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CO_2 fluxes in a recently restored salt marsh

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ABSTRACT

Blue carbon ecosystems are not only known to be one of the most important carbon sinks, but also their restoration is considered a nature-based tool for mitigating climate change impacts. Further research on restored salt marshes is essential to understand the recuperation of natural carbon dynamics and provide insights into short-term effects and a basis for long-term monitoring. In this study, we assess the net CO_2 exchange with the atmosphere over a year in a recently restored salt marsh in Trebujena, southern Spain. We measured CO_2 fluxes every two months from bare and vegetated sediments that were terrestrialised, under both dark and light conditions, and examined their relationships with the environmental variables measured *in situ* (i.e. sediment temperature, moisture, salinity, pH, organic carbon, and inorganic carbon). Additionally, CO_2 flux measurements were taken on the flooded area at the water-air interface. Our results indicate that CO_2 fluxes were significantly influenced by sediment temperature, moisture, and salinity. Bare and vegetated sediments were CO_2 sources because the meadow's uptake was insufficient to offset emissions from terrestrialised sediments, suggesting a degraded physiological state of the vegetation. In contrast, the flooded area was a net CO_2 sink, suggesting that the recovery of the natural hydrological regime would be advisable to promote the restoration of the carbon dynamics.

1. Introduction

Coastal wetlands such as mangroves, salt marshes, or seagrass meadows are recognised as the primary blue carbon ecosystems (BCEs). They constitute global carbon sinks (i.e Chmura et al., 2003; Duarte et al., 2005; McLeod et al., 2011), due to their significant capacity to store and sequester carbon (Bindoff et al., 2019). These wetlands are characterised by high productivity driven by diverse primary producers, including cyanobacteria, algae, and vascular plants (Chmura, 2009). Through photosynthesis, plants fix carbon, and their biomass forms the decaying organic material in the sediment. Furthermore, the vegetation meadow increases the sedimentation rate of both autochthonous and allochthonous material (Nardin et al., 2016).

Additionally, these wetlands typically feature a water-saturated and saline sediment, promoting environmental conditions that limit the microbial consumption and remineralization of organic matter (OM) through respiratory metabolism (Van Horn et al., 2014). Moreover, high sulphate concentrations typical of saline wetlands inhibit methanogenesis, resulting in comparatively low methane emissions (Jørgensen and Kasten, 2006; Rosentreter, 2022). As a result, a substantial portion of the settled organic carbon (OC) remains preserved and buried within the sediment for extended periods of time, effectively acting as long-term carbon sinks (Chmura, 2009).

It has been estimated that over a year, the net ecosystem production of BCEs vegetated habitats is 3388 Tg y^{-1}, while the burial rate of OC is 111.4 Tg y^{-1} (Duarte et al., 2005). Beyond their role in the global carbon cycle, they provide a wide range of nature's contributions to people (NCP), including habitat creation and maintenance, regulation of coastal water quality, formation, protection, and decontamination of soil and sediments, food and feed, and supporting identities (Díaz et al., 2018).

Despite all these contributions, coastal wetlands are considered the most degraded ecosystems on a global scale (Barbier et al., 2011), with more than 50% of their total surface lost in the 20th century (Li et al.,

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2018). In the Mediterranean region, the main threats to these ecosystems and, more precisely, salt marshes, are desiccation and changes in their hydrological dynamics (Alvarez-Cobelas et al., 2001).

Draining a salt marsh compromises its carbon reserves. These hydrological alterations directly modify sediment moisture, temperature, and salinity, which are known to regulate microbial metabolism and CO_2 exchange in salt marsh sediments (Raich and Potter, 1995; Almagro et al., 2009; Stolpmann et al., 2025). The exposure of highly organic sediment to the air enhances the aerobic microbial respiration and drives carbon mineralization (Marcé et al., 2019). Moreover, drained surfaces present higher sediment temperature, accelerating microbial metabolic rates, further raising the CO_2 emission to the atmosphere (Lloyd and Taylor, 1994).

Consequently, restoring salt marshes may be a nature-based solution to mitigate the effects of climate change. However, very few studies have quantified net CO_2 exchange in Mediterranean restored salt marshes, and the net behaviour of the ecosystem as a source or a sink was contradictory between them (Shahan, 2022; Helman et al., 2026). Considering that the principal approaches to salt marsh restoration are the recovery of the tidal regime, the sediment characteristics, and the autochthonous vegetation, or the active construction of new salt marshes, restoration success could be evaluated by indicators such as biodiversity, vegetation biomass, sediment characteristics, ecosystem metabolism, and carbon dynamics (Billah et al., 2022).

The objective of this study was to assess the net CO_2 exchange between a recently restored salt marsh wetland and the atmosphere, as well as provide management advice to prevent disproportionate re-emission of previously stored carbon.

Although full recovery of ecosystem structure and functions may require up to 50 years (Billah et al., 2022; Moreno-Mateos et al., 2012), it remains unclear whether recently restored salt marshes can rapidly regain a net atmospheric CO_2 sink function. Furthermore, in these ecosystems, initial vegetation establishment is often heterogeneous, leading to a mosaic of vegetated and bare sediments. This spatial heterogeneity can influence local CO_2 fluxes and may affect the ecosystem-scale carbon balance. Therefore, studying recently restored ecosystems can contribute to the understanding of the short-term restoration effects on carbon dynamics and provide a basis for tracking their long-term development. Based on this context, we hypothesize that (1) the restored salt marsh acts as an atmospheric CO_2 sink; (2) the meadow contributes substantially to this sink through photosynthetic CO_2 uptake; and (3) the main sedimentary variables influencing CO_2 fluxes are sediment moisture, temperature, and salinity.

