quantify their climate benefits (Jones et al., 2024).

Currently, estimates of climate mitigation capacity of wetland restoration are highly variable (Griscom et al., 2017), stemming from incomplete understanding of several climate relevant processes. A

common identified issue is the lack of widespread data on how GHG exchanges, in particular CH₄ and N₂O emissions, respond to coastal wetland restoration (Rosentreter et al., 2021). While the climatic effect of restoration projects in other ecosystems might be well represented by simple C balance assessments, in wetlands systems monitoring of these non-CO₂ GHG exchanges, and consideration of their time-horizon dependent warming effects is essential to accurately quantify net climatic impact (Macreadie et al., 2019). Transient increases in CH₄ emissions from restored wetlands can, considering radiative forcings and atmospheric lifetimes of GHGs, considerably delay climatic benefits of increased C storage (Schuster et al., 2024). Therefore, wetland restoration actions that achieve timely reductions of CH₄ emissions, such as those of Curonian Lagoon and to a lesser extent Camargue and Marjal dels Moros, become especially relevant to meeting climatic mitigation targets. Additionally, the importance of lateral C and off-site GHG exchanges is increasingly being recognized, and future studies should therefore aim to obtain a more complete assessment of watershed-level budgets that support management decisions (Jones et al., 2024; Regnier et al., 2022). Finally, appropriate pre-restoration baseline reference condition measurements are essential to provide actionable knowledge to managers, thereby allowing quantification of actual benefits of alteration-specific reversals.

Given the ample and clear benefits of coastal wetland restoration on the provisioning of other ecosystem services, widespread restoration of degraded systems should nonetheless be pursued. We advocate taking advantage of recent policy momentum, exemplified by the EU Nature Restoration Regulation (Kampa et al., 2025), to gather more evidence on the effects of coastal wetland restoration on GHG exchange, enabling us to quantify more precisely the magnitude, consistency and reliability of potential associated climatic benefits.

5. Conclusions

This study examined how the conservation status and system-specific restoration actions of diverse European coastal wetlands influence atmospheric exchanges of CO₂ and CH₄ and their combined effects on climate forcing expressed as CO₂-eq. The results of this study show that GHG fluxes respond differently to degradation and restoration actions depending on the wetland type and associated main biogeochemical drivers. In particular, CO₂ fluxes responded primarily to landscape-scale changes in vegetation cover and inundation, whereas CH₄ exchanges were more sensitive to environmental modification and readily responded to less evident changes in water quality, salinity, and hydrodynamics.

These contrasting responses, together with the different relative contributions of CO₂ and CH₄ to net climatic forcing, translated into wetland-specific CO₂-eq exchange patterns associated with restoration and conservation. Replantation of seagrass meadows consistently emerged as an effective restoration measure associated with significant reductions in surface-atmosphere CO₂-eq exchanges under both 100-year and 20-year CH₄ warming scenarios, while eutrophication reversal through improved water treatment was associated with significant reductions under the 20-year scenario. Other actions, such as the reestablishment of natural salinity and hydrodynamics regimes, showed signs of reducing CH₄ emissions, but high CO₂ flux variability precluded detection of significant reductions in combined CO₂-eq emissions with the measured data.

While this study did not assess potential changes in N₂O emissions, the observed patterns for CO₂ and CH₄ contribute to the growing body of evidence supporting wetland restoration as a promising nature-based solution for climate change mitigation. At the same time, the findings of our study underscore the importance of considering multiple GHGs and their specific biogeochemistry when evaluating the climatic impact of wetland restoration projects. Further research should therefore aim to simultaneously quantify complete exchange budgets of CO₂, CH₄ and N₂O over management-relevant timeframes to better characterize the

functional recovery process and obtain more complete assessments of the climatic implications associated with wetland restoration.

Within the scope of this study, restoration projects implemented across a range of European coastal wetland types showed no evidence of significant detrimental effects in terms of CO₂-eq. Instead, the results demonstrate that restoration was generally associated with maintained or improved CO₂-eq exchange profiles favoring climate change mitigation. Combined with ample evidence for other ecosystem service co-benefits, the results of our study support current regulatory efforts aimed at recovering historically degraded European wetlands while underscoring the need for targeted, ecosystem-specific restoration strategies to maximize potential climate mitigation benefits.

Declaration of generative AI and AI-assisted technologies in the manuscript preparation process

During the preparation of this work the authors used ChatGPT-5.2 in order to identify potential improvements in text readability and for coding syntax support during data processing. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the published article.

