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CO_2 influx and efflux circadian cycles in bare dry lake sediments

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Abstract. Permanent and temporary drying of inland waters expands the surface area of exposed sediments, potentially altering total ecosystem CO_2 fluxes. However, the response of CO_2 fluxes from dry sediments to episodic rewetting, and the relative roles of biotic and abiotic exchange mechanisms in shaping net fluxes, remain poorly understood. Here, we conducted a field rewetting experiment on long-term exposed sediments of Lake Gallocanta (Spain) to assess rewetting-induced variations in CO_2 fluxes. CO_2 exchanges between sediments and the atmosphere were measured before and after rewetting using closed gas chambers, and the isotopic composition of emitted CO_2 ($\delta^{13}C$-CO_2) was analyzed. Sediment samples were also collected to characterize key physicochemical properties (e.g., water activity, temperature, pH) and to assess changes in microbial community composition. In addition, a numerical model integrating gas flux and isotope data was developed to disentangle biotic and abiotic contributions to total CO_2 emissions. Contrary to expectations, rewetting had minimal influence on CO_2 flux magnitudes, which instead exhibited a pronounced circadian pattern of efflux and influx. Although rewetting substantially altered microbial community structure, these changes did not indicate that biological carbon fixation explained the observed CO_2 influx. Model simulations incorporating both biotic and abiotic processes indicated that abiotic mechanisms, most likely carbonate weathering, dominated CO_2 influx, whereas aerobic respiration accounted for midday efflux. Overall, our results highlight the critical role of abiotic processes in regulating CO_2 dynamics from long-term desiccated lake sediments and suggest that net CO_2 fluxes may not reliably indicate organic carbon remobilization under dry lake conditions.

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1 Introduction

Many lakes, especially in arid and semi-arid regions such as the Mediterranean, are facing more recurrent permanent or temporary drying due to climate change and water withdrawals (Pekel et al., 2016; Marce et al. 2019). On a global scale, 90,000 km^2 of permanent surface water disappeared between 1984 and 2015, and approximately 70% of permanent waters have been lost in the Middle East and Central Asia due to extreme drought and human impacts (Pekel et al., 2016). During these dry periods, sediments are exposed to atmospheric oxygen, which stimulates mineralization of sediment organic matter, turning them into hotspots of CO_2 emissions (Catalán et al. 2014; Gomez-Gener et al. 2015), and potentially increasing global CO_2 emissions from inland waters by 6 to 10% (Marcé et al. 2019; Keller et al. 2020).

Variations in sediment water content and oxygen availability are key proxies for microbially mediated biogeochemical processes, as they control major shifts in redox conditions (Reverey et al., 2016, 2018; Marce et al., 2019). CO_2 fluxes are primarily influenced by circadian temperature fluctuations (Koschorreck et al., 2022), organic matter content (Keller et al., 2020), and the duration since desiccation (Arce et al., 2021). Elevated CO_2 emissions from drying sediments are typically associated with enhanced aerobic microbial growth during early desiccation, driven by increased oxygen availability (Fromin et al., 2010) and labile organic carbon (Arce et al., 2021). As desiccation progresses, extended drying of exposed lake sediments alters nutrient availability and physicochemical properties (Reverey et al., 2016), consequently reshaping microbial community structure and activity (Romani et al., 2017; Arce et al., 2021; Miao, 2023). Prolonged dry conditions can suppress microbial activity by inducing water limitation, leading to cell dormancy or death (Sabater et al., 2016). The microbial community thus comprises both active and dormant microorganisms, but CO_2 efflux predominantly arises from the active fraction (Werth & Kuzyakov, 2010). In soils, the proportion of active bacteria is typically below 3.5% (Bloem et al., 1992; Blagodatskaya & Kuzyakov, 2013), whereas up to 60% of cells remain potentially active and can resume metabolism within hours (1–3 h) after rewetting (Placella et al., 2012). Moreover, some microorganisms adapted to low-moisture conditions can persist through desiccation until favorable conditions return (Pohlon et al., 2013; Romani et al., 2013). Rewetting events are known to trigger transient CO_2 pulses associated with enhanced microbial respiration (Birch, 1958). In long-term desiccated sediments, rewetting can either stimulate (Arce et al., 2019; von Schiller et al., 2019) or suppress CO_2 emissions (Koschorreck et al., 2022), suggesting context-dependent responses. However, the effects of short rewetting events, such as those caused by small rainfall pulses, on microbial community composition, activity, and carbon dynamics remain poorly understood (Arce et al., 2021; Coulson et al., 2022). Integrating analyses of both bulk (DNA-based) and potentially active (based on complementary DNA (cDNA) as a proxy for RNA) microbial profiles provides a powerful approach to elucidate bacterial responses to episodic rain events and to disentangle the abiotic and biotic drivers underlying CO_2 fluxes from soils (Aanderud et al., 2016).