2. Materials and Methods

2.1. Study area

In the mid-20th century, all the Guadalquivir salt marshes except for those in Doñana National Park were drained for agricultural purposes. However, because of the highly saline sediments, most of them were abandoned (Ruiz and Hortas, 2014), and consequently underwent a process of terrestrialisation. Here, halophilic vegetation established over the dried sediments (Marcé et al., 2019).

In 2019, the World Wildlife Fund (WWF) carried out a 6-ha restoration of a terrestrialised salt marsh area called "Adventus" (36° 53' 30"

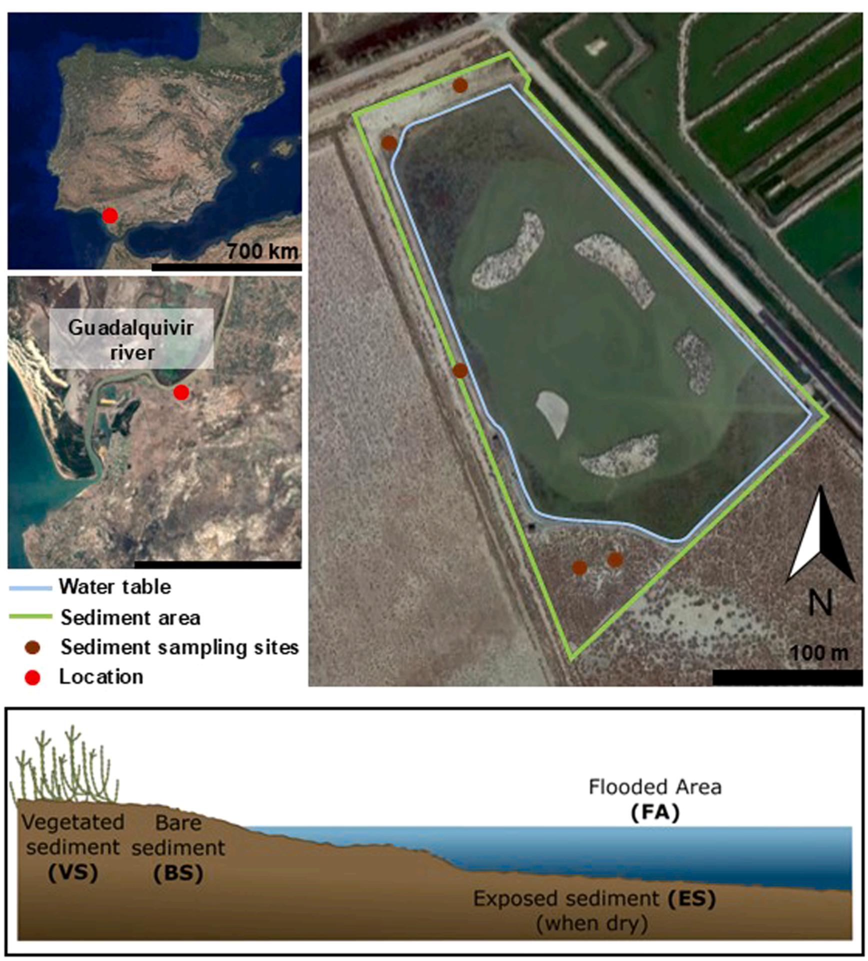

Fig. 1. Location map of the restored salt marsh in Trebujena and sampling sites. The diagram indicates the sampling points: (VS) vegetated sediment, (BS) bare sediment, (FA) flooded area and (ES) exposed sediment when the salt marsh was drained.

N; 6° 13’ 53” W), 0.11 km from the Guadalquivir estuary left margin, in Trebujena, southern Spain, (Fig. 1). They aimed to recover biodiversity and ecological values of the salt marsh alongside studying the possibility of the ecosystem being a net atmospheric CO_2 sink.

Their strategy for this restoration project was the active construction of a new salt marsh. The restoration began with the excavation of a basin for a permanently flooded area (FA) with an extension of 5 ha and a mean depth of 0.5 m. Inside, 5 artificial islands were built for breeding bird species. Surrounding the basin, a trail and two bird observatories were made to incentivize ecotourism in the area.

The Adventus salt marsh hydrology is managed by a shrimp (*Palaemonete varians*) aquaculture company that also extracts them from the salt marsh. Water is pumped from the Guadalquivir River to a sedimentary pond where the suspended solids precipitate, reducing the allochthonous input of OM. Water is then conducted by a gravitational gradient to the FA and could be drained as needed through the respective gates. The design of the FA prevents water from exceeding the basin boundaries and flooding the surrounding terrestrialised sediments, making the two compartments almost independent. The area is vegetated with native species such as *Sarcocornia* sp. and *Suaeda vera.* These species are adapted to high salinity conditions and water-logged sediments (Ventura and Sagi, 2013; Calone et al., 2022).

2.2. Study design

To study the CO_2 net ecosystem exchange of the restored salt marsh and its main drivers, a total of 8 sampling campaigns were conducted during February and April in 2022 and every 2 months between January and November in 2023. Sediment and vegetation samples, and CO_2 measurements were taken in 5 designated sampling sites over the terrestrialised sediment. Within each site, 2 random sampling points were established for bare sediments (BS) and vegetated sediments (VS), 1–0.5 m apart. Sampling points within sites varied between sampling campaigns, depending on vegetation coverage. On the FA, measurements were conducted in 5 non-fixed sites (Fig. 1).

Additionally, a controlled drainage event of the FA for management purposes provided an opportunity to study the effect of desiccation in the salt marsh. For this, 3 transects, with 4 sampling points over the recently exposed sediments (ES) each, were established from the shoreline to the inner part of the drained area, in a salinity gradient.