CRediT authorship contribution statement

Miguel Cabrera-Brufau: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation. **Camille Minaudo:** Writing – review & editing, Methodology, Investigation, Data curation. **Katrin Attermeyer:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Alba Camacho-Santamans:** Writing – review & editing, Methodology, Investigation. **Rafael Carballeira:** Writing – review & editing, Methodology, Investigation. **Benjamin Misteli:** Writing – review & editing, Methodology, Investigation. **Jorge Montes-Pérez:** Writing – review & editing, Methodology, Investigation. **Daniel Morant:** Writing – review & editing, Methodology, Investigation. **Biel Obrador:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Antonio Picazo:** Writing – review & editing, Methodology, Investigation. **Carlos Rochera:** Writing – review & editing, Methodology, Investigation. **Mihai Adamescu:** Writing – review & editing, Investigation. **Raquel Ambrosio:** Writing – review & editing, Investigation. **Giancarlo Bachi:** Writing – review & editing, Investigation. **Nina Bègue:** Writing – review & editing, Investigation. **Martynas Bučas:** Writing – review & editing, Investigation. **Lidia Cañas Ramírez:** Writing – review & editing, Methodology, Investigation. **Marco Carloni:** Writing – review & editing, Investigation. **Lamara Cavalcante:** Writing – review & editing, Investigation. **Constantin Cazacu:** Writing – review & editing, Investigation. **Giovanni Checucci:** Writing – review & editing, Investigation. **J. Pedro Coelho:** Writing – review & editing, Investigation. **Valentin Dinu:** Writing – review & editing, Investigation. **Valtere Evangelista:** Writing – review & editing, Investigation. **Ilenia Férez Martín:** Writing – review & editing, Methodology, Investigation. **Jonas Gintauskas:** Writing – review & editing, Investigation. **Relu Giuca:** Writing – review & editing, Investigation. **Anis Guelmami:** Writing – review & editing, Investigation. **Mirco Guerazzi:** Writing – review & editing, Investigation. **Samuel Hilaire:** Writing – review & editing, Investigation. **Marija Katarzyte:** Writing – review & editing, Investigation. **Ana I. Lillebo:** Writing – review & editing, Project administration, Investigation, Funding acquisition, Conceptualization. **Raquel Lizán:** Writing – review & editing, Investigation. **Bruna R.F. Oliveira:** Writing – review & editing, Investigation. **Vitor H. Oliveira:** Writing – review & editing, Investigation. **Marta Pedrón:** Writing – review & editing, Investigation. **Jolita Petkuvienė:** Writing – review & editing, Investigation. **Tudor Racoviceanu:** Writing – review & editing, Investigation. **Michael Ronse:** Writing – review & editing, Investigation. **Chiara Santinelli:** Writing – review & editing, Investigation. **Ana I. Sousa:** Writing – review & editing, Investigation. **Wouter Suykerbuyk:** Writing – review & editing, Investigation.

Edvinas Tiškus: Writing – review & editing, Investigation. **Claudia Tropea:** Writing – review & editing, Investigation. **Diana Vaičiūtė:** Writing – review & editing, Investigation. **Silvia Valsecchi:** Writing – review & editing, Investigation. **Marinka van Puijenbroek:** Writing – review & editing, Investigation. **Mourine J. Yegon:** Writing – review & editing, Investigation. **Antonio Camacho:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Daniel von Schiller:** Writing – review & editing, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Funding

Funding for this research came from the project RESTORE4Cs - *Modelling RESTORation of wetlands for Carbon pathways, Climate Change mitigation and adaptation, ecosystem services, and biodiversity, Co-benefits* (DOI: <https://doi.org/10.3030/101056782>), funded by the European Union under the Horizon Europe research and innovation programme (Grant Agreement ID: 101056782). The views and opinions expressed are those of the author(s) only and do not necessarily reflect those of the European Union or the granting authority. Neither the European Union nor the granting authority can be held responsible for them. We also acknowledge the support of FCT – Fundação para a Ciência e a Tecnologia I.P., to CESAM-Centro de Estudos do Ambiente e do Mar, under the project references UID/50017/2025 (doi.org/10.54499/UID/50017/2025) and LA/P/0094/2020 (doi.org/10.54499/LA/P/0094/2020). We thank Sara Ribeiro for logistical support. Work by the University of Valencia was also co-supported by projects CLIMAWET-CONS (PID2019-104742RB-I00), funded by the Agencia Estatal de Investigación of the Spanish Government, and by the project ECCAEL (PROMETEO CIPROM-2023-031), funded by the Generalitat Valenciana, both granted to Antonio Camacho. Daniel von Schiller is a Serra Hünter Fellow.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecoleng.2026.108080>.

Data availability

Data presented in this article is deposited at LifeWatch ERIC (<https://doi.org/10.48372/C29B-QW38>) and will be fully accessible after December 31st, 2027. During the embargo period, data will be made available upon reasonable request. The code to reproduce the results of this article is archived at Zenodo (<https://doi.org/10.5281/zenodo.21129514>).