Beyond biotic pathways, several abiotic processes, often overlooked in studies of carbon gas fluxes, can also influence CO_2 exchange dynamics. These include carbonate weathering, photodegradation of organic carbon by UV radiation,

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and CO_2 adsorption or desorption by mineral particles (Rey, 2015; Light et al., 2019; Marce et al., 2019). In particular, the reversible carbonate equilibrium represents a key component of abiotic fluxes in arid and semi-arid soils, potentially leading to either CO_2 efflux through carbonate precipitation (Eq. 1) (Soper et al., 2017) or CO_2 influx through carbonate dissolution (Eq. 2) (Xie et al., 2009; Hamerlynck et al., 2013; Ma et al., 2013; Fa et al., 2016). The equilibrium reactions can be summarized as follows:

$$CO_2 + H_2O \leftrightarrow HCO_3^- + H^+ \quad (1)$$

$$CaCO_3 + H^+ \leftrightarrow Ca^{+2} + HCO_3^- \quad (2)$$

Previous studies have reported abiotic nocturnal CO_2 influxes in saline and alkaline soils (Xie et al., 2008; Ma et al., 2013; Wang et al., 2020). For instance, Ma et al. (2013) observed an atypical CO_2 uptake in sterilized saline/alkaline soils during nighttime, followed by a daytime efflux, both significantly correlated with soil pH, humidity, and temperature. Evidence suggests that abiotic CO_2 influxes can occur under both wet (Fa et al., 2016) and dry (Hamerlynck et al., 2013) conditions. Disentangling biotic from abiotic CO_2 fluxes is particularly challenging in water-limited ecosystems, where even minor variations in soil moisture can rapidly alter soil physicochemical properties. Precipitation events typically stimulate biotic CO_2 emissions while simultaneously reducing the relative contribution of abiotic fluxes (Inglima et al., 2009). Increases in soil moisture can enhance microbial respiration but also promote carbonate dissolution (Schlesinger, 1985; Gallagher et al., 2020), which consumes CO_2 and may mask biological respiration. Conversely, nighttime temperature drops can enhance abiotic CO_2 uptake through carbonate precipitation by increasing CO_2 solubility and the pH of thin water films on soil particle surfaces (Kim et al., 2024). Although dew accumulation can stimulate microbial dark CO_2 respiration in arid environments (Belnap & Lange, 2003), concurrent abiotic CO_2 influxes may offset or obscure this biotic activity (Kim et al., 2024).

Despite increasing evidence of both biotic and abiotic mechanisms influencing CO_2 fluxes in arid soils, clear process-based discrimination of inorganic CO_2 uptake and release pathways remains lacking. This gap in understanding may lead to systematic over- or underestimation of biologically driven sediment CO_2 emissions. Similar to saline and alkaline soils (Parsons et al., 2004; Ball et al., 2009), distinguishing abiotic from biotic controls on CO_2 fluxes in dry sediments is challenging because both are regulated by common environmental drivers such as temperature, moisture availability, and pH (Rey, 2015; Marce et al., 2019). Moreover, the paucity of information on abiotic carbon exchange mechanisms is even more pronounced in desiccated aquatic sediments (Light et al., 2019; Marce et al., 2019).