2.3. Sediment and vegetation analysis

In BS, VS, and ES, the salinity and pH of the sediment were assessed in a 1:2.5 sediment and distilled water dissolution (Shao et al., 2022), using a salinity (Crison 5060) and a pH probe (Hach 5053 T), respectively. Sediment temperature was determined by a penetration probe (Hach 5053 T) directly in the sediment while CO_2 flux measurements were conducted. Sediment temperature and moisture in the ES during the drainage event were determined using a dielectric sensor (HydraProbe, Stevens).

A sample of the top 5 cm of the terrestrialised sediment was collected in every sampling point. 5 g out of every sample was dried at 105°C in a muffle furnace until constant weight to assess the moisture content referred to their dry weight. Then, the samples were heated at 550°C for 4 h and 950°C for 2 h to quantify the OM and inorganic carbon (IC), respectively, by the loss-on-ignition (LOI) method (Heiri et al., 2001). OC was estimated from the OM values using Craft et al. (1991). equation for tidal salt marshes as recommended by the IUCN 2014 manual (Fourqurean et al., 2014).

In VS, all the vegetation inside the chamber was collected and weighed after the CO_2 measurement.

2.4. Flux measurements

CO_2 fluxes in the terrestrialised sediments were measured using a canopy assimilation transparent chamber (CPY-5) (PP Systems, Amesbury, USA) connected to an EGM-5 Infrared Gas Analyser (IRGA) (PP Systems, Amesbury, USA). The chamber was sealed air-tight on top of the sediment, and the CO_2 concentration inside the chamber was recorded every second for 180 s. The chamber was vented between every incubation measurement. Aboveground biomass CO_2 fluxes estimations were obtained by subtracting BS from VS CO_2 fluxes.

To recreate nighttime dark conditions, an opaque cover was placed over the CO_2 flux measuring chamber. To test for potential bias introduced by daytime dark measurements, during the October 2023 sampling campaign, CO_2 fluxes in BS and VS were also measured at nighttime in the same sampling points. No significant differences were observed between nighttime and daytime dark fluxes (repeated-measures ANOVA, $p > 0.05$), supporting the methodological approach.

For sampling the ES, an opaque soil respiration chamber (SRC-2) (PP Systems, Amesbury, USA) was used. Incubations lasted for 180 s.

Changes in CO_2 concentration inside the incubation chambers were used to calculate the CO_2 flux in g CO_2 m^{-2} h^{-1}, normalised to the pressure and temperature measured by the IRGA inside the chamber.

FA CO_2 fluxes were measured using the same EGM-5 IRGA connected to a floating chamber designed following (Frankignoulle, 1988), with an area of 0.2 m^2 and a volume of 0.03 m^3. CO_2 concentration was recorded every second inside the chamber during 300 s incubations for flux calculation.

A total of 239 chamber incubations were used for this study. For all of them, the relationship between CO_2 concentration and time was visually inspected to assess data quality before flux calculation. The criterion established for accepting the measurement was a coefficient of determination (R^2) > 0.7 for the linear regression. For neutral plots, exhibiting minimal slope (< 0.02), the R^2 criterion was not considered appropriate; instead, fluxes were evaluated based on signal stability. The incubations that did not follow these criteria were excluded.

Daily CO_2 fluxes in BS and VS were estimated by multiplying dark and light conditions measurements by the corresponding light and dark hours of each sampling day and integrating over the photoperiod.

2.5. Flux upscaling and meadow physiological state

The LandViewer product from EOS Data Analytics (EOSDA) (EOS Data Analytics (EOSDA), 2025) was used to obtain the Normalized Difference Vegetation Index (NDVI) for the restored area. The imagery selected was the closest available to each sampling campaign from the Sentinel-2 satellite with a cloud coverage below 20% and a solar incidence angle between 30° and 70°.

Upscaled CO_2 flux was estimated by multiplying daily CO_2 flux averages from BS, VS, and FA surfaces by their extension as expressed by the NDVI.

To study how the meadow was affected by environmental factors, the maximum NDVI value ($NDVI_{max}$) was used as a proxy of its physiological state; the higher the $NDVI_{max}$ value, the better the state of the vegetation. Relationships between the $NDVI_{max}$ value and mean values from sedimentary variables measured in VS were used to assess the main stressors affecting the vegetation.

2.6. Statistical analyses

No significant differences were found between sedimentary variables measured in BS and VS during the study period, so the overall data is used to describe the environmental and sedimentary characteristics of the salt marsh. However, to test the effect of the environmental factors on CO_2 fluxes, BS and VS data were analysed independently. Linear regression tests were carried out, where CO_2 fluxes were the dependent variable and environmental properties were the independent variables. To better explore the relation between the ES CO_2 fluxes and sediment salinity, only data under the same conditions of sediment temperature and moisture content were used. Also, additional linear regressions, correlations, and non-linear fit models were performed between different environmental variables. For all correlations, the confidence level was set at 95%.

Statistical differences between daily CO_2 fluxes in BS, VS, and FA were tested by a non-parametric Kruskal-Wallis test at a significance level of $p < 0.05$. Differences in the distributions were assessed using Dunn's post hoc test with a Bonferroni correction. For this analysis, only 2023 data points were used, so CO_2 fluxes between February and April were not overrepresented. To test whether mean CO_2 fluxes in light conditions were statistically different from measurements under dark conditions, both in BS and VS, a non-parametric Wilcoxon signed-rank test at a significance level of $p < 0.05$ was used.

All data were previously tested for normality and homogeneity of variance using a Shapiro-Wilk and a Levene's F test, respectively. Non-parametric data distributions are referred to as median (first quartile, Q_1; third quartile, Q_3), whereas parametric distributions are referred to as mean ± standard deviation (SD).

3. Results

3.1. Environmental variables

Environmental variables showed distinct temporal patterns and significant relations among them, reflecting both seasonal forcing and sediment biogeochemical controls. Summary statistics for all environmental variables are presented in Table 1.