References

- Airolidi, L., Beck, M., 2007. Oceanography and Marine Biology. In: Oceanography and Marine Biology: An Annual Review. CRC Press. <https://doi.org/10.1201/9781420050943>.
- Bernal, B., Murray, L.T., Pearson, T.R.H., 2018. Global carbon dioxide removal rates from forest landscape restoration activities. Carbon Balance Manag. 13 (1), 22. <https://doi.org/10.1186/s13021-018-0110-8>.
- Bertolini, C., da Mosto, J., 2021. Restoring for the climate: a review of coastal wetland restoration research in the last 30 years. Restor. Ecol. 29, e13438. <https://doi.org/10.1111/rec.13438>.
- Bianchi, A., Larmola, T., Kekkonen, H., Saarnio, S., Lång, K., 2021. Review of greenhouse gas emissions from rewetted agricultural soils. Wetlands 41, 108. <https://doi.org/10.1007/s13157-021-01507-5>.
- Bonaglia, S., Cheung, H.L.S., Politi, T., Vybernaite-Lubiene, I., McKenzie, T., Santos, I.R., Zilius, M., 2025. Eutrophication and urbanization enhance methane emissions from coastal lagoons. Limnol Oceanogr Lett 10, 140–150. <https://doi.org/10.1002/lo2.10430>.
- Cabrera-Brufau, M., Minaudo, C., 2026. MCabreraBrufau/Restore4Cs_GHG_chamber_fluxes: Static Chamber CO₂ and CH₄ Flux Calculation Workflow (RESTORE4Cs Project) (v1.0.0). Zenodo. <https://doi.org/10.5281/zenodo.19184152>.
- Cabrera-Brufau, M., Minaudo, C., von Schiller, D., Obrador, B., Attermeyer, K., Camacho, A., 2025. Instantaneous Fluxes of Carbon Dioxide (CO₂) and Methane (CH₄) of Six European Coastal Wetlands Under Different Ecological Status Measured Seasonally With Static Chambers [Data set]. LifeWatch ERIC. <https://doi.org/10.48372/C29B-QW38>.
- Cabrera-Brufau, M., Minaudo, C., Attermeyer, K., Camacho-Santamans, A., Carballeira, R., Misteli, B., Montes-Pérez, J.J., Morant, D., Obrador, B., Picazo Mozo, A., Rochera, C., von Schiller, D., Camacho, A., 2026. Raw GHG Static Chamber Data of RESTORE4Cs Project (CO₂ and CH₄ Concentration Time Series and Incubation Details) [Data set]. Zenodo. <https://doi.org/10.5281/zenodo.18803756>.
- Camacho, A., Picazo, A., Rochera, C., Santamans, A., Morant, D., Miralles-Lorenzo, J., Castillo-Escrivá, A., 2017. Methane emissions in Spanish Saline Lakes: current rates, temperature and salinity responses, and evolution under different climate change scenarios. Water 9, 659. <https://doi.org/10.3390/w9090659>.
- Camacho-Santamans, A., Morant, D., Rochera, C., Picazo, A., Camacho, A., 2025. Towards an enhancement of the climate change mitigation capacity of inland saline shallow lakes through hydrological regime and vegetation management: a modelling approach. Water Int. 50, 197–224. <https://doi.org/10.1080/02508060.2024.2311997>.
- Canadell, J.G., Monteiro, P.M.S., 2023. Global carbon and other biogeochemical cycles and feedbacks. In: climate Change 2021 – the Physical Science Basis. Cambridge University Press, pp. 673–816. <https://doi.org/10.1017/9781009157896.007>.
- 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, 470. <https://doi.org/10.1038/s43247-024-01635-w>.
- Darusman, T., Murdiyarso, D., Impron, Anas, I., 2023. Effect of rewetting degraded peatlands on carbon fluxes: a meta-analysis. Mitig. Adapt. Strat. Glob. Chang. 28 (3), 10. <https://doi.org/10.1007/s11027-023-10046-9>.
- Davidson, I.C., Cott, G.M., Devaney, J.L., Simkanin, C., 2018. Differential effects of biological invasions on coastal blue carbon: a global review and meta-analysis. Glob. Chang. Biol. 24, 5218–5230. <https://doi.org/10.1111/gcb.14426>.