This study aims to quantify the effects of rewetting on CO_2 fluxes from long-term dried lake sediments and to elucidate the relative contribution of abiotic and biotic processes governing CO_2 exchanges between sediments and the atmosphere. To this end, a field rewetting experiment was conducted in the long-term desiccated sediments of Lake Gallocanta (Spain). Rewetting-induced variations in CO_2 fluxes were measured, and compositional changes in the bulk (DNA-based) and active (cDNA-based) fractions of the microbial community were analyzed through 16S rRNA amplicon sequencing. Additionally, the stable isotopic signature of emitted CO_2 ($^{13}C–CO_2$) was used to differentiate

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between biotic and abiotic sources of emissions. We hypothesize that microorganisms adapted to extreme desiccation can rapidly reactivate upon rewetting, increasing cDNA activity and consequently enhancing CO_2 fluxes through biological respiration upon rewetting. Moreover, we hypothesize that CO_2 fluxes are driven by the combination of abiotic (e.g., carbonate weathering) and biotic (microbial respiration) processes.

2 Methods

2.1 Study site, rewetting experiments design and sampling

Field experiments were conducted in lake Gallocanta, an endorheic shallow saline lake located in the Iberian Peninsula (NE Spain; 40°58′ N,01°30′ W), with an approximate altitude of 1,000 m above sea level. The Gallocanta basin has a dry semiarid climate, characterized by an average annual temperature of 11 °C, and an average annual rainfall of 488 mm (Castaneda et al., 2020). The precipitation regime is highly seasonal, and has a maximum in spring and fall seasons, resulting in rapid and significant fluctuations in the water level of the lake (Castaneda et al., 2015). Additionally, land-use changes from pasture to agricultural farming in the lake basin have been compromising the water sources feeding the lake. As a consequence, Gallocanta lake has experienced severe droughts since the 1980s (Comín et al.,1992; Luzon et al., 2007 & 2009), which resulted in the offshore sediments emergence (Castaneda et al., 2020). The lake basin is rich in gypsum and carbonates (Schütt, 1998; Corzo et al., 2005) and the sediments present variable concentrations of salt and organic matter. The intermittently desiccated marginal lacustrine sub-environment of the lake is characterized by carbonate-rich (30-40%) and organic-low (3.3% total organic carbon) brown or gray mud (Luzon et al., 2007).

The rewetting field experiment was performed at the southeastern side of the lake (40° 56' N and 1° 28' W), a bare lacustrine terrace that has been dry at least since 1984, and retained a very sparse vegetation cover, halophytes compose most of the vegetation in marshes. Within that terrace, we selected an area with bare sediments without vegetation to perform the experiment between the 9th and 13th of July 2018. Details of the field sampling design are given in Fig. S1. Ten squared plots (5 control and 5 rewetted) of 1.5×1.5 m dimensions with an inner square of 1×1 m were delimited. The first day, we measured the basal/initial conditions (T0). Then, on the morning of the second day we mimicked a 28 mm rain event with distilled water on 5 of the plots (i.e., the rewetting treatment), while the other 5 plots were kept dry. All the plots were monitored for four days. CO_2 fluxes were measured 12 times, named as the hours since rewetting, where T0 is before rewetting, T1 is one hour after rewetting, and so on (T0, T1, T6, T13, T15, T23, T30, T36, T37, T53, T61 and T65). Sediment samples to monitor the changes in physicochemical properties were collected in 6 out of the 12 time intervals (T0 (Initial)) and times T6, T23, T30, T53 and T61 (Fig. S1). Samples were collected using small cores (2 cm diameter and 10 cm depth) and kept in 50 mL Falcon tubes at 4 °C until their analysis in the laboratory. For molecular analyses, a two-gram sediment sample from each plot was collected at times T0, T6, T30 and T60 and preserved in a sterile Falcon tube containing 3 mL of RNAlater (ThermoFisher Scientific). Tubes were immediately frozen to –20 ºC upon collection until arrival at the laboratory, where they were stored at –80 ºC until processing. Samples and measurements were only taken in the inner square of the plots, to avoid border

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effects. Ambient meteorological conditions were continuously recorded during the whole duration of the field experiment (Kestrel 4000). The air temperature varied between 13 and 29 °C with a mean of 22 °C. Wind speed, atmospheric pressure, and relative humidity were 3.3 ± 2.2 m s^{-1}, 904 ± 2.0 hPa, and 59% ± 18%, respectively.