Sediment temperature showed a clear seasonal pattern, with minimum values recorded in November 2023 and maximum values in July 2023. Sediment moisture also varied seasonally and was positive and significantly related to sediment temperature ($R^2 = 0.42$, $p < 0.05$). In addition, accumulated precipitation during the 15 days before each sampling campaign was positively related to mean sediment moisture content ($R^2 = 0.57$, $p < 0.05$). Annual precipitation in the study area was 358.4 mm in 2022 and 304.4 mm in 2023 (Instituto de Investigación y Formación Agraria y Pesquera IFAPA, 2025).

Regarding sediment chemical properties, a significant relationship was observed between OC content and sediment salinity (Fig. 2A). This relationship was best described by a logistic model (AIC = 111.63; $R^2 = 0.63$; $p < 0.05$), with OC content increasing with salinity in the 0–10 g L^{-1} range and reaching its highest values at salinities above 10 g L^{-1} . Additionally, OC content was negatively correlated with IC content in sediments (Pearson's correlation coefficient r = -0.62, $p < 0.05$) (Fig. 2B).

3.2. CO_2 fluxes

CO_2 fluxes differed among compartments and between light and dark conditions, reflecting contrasting metabolic responses of BS, VS, and FA. The median CO_2 emissions measured in BS under light conditions were higher ($p < 0.05$) than under dark conditions (median = 0.13 [Q_1 = 0.04; Q_3 = 0.29] g CO_2 m^{-2} h^{-1} in light; 0.11 [0.05; 0.17] g CO_2 m^{-2} h^{-1} in dark) (Fig. 3). Otherwise, the median CO_2 flux in VS was significantly lower ($p < 0.05$) in light than in dark conditions, showing an uptake and an emission respectively (-0.21 [-0.67; 0.11] g CO_2 m^{-2} h^{-1} in light; 0.37 [0.22; 0.80] g CO_2 m^{-2} h^{-1} in dark) (Fig. 3). However, the CO_2 uptake was not intense enough to counteract the CO_2 emission measured under dark conditions. The FA always exhibited a CO_2 uptake from the atmosphere during daytime (-0.03 [-0.04; −0.01] g CO_2 m^{-2} h^{-1}).

Table 1
Summary statistics of environmental variables measured during the study period in the Adventus salt marsh. Minimum (Min), maximum (Max), and Mean ± Standard deviation (SD) values are provided for sediment temperature (°C), moisture (%), organic carbon (OC, %) and inorganic carbon (IC, %) contents, salinity (g L^{-1}) and pH.

Sedimentary variable	Min	Max	Mean ± SD
Temperature (°C)	12.4	48.6	27.0 ± 9.2
Moisture (%)	2.0	59.0	21.4 ± 13.3
OC (%)	2.3	7.7	5.6 ± 1.3
IC (%)	4.8	13.2	8.1 ± 2.1
Salinity (g L^{-1})	0.4	67.7	15.4 ± 14.0
pH	6.6	8.9	7.9 ± 0.5

3.3. Drivers of sediment CO_2 flux

In BS, sediment moisture content was negatively related to the CO_2 fluxes, with high moisture leading to CO_2 uptake and drier conditions resulting in CO_2 emissions. Although the relationship in light conditions was stronger than in dark ($R^2 = 0.23$, $p < 0.05$ in light; $R^2 = 0.10$, $p < 0.05$ in dark), there were no significant differences between slopes ($p > 0.05$). The most intense CO_2 uptake was depicted in sediments with a moisture content over 37%.

A direct relationship between BS temperature and CO_2 fluxes was found, explaining a greater proportion of the variability under light than under dark conditions ($R^2 = 0.28$, $p < 0.05$ in light; $R^2 = 0.18$, $p < 0.05$ in dark); however, slopes were not different ($p > 0.05$). CO_2 uptake was observed mostly in sediments with temperatures under 20°C.

During the drainage of the salt marsh FA, dark CO_2 fluxes were measured in ES across a salinity gradient. Without the effect of moisture and temperature masking the influence of salinity on the CO_2 emission, an inverse relationship between these variables ($R^2 = 0.50$, $p < 0.05$) was observed. In addition, during this drainage event, in the ES, the highest CO_2 emission (0.46 g CO_2 m^{-2} h^{-1}) was measured.

Regarding VS, no significant relationships were found between the CO_2 fluxes and the environmental variables studied. Nonetheless, aboveground biomass CO_2 fluxes were significantly related to the sediment moisture and to the fresh weight of the vegetation. In both cases, the relationships found were negative under light conditions and positive in dark ($R^2 = 0.11$, $p < 0.05$ in light and $R^2 = 0.13$, $p < 0.05$ in dark; $R^2 = 0.37$, $p < 0.05$ in light and $R^2 = 0.20$, $p < 0.05$ in dark, respectively) (Fig. 4). $NDVI_{max}$ values were also positively related to moisture content and negatively to sediment temperature and salinity ($R^2 = 0.53$, $p < 0.05$; $R^2 = 0.47$, $p < 0.05$; $R^2 = 0.45$, $p < 0.05$ respectively) (Fig. 5). The highest $NDVI_{max}$ value (0.63) was observed under a low mean temperature and salinity, and high moisture content (18.3°C; 6.9 g L^{-1}; 39.7%, respectively).

3.4. CO_2 fluxes upscaling

Integrating 2023 CO_2 fluxes under light and dark conditions allowed us to estimate daily net CO_2 fluxes. Daily, BS emitted at a median rate of 2.93 (1.25; 4.77) g CO_2 m^{-2} d^{-1}, which did not differ ($p > 0.05$) from the median CO_2 emission rate from VS (2.79 [0.07; 4.20] g CO_2 m^{-2} d^{-1}). The FA captured CO_2 at a median rate of −0.55 (-0.81; −0.18) g CO_2 m^{-2} d^{-1}, being significantly lower ($p < 0.05$) than the median emission from BS and VS (Fig. 6). However, the lack of dark measurements in the FA could lead to an overestimation of the CO_2 uptake.