- European Environment Agency, 2024. Europe's State of Water 2024 – The Need for Improved Water Resilience. Publications Office of the European Union. <https://doi.org/10.2800/02236>.
- European Union, 2024. Regulation (EU) 2024/1991 of the European Parliament and of the Council of 24 June 2024 on Nature Restoration and Amending Regulation (EU) 2022/869.
- 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., Hugelius, G., Joosten, H., Barthelmes, A., Prigent, C., Aires, F., Hoyt, A.M., Davidson, N., Finlayson, C.M., Lehner, B., Jackson, R.B., McIntyre, P.B., 2023. Extensive global wetland loss over the past three centuries. Nature 614 (7947), 281–286. <https://doi.org/10.1038/s41586-022-05572-6>.
- Ge, M., Korrensalo, A., Laiho, R., Kohl, L., Lohila, A., Pihlatie, M., Li, X., Laine, A.M., Anttila, J., Putkinen, A., Wang, W., Koskinen, M., 2024. Plant-mediated CH₄ exchange in wetlands: a review of mechanisms and measurement methods with implications for modelling. Sci. Total Environ. <https://doi.org/10.1016/j.scitotenv.2023.169662>.
- Graves, S., Piepho, H.-P., Sundar Dorai-Raj, L.S., 2024. , with help from multcompView: Visualizations of Paired Comparisons. <https://doi.org/10.32614/CRAN.package.multcompView>.
- Griscom, B.W., Adams, J., Ellis, P.W., Houghton, R.A., Lomax, G., Miteva, D.A., Schlesinger, W.H., Shoch, D., Sikkamäki, J.V., Smith, P., Woodbury, P., Zganjar, C., Blackman, A., Campari, J., Conant, R.T., Delgado, C., Elias, P., Gopalakrishna, T., Hamsik, M.R., Herrero, M., Kiesecker, J., Landis, E., Laestadius, L., Leavitt, S.M., Minnemeyer, S., Polasky, S., Potapov, P., Putz, F.E., Sanderman, J., Silvius, M., Wollenberg, E., Fargione, J., 2017. Natural climate solutions. Proc. Natl. Acad. Sci. 114, 11645–11650. <https://doi.org/10.1073/pnas.1710465114>.
- Hartig, F., 2024. DHARMA: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. <https://doi.org/10.32614/CRAN.package.DHARMA>.
- He, T., Ding, W., Cheng, X., Cai, Y., Zhang, Y., Xia, H., Wang, X., Zhang, J., Zhang, K., Zhang, Q., 2024. Meta-analysis shows the impacts of ecological restoration on greenhouse gas emissions. Nat. Commun. 15, 2668. <https://doi.org/10.1038/s41467-024-46991-5>.
- Hutchinson, G.L., Mosier, A.R., 1981. Improved soil cover method for field measurement of nitrous oxide fluxes. Soil Sci. Soc. Am. J. 45, 311–316. <https://doi.org/10.2136/sssaj1981.03615995004500020017x>.
- IPCC, 2023. Climate Change 2021 – the Physical Science Basis. Cambridge University Press, Cambridge. <https://doi.org/10.1017/9781009157896>.
- Jones, S.F., Arias-Ortiz, A., Baldocchi, D., Eagle, M., Friess, D.A., Gore, C., Noe, G., Nolte, S., Oikawa, P., Paytan, A., Raw, J.L., Roberts, B.J., Rogers, K., Schutte, C., Stagg, C.L., Thorne, K.M., Ward, E.J., Windham-Myers, L., Yando, E.S., 2024. When and where can coastal wetland restoration increase carbon sequestration as a natural climate solution? Cambridge Prisms: Coastal Futures. <https://doi.org/10.1017/cft.2024.14>.
- Kampa, E., Elkina, E., Otero, M., 2025. Unlocking potential of coastal wetlands in Europe: Integration into National Restoration Plans. Policy Brief. RESTORE4Cs project. https://www.restore4cs.eu/wp-content/uploads/2025/09/RESTORE4Cs_Policy-Brief-2_EN.pdf.