2.2 Measurements of CO_2 Fluxes and $\delta^{13}C$-CO_2

Sediment CO_2 fluxes were measured using an enclosed chamber method as previously described by Obrador et al. (2018). We installed two collars in each plot before the experiment to avoid disturbances. Then, we attached an opaque chamber with a surface area (S) of 0.0186 m^2 and 1.388 L of inner volume (V) to one of the collars. The chamber was connected to an infrared gas analyzer with a 4.8 s resolution and 1% accuracy (IRGA EGM-5, PP-Systems, Amesbury, USA). The CO_2 concentration within the chamber was monitored until at least 10 µatm of change in CO_2 was reached, with a maximum duration of 300 s and a minimum of 120 s. Then, CO_2 fluxes (F_{CO2}, mmol m^{-2} day^{-1}) were calculated by using the change in the concentration of CO_2 inside the chamber, according to Eqn (3):

$$F_{CO_2} = \left(\frac{dpCO_2}{dt}\right)\left(\frac{V}{RTS}\right) \quad (3)$$

where $\frac{dpCO2}{dt}$ is the slope of the gas accumulation inside the chamber, V is the chamber volume (L), S is the surface area (m^2), T is the air temperature during the measurement (K°), and R is the ideal gas constant (0.082 L atm mol^{-1} K^{-1}). Positive fluxes indicate CO_2 emission from the sediment to the atmosphere (i.e., efflux), whereas negative fluxes indicate CO_2 uptake by sediment (i.e., influx).

In parallel to the CO_2 flux measurements at times T0, T6, T23, T30, and T61, we installed a second chamber of the same characteristics in the second collar, covered with a wet cloth for cooling, to collect additional gas samples to determine changes in the ^{13}C-CO_2 isotopic signature of the gas inside the chamber. During each deployment, we sampled the gas in the chamber 5 times during a variable period (for Keeling plots: median = 1.6 h, SD = 0.6 h; for Rayleigh plots: median = 2.1 h, SD = 1.2 h), depending on the current CO_2 emissions from the plot as measured with the first chamber. The first gas sample was taken immediately after deploying the chamber on the collar, together with an atmospheric sample, used to correct for contamination through the vent during sampling. Then, 60 mL of chamber gas were sampled with a plastic syringe with stopcock, and pressurized into a 12 mL Exetainer vial. The chamber was vented by opening an additional vent for that purpose to avoid generating under pressure during sampling. Samples were processed for $\delta^{13}C$ and pCO_2 using a PICARRO gas isotopic analyzer (Picarro G2201-i cavity ringdown spectrometer (Picarro Inc., Santa Clara, USA) at CREAF-UAB (Spain), after transferring the over-pressurized gas from the Exetainers into a gas-tight syringe.

2.3 Sediment physicochemical parameters

Water content and ash-free dry weight (AFDW, %) were determined gravimetrically by heating the sediments first at 100 °C until stable weight and then at 450 °C in a clean furnace for 4 hr (Dean, 1974). A mixture of sediment sample and deionized water (Milli-Q, Merck, Germany) were mixed by 1/1 (*vol*), and pH and conductivity were measured in

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the suspension using the conventional electrodes (WTW, Germany). Water activity (aw) was measured with an Aqualab Pawkit Water Activity Meter (± 0.02 aw accuracy) (METER Group, USA). Sediment temperature was measured *in situ* with a soil probe.