CO_2 daily fluxes were upscaled to the BS, VS, and FA extensions at the moment of sampling. These upscaled values represent approximate CO_2 exchanges at the ecosystem scale but are not predictive. We estimated that the whole extension of BS on average emitted 20.87 ± 14.00 T CO_2 $year^{-1}$. The emission from the BS was not statistically different ($p > 0.05$) from the VS, averaging 18.17 ± 23.13 T CO_2 $year^{-1}$. On the other hand, the FA during the study period showed a mean uptake of −9.24 ± 8.18 T CO_2 $year^{-1}$. The mean net CO_2 exchange at the ecosystem scale during the study period was an estimated emission of 36.85 ± 38.44 T CO_2 $year^{-1}$.

Remarkably, the VS only acted as a CO_2 sink during the November sampling campaign, with an uptake of −26.59 ± 12.20 T CO_2 $year^{-1}$, even offsetting the BS CO_2 emission recorded that day (12.94 ± 8.82 T CO_2 $year^{-1}$). The FA also acted as an atmospheric CO_2 sink (-6.98 ± 1.62 T CO_2 $year^{-1}$). As a result, during the November sampling

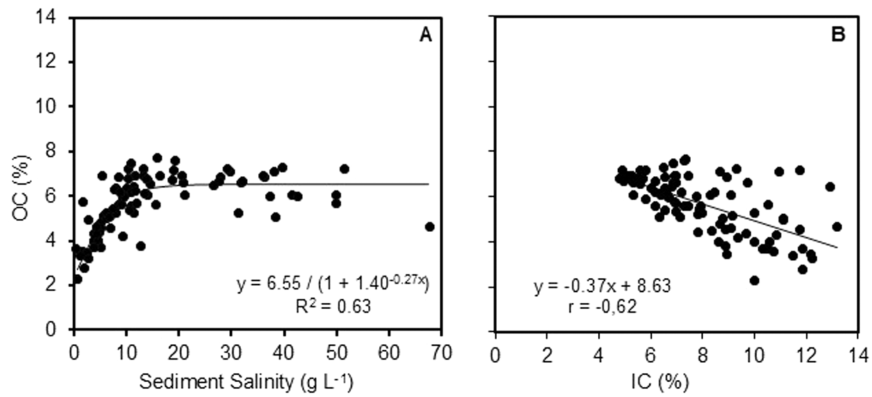

Fig. 2. Relationships between sediment organic carbon content (OC, %) and salinity (g L^{-1}) $p < 0.05$ (A), and between sediment organic carbon and inorganic carbon contents (IC, %) $p < 0.05$ (B).

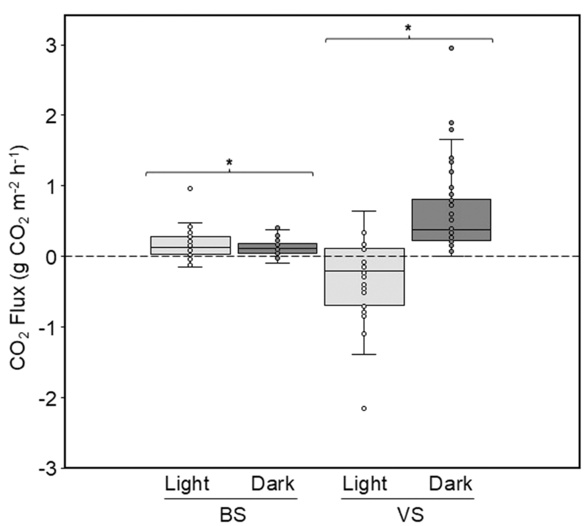

Fig. 3. CO_2 fluxes (g CO_2 m^{-2} h^{-1}) from bare sediment and vegetated sediment, in light and dark conditions. The whiskers indicate the variability outside the boxes (superior and inferior quartiles), the middle line is the median and the dots are flux values, negative values represent CO_2 uptake, while positive values CO_2 emission. Asterisks show significant differences between groups, $p < 0.05$.

campaign, the net ecosystem uptake was −20.62 T CO_2 $year^{-1}$. During every other sampling campaign, the ecosystem acted as a net source of CO_2 to the atmosphere.

4. Discussion

The focus of restoration actions has a direct influence on carbon cycling in coastal wetlands (Baldino et al., 2026). Our results show that both BS and VS acted as net CO_2 sources, offsetting the CO_2 uptake by the FA. This finding highlights that restored wetlands may not necessarily function as carbon sinks, and that restoration outcomes should be evaluated not only in terms of vegetation establishment but also in terms of biogeochemical functioning.

4.1. Environmental characterisation of the salt marsh

The significant relationships between salinity, OC, and IC suggest that multiple interacting biogeochemical processes control carbon dynamics in the sediment. Below, we discuss the mechanisms that may explain these patterns.

The relationship between sediment salinity and OC content could be attributed to the limiting effect of salinity over sediment microorganisms' metabolism, which prevents the OC from being remineralised, resulting in OC burial (Van Horn et al., 2014; Setia et al., 2010; Zhang et al., 2021; Chen et al., 2022). A salinity of 10 g L^{-1} would be the threshold at which the Adventus salt marsh microbial community metabolism would decline, decreasing the rate at which the OC is consumed.