- Kasak, K., Espenberg, M., Anthony, T.L., Tringe, S.G., Valach, A.C., Hemes, K.S., Silver, W.L., Mander, Ü., Kill, K., McNicol, G., Szutu, D., Verfaillie, J., Baldocchi, D. D., 2021. Restoring wetlands on intensive agricultural lands modifies nitrogen cycling microbial communities and reduces N₂O production potential. *J. Environ. Manage.* 299, 113562. <https://doi.org/10.1016/j.jenvman.2021.113562>.
- Koebisch, F., Winkel, M., Liebner, S., Liu, B., Westphal, J., Schmiedinger, I., Spitz, A., Gehre, M., Jurasinski, G., Köhler, S., Unger, V., Koch, M., Sachs, T., Böttcher, M.E., 2019. Sulfate deprivation triggers high methane production in a disturbed and rewetted coastal peatland. *Biogeosciences* 16, 1937–1953. <https://doi.org/10.5194/bg-16-1937-2019>.
- Lenth, R.V., 2025. emmeans: Estimated Marginal Means, aka Least-Squares Means. <https://doi.org/10.32614/CRAN.package.emmeans>.
- Leo, K.L., Gillies, C.L., Fitzsimons, J.A., Hale, L.Z., Beck, M.W., 2019. Coastal habitat squeeze: a review of adaptation solutions for saltmarsh, mangrove and beach habitats. *Ocean Coast. Manag.* 175, 180–190. <https://doi.org/10.1016/j.ocecoaman.2019.03.019>.
- Lin, C.-W., Lin, W.-J., Ho, C.-W., Kao, Y.-C., Yong, Z.-J., Lin, H.-J., 2024. Flushing emissions of methane and carbon dioxide from mangrove soils during tidal cycles. *Sci. Total Environ.* 919, 170768. <https://doi.org/10.1016/j.scitotenv.2024.170768>.
- Lorke, A., Bodmer, P., Noss, C., Alshboul, Z., Koschorreck, M., Somlai-Haase, C., Bastviken, D., Flury, S., McGinnis, D.F., Maack, A., Müller, D., Premke, K., 2015. Technical note: drifting versus anchored flow chambers for measuring greenhouse gas emissions from running waters. *Biogeosciences* 12, 7013–7024. <https://doi.org/10.5194/bg-12-7013-2015>.
- Lovley, D.R., Klug, M.J., 1983. Sulfate reducers can outcompete methanogens at freshwater sulfate concentrations. *Appl. Environ. Microbiol.* 45, 187–192. <https://doi.org/10.1128/aem.45.1.187-192.1983>.
- Macreadie, P.I., Anton, A., Raven, J.A., Beaumont, N., Connolly, R.M., Friess, D.A., Kelleway, J.J., Kennedy, H., Kuwae, T., Lavery, P.S., Lovelock, C.E., Smale, D.A., Apostolaki, E.T., Atwood, T.B., Baldock, J., Bianchi, T.S., Chmura, G.L., Eyre, B.D., Fourqurean, J.W., Hall-Spencer, J.M., Huxham, M., Hendriks, I.E., Krause-Jensen, D., Laffoley, D., Luisetti, T., Marbà, N., Masque, P., McGlathery, K.J., Megonigal, J.P., Murdiyarso, D., Russell, B.D., Santos, R., Serrano, O., Silliman, B.R., Watanabe, K., Duarte, C.M., 2019. The future of blue carbon science. *Nat. Commun.* 10, 3998. <https://doi.org/10.1038/s41467-019-11693-w>.
- Maes, J., Teller, A., Erhard, M., Condé, S., Vallecillo, S., Barredo, J.I., Luisa, M., Malak, D. A., Trombetti, M., Viaggi, O., Zulfian, G., Addamo, A.M., Grizzetti, B., Somma, F., Hagyo, A., Vogt, P., Polce, C., Jones, A., Marin, A.I., Ivits, E., Mauri, A., Rega, C., Czucz, B., Ceccherini, G., Pisoni, E., Ceglar, A., De Palma, P., Cerrani, I., Meroni, M., Caudullo, G., Lugato, E., Vogt, J.V., Spinoni, J., Cammalleri, C., Bastrup-birk, A., Miguel, J.S., Román, S.S., Kristensen, P., Christiansen, T., De Roo, A., Cardoso, A.C., Pistocchi, A., Del, I., Alvarellos, B., Tsiamis, K., Gervasini, E., Deriu, I., La Notte, A., Viñas, R.A., Vizzarri, M., Camia, A., Kakoulaki, G., Bendito, E.G., Panagos, P., Ballabio, C., Scarpa, S., Orgiazzi, A., Ugalde, O.F., Santos-martin, F., 2020. Mapping and Assessment of Ecosystems and their Services: an EU Ecosystem Assessment. *ISPRRA*. <https://doi.org/10.2760/757183>.
- Maier, M., Weber, T.K.D., Fiedler, J., Fuß, R., Glatzel, S., Huth, V., Jordan, S., Jurasinski, G., Kutzbach, L., Schäfer, K., Weymann, D., Hagemann, U., 2022. Introduction of a guideline for measurements of greenhouse gas fluxes from soils using non-steady-state chambers. *J. Plant Nutr. Soil Sci.* 185, 447–461. <https://doi.org/10.1002/jpln.202200199>.
- McGillycuddy, M., Warton, D.I., Popovic, G., Bolker, B.M., 2025. Parsimoniously fitting large multivariate random effects in glmmTMB. *J. Stat. Softw.* 112, 1–19. <https://doi.org/10.18637/jss.v112.i01>.
- 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, e93507. <https://doi.org/10.1371/journal.pone.0093507>.