Otherwise, OC was negatively correlated with IC content in the sediments, suggesting that different processes might be potentially

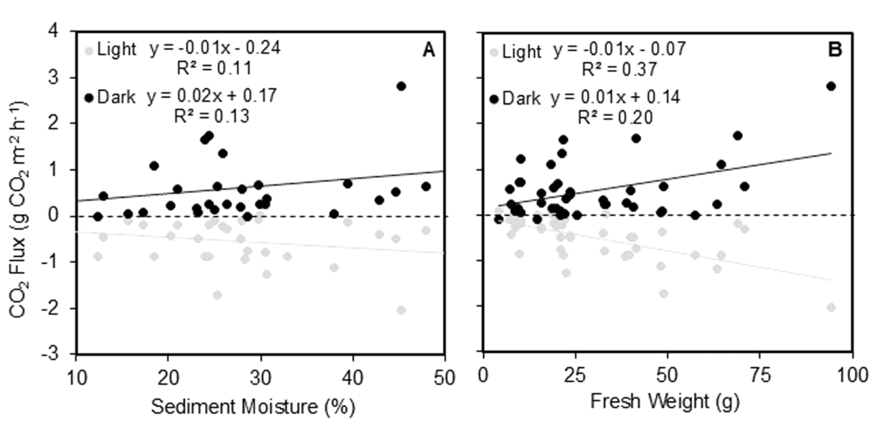

Fig. 4. Relationships between the aboveground biomass CO_2 fluxes of the vegetation (g CO_2 m^{-2} h^{-1}) and moisture content in sediments (%), $p < 0.05$ (A), and the fresh weight of the vegetation (g), $p < 0.05$ (B). Light measurements are gray and dark measurements black. Negative CO_2 flux values represent uptake, while positive values an emission. Slopes were different between each other, $p < 0.05$.

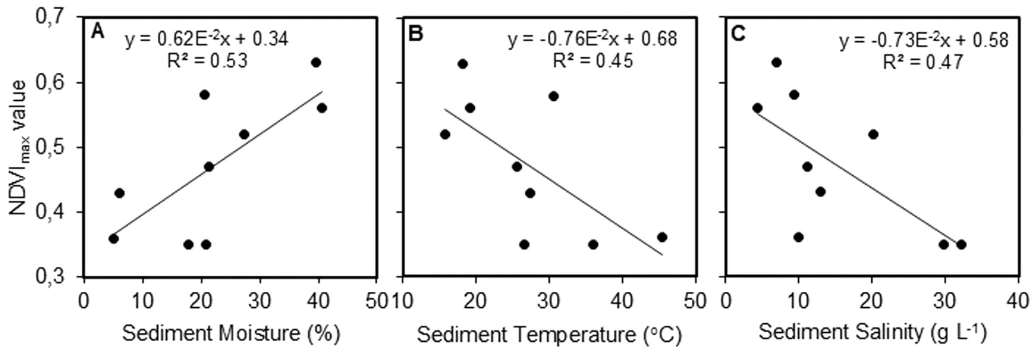

Fig. 5. Relationship between the Normalized Difference Vegetation Index maximum value ($NDVI_{max}$) and sedimentary variables measured in vegetated sediments: (A) moisture content (%), (B) temperature (°C) and (C) salinity (g L^{-1}), $p < 0.05$.

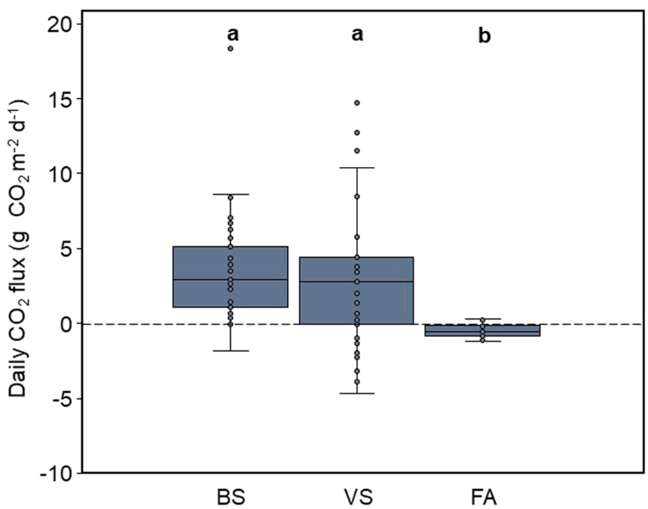

Fig. 6. Daily CO_2 fluxes (g CO_2 m^{-2} d^{-1}) from bare sediment (BS), vegetated sediment (VS) and the flooded area (FA). The whiskers indicate the variability outside the boxes (superior and inferior quartiles), the middle line is the median and the dots are flux values, negative values represent CO_2 uptake, while positive values CO_2 emission. Letters "a" and "b" show the significantly different groups, $p < 0.05$.

involved in this pattern. Anaplerotic fixation, as microorganisms and plant roots can fix CO_2 under both aerobic and anaerobic conditions to synthesize intermediaries of the citric acid cycle (Nel and Cramer, 2019). Similarly, autotrophic microbial metabolic pathways involving IC fixation could contribute to this pattern (Shao et al., 2022; Nel and Cramer, 2019). Both processes would decrease IC content while concomitantly increasing microbial biomass and, eventually, the OC content in the sediment. In contrast, in low-OM sediments and in the presence of calcium ions (Ca^{2+}), halophilic bacteria may promote carbonate precipitation, increasing IC content where OC is low (Delgado et al., 2008).

4.2. Environmental controls and processes driving sediment CO_2 fluxes

CO_2 fluxes measured in the different compartments of the Adventus salt marsh were compared with values reported for other coastal wetlands to contextualize the observed emission and uptake patterns and assess the functioning of the restored ecosystem.