- Minaudo, C., von Schiller, D., Misteli, B., Morant, D., Adamescu, M., Attermeyer, K., Basset, A., Carballeira, R., Cazacu, C., Coelho, J.P., Guelmami, A., Hilaire, S., Miralles, J., Obrador, B., Petkuvienė, J., Picazo, A., Rochera, C., Santinelli, C., Teixeira, H., Titocci, J., Vaicute, D., Camacho, A., 2023. Methodological Manual. Deliverable D4.2 Horizon RESTORE4Cs Project GA ID: 101056782.
- Minaudo, C., Cabrera-Brufau, M., Montes-Pérez, J.J., Attermeyer, K., Camacho, A., Camacho-Santamans, A., Cazacu, C., Giuca, R., Lillebø, A., Misteli, B., Morant, D., Obrador, B., Oliveira, B.R.F., Petkuvienė, J., Mozo, A.P., Rochera, C., von Schiller, D., 2026. Uncertainty in aquatic greenhouse gas flux estimates arises from subjective processing of floating chamber time series. *Limnol. Oceanogr. Methods* 2026, e70054. <https://doi.org/10.1002/lom3.70054>.
- Miralles-Lorenzo, J., Picazo, A., Rochera, C., Morant, D., Casamayor, E.O., Menéndez-Serra, M., Camacho, A., 2025. Environmental gradients and conservation status determine the structure and carbon-related metabolic potential of the prokaryotic communities of Mediterranean inland saline Shallow Lakes. *Ecol. Evol.* 15, e71286. <https://doi.org/10.1002/ee3.71286>.
- Misteli, B., Attermeyer, K., Rochera, C., Lillebø, A.I., Camacho, A., 2025a. How Can Coastal Wetland Restoration Mitigate Climate Change? What we Know and What Is Still Unclear. Policy Brief. Restore4Cs project. https://www.restore4cs.eu/wp-content/uploads/2025/12/EN-Policy-Brief-9-v7_Final-1.pdf.
- Misteli, B., Morant, D., Camacho, A., Adamo, M., Bachi, G., Bègue, N., Bučas, M., Cabrera-Brufau, M., Carballeira, R., Cavalcante, L., Cazacu, C., Coelho, J., Doebeke, C., Dinu, V., Guelmami, A., Giuca, R., Katarzytė, M., Lillebø, A., Marin, A., Marangi, C., Minaudo, C., Montes-Pérez, J., Obrador, B., Oliveira, B., Petkuvienė, J., Picazo, A., van Puijenbroek, M., Ronse, M., Rochera, C., Sánchez, A., Santinelli, C., Sousa, A., von Schiller, D., Attermeyer, K., Tropea, C., Vaiciūtė, D., 2025b. Coastal wetland restoration and greenhouse gas pathways: a global meta-analysis. *EarthArXiv Preprint*. <https://doi.org/10.31223/X51B39>.
- 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. <https://doi.org/10.1007/s10980-012-9758-8>.
- Morant, D., Picazo, A., Rochera, C., Santamans, A.C., Miralles-Lorenzo, J., Camacho, A., 2020a. Influence of the conservation status on carbon balances of semiarid coastal Mediterranean wetlands. *Inland Waters* 10, 453–467. <https://doi.org/10.1080/20442041.2020.1772033>.
- Morant, D., Picazo, A., Rochera, C., Santamans, A.C., Miralles-Lorenzo, J., Camacho-Santamans, A., Ibañez, C., Martínez-Eixarch, M., Camacho, A., 2020b. Carbon metabolic rates and GHG emissions in different wetland types of the Ebro Delta. *PLoS One* 15, e0231713. <https://doi.org/10.1371/journal.pone.0231713>.
- Morant, D., Rochera, C., Picazo, A., Miralles-Lorenzo, J., Camacho-Santamans, A., Camacho, A., 2024. Ecological status and type of alteration determine the C-balance and climate change mitigation capacity of Mediterranean inland saline shallow lakes. *Sci. Rep.* 14, 29065. <https://doi.org/10.1038/s41598-024-79578-7>.
- Moreno-Mateos, D., Power, M.E., Comin, F.A., Yockteng, R., 2012. Structural and functional loss in restored wetland ecosystems. *PLoS Biol.* 10, e1001247. <https://doi.org/10.1371/journal.pbio.1001247>.
- Moreno-Mateos, D., Barbier, E.B., Jones, P.C., Jones, H.P., Aronson, J., López-López, J.A., McCrackin, M.L., Meli, P., Montoya, D., Rey Benayas, J.M., 2017. Anthropogenic ecosystem disturbance and the recovery debt. *Nat. Commun.* 1 (8), 14163. <https://doi.org/10.1038/ncomms14163>.
- Neubauer, S.C., 2021. Global Warming potential is not an ecosystem property. *Ecosystems* 24, 2079–2089. <https://doi.org/10.1007/s10021-021-00631-x>.
- O'Connor, J.J., Fest, B.J., Sievers, M., Swearer, S.E., 2020. Impacts of land management practices on blue carbon stocks and greenhouse gas fluxes in coastal ecosystems—a meta-analysis. *Glob. Chang. Biol.* 26, 1354–1366. <https://doi.org/10.1111/gcb.14946>.