In BS, CO_2 emission rates were lower than those reported for the restored Lake Markermeer in the Netherlands (Tak et al., 2023), and similar to values described for a Mediterranean saline wetland (Thomas et al., 2022). Although both studies were undertaken under similar sedimentary conditions regarding temperature, moisture, OM content, and texture, Lake Markermeer was a degraded estuary restored into a freshwater wetland (Tak et al., 2023), whereas the Mediterranean wetland was saline (Thomas et al., 2022). Therefore, the salinity difference could be the main reason for the respective difference and similarity between the two studies and the CO_2 emissions we measured. At the same time, the negative relationship between CO_2 emission and salinity in ES may indicate an osmotic stress caused by salinity, hindering the microbial capacity to consume OM (Van Horn et al., 2014). This process is also consistent with the sediment OC-salinity relationship described in Section 4.1. However, the main drivers of CO_2 fluxes from BS in the Adventus salt marsh were sediment moisture and temperature. Both factors were negative and highly correlated with each other; therefore, their separate effects on gas exchange were difficult to assess from field observations.

The relationship between sediment moisture and CO_2 emission has been previously described as a quadratic function, where soil microorganisms have a sediment moisture optimum at which aerobic respiration peaks, but outside this range, it is limited (Linn and Doran, 1984; Bowden et al., 1998; Qi and Xu, 2001). In contrast, CO_2 emission typically increases exponentially with sediment temperature (Lloyd and Taylor, 1994; Boone et al., 1998; Duan et al., 2019). On the high-moisture and low-temperature extreme, a saturating moisture level could turn the sediments anoxic (Skopp et al., 1990). In such a situation, water acts as a physical barrier impeding gas diffusion at the sediment-atmosphere interface, and the aerobic respiration, driving OM remineralization, is reduced (Tiedje et al., 1984). Under low-temperature conditions, microbial respiration rates are increasingly constrained by activation energy, resulting in reduced CO_2 emissions (Lloyd and Taylor, 1994). Conversely, under low-moisture and high-temperature conditions, the expected responses of CO_2 fluxes to individual environmental drivers were not observed. Instead, both moisture-CO_2 flux and temperature-CO_2 flux relationships appeared linear. This deviation from the expected patterns could reflect an interaction between sediment moisture and temperature. Low moisture conditions may limit microbial activity and reduce the sensitivity of respiration rates to temperature increases (Wang et al., 2014), preventing the typical exponential response (Lloyd and Taylor, 1994; Qi and Xu, 2001; Duan et al., 2019; Wu et al., 2021). As a result, respiration is not completely inhibited but remains lower than expected under optimal moisture conditions (Wang et al., 2014; Zhou et al., 2014). Consequently, the elevated CO_2 emissions observed under low-moisture conditions may partly reflect the effect of increased temperatures.

Regarding the differences between CO_2 fluxes measured in light and dark conditions in BS, both median values depicted a net emission to the atmosphere, which may be driven by microbial respiration (Raich and Tufekcioglu, 2000; Han et al., 2007). However, the CO_2 emission was significantly higher in light than in dark conditions. This difference could be attributed to abiotic processes such as an increase in temperature inside the chamber or the effect of light itself. Solar radiation can be responsible for the photodegradation of OM, emitting CO_2 during the process (Wang et al., 2014; Brandt et al., 2009; Rutledge et al., 2010). Despite overall net CO_2 emissions, CO_2 uptake was observed in both light and dark conditions. In light conditions, the uptake could have been mainly driven by the photosynthetic biofilms that developed over the moist sediments. In a study by Chen and Lee (Chen and Lee, 2024) the sediment of unvegetated tidal flats was estimated to be a net CO_2 sink or a weak source. They attributed the CO_2 uptake to seasonality and microphytobenthos abundance. However, dark CO_2 uptake in BS remains understudied. Abiotic dark influx is often described in drylands, mostly in alkaline sediments with a low OM content, under low sediment moisture and temperature conditions (Ma et al., 2013; Sagi et al., 2021). This is related to calcium carbonate ($CaCO_3$) dynamics, where $CaCO_3$ dissolution in the inter-pore spaces of the sediment leads to an influx of atmospheric CO_2 (Ma et al., 2013).

Although CO_2 uptake was observed under the lowest sediment temperatures in the Adventus salt marsh, the OM and moisture contents of the sediment were high. Under these conditions, respiration should hinder the abiotic uptake (Sagi et al., 2021). Therefore, abiotic mechanisms alone are unlikely to explain the observed uptake, suggesting that biotic processes played a dominant role. Biotic processes such as chemoautotrophic metabolisms (i.e. denitrification, sulphur oxidation, or dissimilatory nitrate reduction to ammonium) or dark anaplerotic CO_2 fixation might be involved in dark CO_2 uptakes (Nel and Cramer, 2019). However, in a comparative study of soils with different properties, the highest dark anaplerotic CO_2 fixation rates were at 50% soil moisture, 25℃, and low nutrient contents (Nel and Cramer, 2019). Thus, further research is needed to better understand the dark CO_2 uptake in organic sediments under high-moisture and low-temperature conditions.

In vegetated sediments, the principal carbon input is photosynthesis, whereas the main carbon loss is due to respiratory metabolisms (Carrasco-Barea et al., 2018). At our site, the dark CO_2 emission was approximately half of that reported for Lake Markermeer (Tak et al., 2023). In contrast, their CO_2 uptake under light conditions was seven times greater than that observed in our study, resulting in net primary production (Tak et al., 2023). In vegetated salt marsh sediments, primary production has been estimated to be approximately twice the respiration rate (Duarte et al., 2005). While respiration rates at our site were comparable to those reported for salt marshes, primary production did not reach the average values described in the literature. This suggests that vegetation in the Adventus salt marsh was less productive than initially hypothesised.