- Oliveira, B.R.F., Camacho, A., Guelmami, A., Schroder, C., Bègue, N., Bučas, M., Cazacu, C., Ciravegna, E., Coelho, J.P., Constantin, R.G., Hilaire, S., Katarzytė, M., Morant, D., Picazo, A., Polman, N., van Puijenbroek, M., Raoult, J., Rochera, C., Ronse, M., Lillebø, A.I., 2026. European coastal wetlands datasets and their use in decision-support tools for policy restoration objectives. *Environ. Sci. Policy* 179, 104386. <https://doi.org/10.1016/j.envsci.2026.104386>.
- Oreska, M.P.J., McGlathery, K.J., Aoki, L.R., Berger, A.C., Berg, P., Mullins, L., 2020. The greenhouse gas offset potential from seagrass restoration. *Sci. Rep.* 10 (1), 7325. <https://doi.org/10.1038/s41598-020-64994-1>.
- Palmer, M.A., Zedler, J.B., Falk, D.A., 2016. Ecological theory and restoration ecology. In: *Foundations of Restoration Ecology: Second Edition*, pp. 3–26. https://doi.org/10.5822/978-1-61091-698-1_1.
- Peterson, R.A., 2021. Finding optimal normalizing transformations via bestNormalize. *R J* 13, 310–329. <https://doi.org/10.32614/RJ-2021-041>.
- Pörtner, H.-O., Scholes, R.J., Agard, J., Archer, E., Arneth, A., Bai, X., Barnes, D., Burrows, M., Chan, L., Cheung, W.L. (William), Diamond, S., Donatti, C., Duarte, C., Eisenhauer, N., Foden, W., Gasalla, M.A., Handa, C., Hickler, T., Hoegh-Guldberg, O., Ichii, K., Jacob, U., Insarov, G., Kiessling, W., Leadley, P., Leemans, R., Levin, L., Lim, M., Maharaj, S., Managi, S., Marquet, P.A., McElwee, P., Midgley, G., Oberdorff, T., Obura, D., Osman Elasha, B., Pandit, R., Pascual, U., Pires, A.P.F., Popp, A., Reyes-García, V., Sankaran, M., Settele, J., Shin, Y.-J., Sintayehu, D.W., Smith, P., Steiner, N., Strassburg, B., Sukumar, R., Trisos, C., Val, A.L., Wu, J., Aldrian, E., Parmesan, C., Pichs-Madruga, R., Roberts, D.C., Rogers, A.D., Díaz, S., Fischer, M., Hashimoto, S., Lavorel, S., Wu, N., Ngo, H., 2021. Scientific Outcome of the IPBES-IPCC Co-Sponsored Workshop on Biodiversity and Climate Change. <https://doi.org/10.5281/ZENODO.5101125>.
- R Core Team, 2025. R: A Language and Environment for Statistical Computing.
- Ramsar Convention, 1971. Convention on Wetlands of International Importance Especially as Waterfowl Habitat. Ramsar Convention, Ramsar.
- Reddy, K.R., DeLaune, R.D., Inglett, P.W., 2022. Biogeochemistry of Wetlands. CRC Press, Boca Raton. <https://doi.org/10.1201/9780429155833>.
- Regnier, P., Resplandy, L., Najjar, R.G., Ciais, P., 2022. The land-to-ocean loops of the global carbon cycle. *Nature* 603, 401–410. <https://doi.org/10.1038/s41586-021-04339-9>.
- Remeikaitė-Nikienė, N., Lujanienė, G., Malejevas, V., Barisevičiūtė, R., Žilius, M., Garnaga-Budrė, G., Stankevičius, A., 2016. Distribution and sources of organic matter in sediments of the South-Eastern Baltic Sea. *J. Mar. Syst.* 157, 75–81. <https://doi.org/10.1016/j.jmarsys.2015.12.011>.
- Rheault, K., Christiansen, J.R., Larsen, K.S., 2024. goFlux: a user-friendly way to calculate GHG fluxes yourself, regardless of user experience. *J. Open Source Softw.* 9, 6393. <https://doi.org/10.21105/joss.06393>.
- Rissanen, A.J., Jilbert, T., Simojoki, A., Mangayil, R., Aalto, S.L., Khanongnuch, R., Peura, S., Jäntti, H., 2023. Organic matter lability modifies the vertical structure of methane-related microbial communities in lake sediments. *Microbiol. Spectr.* 11. <https://doi.org/10.1128/spectrum.01955-23>.
- Rochera, C., Picazo, A., Morant, D., Miralles-Lorenzo, J., Sánchez-Ortega, V., Camacho, A., 2025. Linking carbon fluxes to flooding gradients in sediments of Mediterranean Wetlands. *ACS EST Water* 5, 2882–2890. <https://doi.org/10.1021/acsestwater.4c00940>.
- Romm, J., Lezak, S., Alshamsi, A., 2025. Are carbon offsets fixable? *Annu. Rev. Env. Resour.* 50, 649–680. <https://doi.org/10.1146/annurev-environ-112823-064813>.
- Rosentire, J.A., Al-Haj, A.N., Fulweiler, R.W., Williamson, P., 2021. Methane and nitrous oxide emissions complicate coastal blue carbon assessments. *Global Biogeochem. Cycles* 35, e2020GB006858. <https://doi.org/10.1029/2020GB006858>.
- Rosentire, J.A., Laruelle, G.G., Bange, H.W., Bianchi, T.S., Busecke, J.J.M., Cai, W.-J., Eyre, B.D., Forbrich, I., Kwon, E.Y., Maavara, T., Moosdorf, N., Najjar, R.G., Sarma, V.V.S.S., van Dam, B., Regnier, P., 2023. Coastal vegetation and estuaries are

- collectively a greenhouse gas sink. *Nat. Clim. Chang.* 13 (6), 579–587. <https://doi.org/10.1038/s41558-023-01682-9>.
- Sadat-Noori, M., Andersen, M.S., Rutledge, H., Glamore, W., 2025. Coastal wetland restoration effects on carbon dynamics: a groundwater perspective. *Rev. Geophys.* 63 (3), e2025RG000895. <https://doi.org/10.1029/2025RG000895>.
- Saunio, M., Bousquet, P., Poulter, B., Peregon, A., Ciais, P., Canadell, J.G., Dlugokencky, E.J., Etiope, G., Bastviken, D., Houweling, S., Janssens-Maenhout, G., Tubiello, F.N., Castaldi, S., Jackson, R.B., Alexe, M., Arora, V.K., Beerling, D.J., Bergamaschi, P., Blake, D.R., Brailsford, G., Brovkin, V., Bruhwiler, L., Crevoisier, C., Crill, P., Covey, K., Curry, C., Frankenberg, C., Gedney, N., Höglund-Isaksson, L., Ishizawa, M., Ito, A., Joos, F., Kim, H.-S., Kleinen, T., Krummel, P., Lamarque, J.-F., Langenfelds, R., Locatelli, R., Machida, T., Maksyutov, S., McDonald, K.C., Marshall, J., Melton, J.R., Morino, I., Naik, V., O'Doherty, S., Parmentier, F.-J.W., Patra, P.K., Peng, C., Peng, S., Peters, G.P., Pison, I., Prigent, C., Prinn, R., Ramonet, M., Riley, W.J., Saito, M., Santini, M., Schroeder, R., Simpson, I.J., Spahni, R., Steele, P., Takizawa, A., Thornton, B.F., Tian, H., Tohjima, Y., Viovy, N., Voulgarakis, A., van Weele, M., van der Werf, G.R., Weiss, R., Wiedinmyer, C., Wilton, D.J., Wiltshire, A., Worthy, D., Wunch, D., Xu, X., Yoshida, Y., Zhang, B., Zhang, Z., Zhu, Q., 2016. The global methane budget 2000–2012. *Earth Syst Sci Data* 8, 697–751. <https://doi.org/10.5194/essd-8-697-2016>.
- Schorn, S., Ahmerkamp, S., Bullock, E., Weber, M., Lott, C., Liebeke, M., Lavik, G., Kuypers, M.M.M., Graf, J.S., Milucka, J., 2022. Diverse methylotrophic methanogenic archaea cause high methane emissions from seagrass meadows. *Proc. Natl. Acad. Sci.* 119. <https://doi.org/10.1073/pnas.2106628119>.
- 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. <https://doi.org/10.1016/j.scitotenv.2024.171218>.
- Schutte, C.A., Moore, W.S., Wilson, A.M., Joye, S.B., 2020. Groundwater-driven methane export reduces salt marsh blue carbon potential. *Global Biogeochem. Cycles* 34 (10), e2020GB006587. <https://doi.org/10.1029/2020GB006587>.
- Singh, N.K., Gourevitch, J.D., Wemple, B.C., Watson, K.B., Rizzo, D.M., Polasky, S., Ricketts, T.H., 2019. Optimizing wetland restoration to improve water quality at a regional scale. *Environ. Res. Lett.* 14, 064006. <https://doi.org/10.1088/1748-9326/ab1827>.
- Suding, K.N., Gross, K.L., Houseman, G.R., 2004. Alternative states and positive feedbacks in restoration ecology. *Trends Ecol. Evol.* 19, 46–53. <https://doi.org/10.1016/j.tree.2003.10.005>.
- Taillardat, P., Thompson, B.S., Garneau, M., Trotter, K., Friess, D.A., 2020. Climate change mitigation potential of wetlands and the cost-effectiveness of their restoration. *Interface Focus* 10, 20190129. <https://doi.org/10.1098/rsfs.2019.0129>.
- Thieurmél, B., Elmarhraoui, A., 2022. suncalc: Compute Sun Position, Sunlight Phases, Moon Position and Lunar Phase. <https://doi.org/10.32614/CRAN.package.suncalc>.
- Vaičiūtė, D., Bučas, M., Bresciani, M., Dabulevičienė, T., Gintauskas, J., Mėzinė, J., Tiškus, E., Umgiesser, G., Morkūnas, J., De Santi, F., Bartoli, M., 2021. Hot moments and hotspots of cyanobacteria hyperblooms in the Curonian Lagoon (SE Baltic Sea) revealed via remote sensing-based retrospective analysis. *Sci. Total Environ.* 769, 145053. <https://doi.org/10.1016/j.scitotenv.2021.145053>.
- Ward, S.E., Bardgett, R.D., McNamara, N.P., Ostle, N.J., 2009. Plant functional group identity influences short-term peatland ecosystem carbon flux: evidence from a plant removal experiment. *Funct. Ecol.* 23, 454–462. <https://doi.org/10.1111/j.1365-2435.2008.01521.x>.
- Wickham, H., 2016. *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.
- Wickham, H., Pedersen, T.L., Seidel, D., 2025. scales: Scale Functions for Visualization. <https://doi.org/10.32614/CRAN.package.scales>.
- Wik, M., Crill, P.M., Varner, R.K., Bastviken, D., 2013. Multiyear measurements of ebullitive methane flux from three subarctic lakes. *J. Geophys. Res. Biogeo.* 118 (3), 1307–1321. <https://doi.org/10.1002/jgrg.20103>.
- Wu, Y., Sun, J., Hu, B., Zhang, G., Rousseau, A.N., 2023. Wetland-based solutions against extreme flood and severe drought: Efficiency evaluation of risk mitigation. *Clim. Risk Manag.* 40, 100505. <https://doi.org/10.1016/j.crm.2023.100505>.
- Zilius, M., Bartoli, M., Bresciani, M., Katarzyte, M., Ruginis, T., Petkuvienė, J., Lubiene, I., Giardino, C., Bukaveckas, P.A., de Wit, R., Razinkovas-Baziukas, A., 2014. Feedback mechanisms between cyanobacterial blooms, transient hypoxia, and benthic phosphorus regeneration in shallow coastal environments. *Estuar. Coasts* 37, 680–694. <https://doi.org/10.1007/s12237-013-9717-x>.
- Zorrilla-Miras, P., Palomo, I., Gómez-Baggethun, E., Martín-López, B., Lomas, P.L., Montes, C., 2014. Effects of land-use change on wetland ecosystem services: a case study in the Doñana marshes (SW Spain). *Landsc. Urban Plan.* 122, 160–174. <https://doi.org/10.1016/j.landurbplan.2013.09.013>.