CO_2 fluxes in VS were not related to any measured environmental variable. Possibly, the annual cycle of the vegetation (Palomo and Niell, 2009) impedes the identification of clear patterns between CO_2 fluxes and environmental variables. The lack of clear relationships is further reinforced by sediment and rhizosphere processes. Part of the carbon uptake by photosynthesis is exuded by the vegetation roots (Curiel Yuste et al., 2007; Zhao et al., 2024). In addition, diverse microbial functional groups (i.e. Cellobiose degraders, fermenters, iron reducers, sulphate reducers, and methanogens) could exchange between them or compete for carbon-based substrates (Yarwood, 2018). Nonetheless, the aboveground biomass, subtracting the effect of sediment processes, showed more intense CO_2 fluxes both in light and dark conditions in high-moisture sediments. Also, CO_2 fluxes were related to the fresh weight of the vegetation, which depicted a positive relationship with sediment moisture. Thus, a higher water content in plant tissues would increase their metabolic rate (Huang et al., 2020). Furthermore, the vegetation physiological state, as expressed by the $NDVI_{max}$ responded negatively to drought, heat, and salinity. This indicates that vegetation is sensitive to the same environmental factors controlling CO_2 fluxes in BS. This highlights a potential indirect linkage between environmental stress and CO_2 dynamics in vegetated systems.

In the Mediterranean region, low tidal amplitudes and limited rainfall lead to seasonal drought, which, together with elevated temperatures and salinity, causes physiological stress in vegetation (Ibañez et al., 2002). Although the Adventus salt marsh is under a Mediterranean climate, it is influenced by the Atlantic Ocean, so it should have a tidal regime that would prevent the seasonal drought. However, its regulated hydrology limits tidal exchange and results in infrequent flooding and a reliance on precipitation, leading to extended stress conditions. This is further supported by the relationship between the accumulated precipitation during the 15 days before the sampling campaign and the sediment moisture content.

Regarding literature, the flooded area in salt marshes is usually considered a CO_2 source to the atmosphere (i.e. Abril et al., 2025; Artigas et al., 2015; Zhao et al., 2024). However, the FA of the Adventus salt marsh acted as a CO_2 sink; this uptake could be attributed to the photosynthetic metabolism of organisms in the water column and carbonate equilibrium dynamics (Otani and Endo, 2018; Chengxin et al., 2005; Dias et al., 2025). Nonetheless, measurements in our study were undertaken in light conditions, which could bias the nighttime processes. Therefore, further measurements, including dark conditions, are needed to fully assess the role of FA in the ecosystem carbon balance.

4.3. Ecosystem net CO_2 balance and implications for salt marsh restoration

Salt marshes are considered highly productive ecosystems with the capacity to store large quantities of carbon in their sediments (Palomo-Ríos et al., 2004; Tong et al., 2013). For this to occur, CO_2 uptake by photosynthesis should be high enough to offset the CO_2 from respiration, resulting in a carbon sink balance (Carrasco-Barea et al., 2018). Moreover, global syntheses suggest that restored salt marshes generally act as net CO_2 sinks across climatic regions (Mason et al., 2023).

In our study, the overall final balance estimations during the study period were a net CO_2 emission from the salt marsh to the atmosphere. The FA acted as a weak CO_2 sink, whereas the BS and VS were net CO_2 sources of higher magnitude. However, spatial heterogeneity could introduce bias into the estimations. The ecosystem shifted to a net CO_2 sink only in the November sampling campaign, when the lowest temperature and relatively high sediment moisture content were recorded.

Due to the defined limits of the FA, its carbon input was unlikely to contribute significantly to the carbon pool in the terrestrialised sediment; as well, the VS exhibited low primary productivity, so its contribution must also have been minimal. Therefore, the carbon emitted from the BS and VS may have another source. Desiccated biofilms could contribute labile OM to the sediment, highly bioavailable to be remineralised (Liu et al., 2022). Additionally, the study period coincided with below-average annual precipitation (Instituto de Investigación y Formación Agraria y Pesquera IFAPA, 2025), which could have shifted the system from a carbon sink to a carbon source under water scarcity, leading to the emission of previously accumulated carbon. This highlights the importance of long-term monitoring of CO_2 flux for an overall view of carbon dynamics and to prevent temporal bias.

The restoration of degraded salt marshes could be a valuable nature-based solution to mitigate the effects of global change and contribute to carbon capture (Artigas et al., 2015). However, the results obtained in this study suggest that natural carbon dynamics might not have been recovered yet in the restored salt marsh. Given that the terrestrialised sediments behaved as CO_2 sources, the current design of the salt marsh and the restoration actions implemented might not contribute to CO_2 sequestration. To promote CO_2 uptake and carbon burial, salt marsh restoration should begin with the recuperation of its natural hydrological regime (Chmura, 2009; Moreno-Mateos et al., 2012; Chen et al., 2022). A restored tidal regime would promote regular sediment inundation and water renewal, independently of rainfall and management interventions. This could increase sediment moisture, regulate salinity, lower sediment temperatures, and improve the physiological state of vegetation, thereby reducing CO_2 emissions in the salt marsh.

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CRediT authorship contribution statement

Sofía Rodríguez-Gómez: Writing – review & editing, Investigation, Conceptualization. **Paula Warren-Jiménez:** Writing – original draft, Investigation, Formal analysis, Data curation, Conceptualization. **Miriam Ruiz-Nieto:** Writing – review & editing, Supervision, Resources, Investigation, Conceptualization. **Jorge Juan Montes-Pérez:** Writing – review & editing, Validation, Methodology, Investigation, Formal analysis, Conceptualization. **Teresa Gil-Gil:** Writing – review & editing, Project administration, Funding acquisition, Conceptualization. **Guillermo Ledesma-Hernández:** Writing – review & editing, Investigation, Conceptualization. **Enrique Moreno-Ostos:** Writing – review & editing, Validation, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work, the authors used ChatGPT AI in order to improve language and readability. 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.

Declaration of Competing Interest

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

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Data availability

The data that has been used is confidential.

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