2.4 Characterization of the sediment microbial community

Frozen sediment samples were thawed and washed to remove the RNAlater buffer. The washing process involved three cycles of the following steps: centrifugation at 8,000×g for 5 minutes, discarding the supernatant, adding 1ml of sterile PBS, homogenizing by vortexing, and repeating the centrifugation. After the final centrifugation, the supernatant was discarded. To facilitate cell lysis in such saline and extremely compact sediments, washed sediment samples were treated with a combination of lysozyme and proteinase K as previously described (Llirós, 2008). Extraction of RNA and DNA was finally accomplished using the RNeasy® PowerSoil® RNA kit (Qiagen) according to manufacturer's instructions, with the following modification: in step 4, samples were vortexed 15 minutes twice. Concentration of DNA and RNA in each extract was determined using QUBIT® 2.0 Fluorometer (Invitrogen Molecular probes Inc., Oslo, Norway). Left-over DNA in the RNA extracts was digested using the Ambion Turbo DNA-free kit (Invitrogen) according to manufacturer instructions. Aliquots of the purified RNA extracts were checked for purity by running a PCR with primers 27F/1492R (Lane, 1991) targeting the bacterial 16S rRNA gene. Afterward, pure RNA extracts were retro-transcribed using SuperScript III First-Strand Synthesis System kit (Thermo Fisher Scientific). The concentration of the resulting cDNA was determined using QUBIT.

The 16S rRNA amplicon sequencing was performed at the Sequencing and Genotyping Unit of the Genomic Facility/SGIker of the University of the Basque Country (Leioa, Spain) following Illumina guidelines for library preparation and high-throughput multiplexed sequencing of the V4 region of the 16S rRNA gene using the universal primer pair 515F/806R (Apprill et al., 2015; Caporaso et al., 2011; Parada et al., 2016). Sequence datasets were deposited in the NCBI Sequence Read Archive (SRA) database under the accession number PRJNA1090308. Sequence reads were processed using QIIME2 release 2020.8 (Bolyen et al., 2019) as described in Sacristán-Soriano et al. (2024). The resulting Amplicon Sequence Variant (ASV) table and taxonomy were then imported into R v4.2.2 (R Core Team, 2021). Samples with less than 7,000 reads were discarded for subsequent analyses. The dataset was filtered to retain ASVs with a minimal proportional abundance in a sample of 0.1% and a prevalence of each feature in all samples of 5% using the *CoDaSeq* package v0.99.6 (Gloor et al., 2017). To rigorously deal with the compositional nature and sparsity of microbiome datasets (Gloor et al., 2017), we estimated the 0 count values using the *zCompositions* package v1.4.0-1 (Palarea-Albaladejo and Martín-Fernandez, 2015) before applying centered log-ratio (CLR) transformation of the data. Taxonomy bar charts between dry and rewetted treatments were plotted in R using *phyloseq v1.36.0* (McMurdie and Holmes, 2013) and *qiime2R* v0.99.4 (Bisanz, 2018).

2.5 Keeling and Rayleigh plot analyses

To discriminate the carbon isotopic signature of the CO_2 being exchanged between the sediments and the atmosphere, we solved a Keeling plot analysis (Eqn. 4) (Keeling, 1958) in each of the 10 plots at times T0, T6, T23, T30, and T61.

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Solving a Keeling plot consists of a linear regression of $\delta^{13}C$ of CO_2 (‰) against $1/pCO_2$. The $\delta^{13}C$ of the source of the emitted CO_2 was obtained as the intercept of the $\delta^{13}C$ value at $1/pCO2 = 0$, by fitting a linear regression to the data:

$$\delta^{13}C(x) = a + bx^1 \quad (4)$$

Where $\delta^{13}C(x)$ is the observed $\delta^{13}C$ value of CO_2 in the chamber at the CO_2 mixing ratio of x (see Section 2.2), and a and b are coefficients obtained by linear fitting. Coefficient a represents the intercept, which gives the isotopic signature of the source of the emitted CO_2 (Fig. A1). We solved the Keeling plots with 5 points for each chamber measurement (see Section 2.2).

However, during large portions of the day, sediments were taking up CO_2 from the atmosphere, and in such conditions solving a Keeling plot is not meaningful. Yet, following the drift of the isotopic carbon signature of an enclosed gas volume in contact with a CO_2 absorbing sediment offers the opportunity to estimate the enrichment factor of the process responsible for the decrease in pCO_2 inside the chamber. Therefore, when the sediments were taking up CO_2, Rayleigh (fractionation) plots were solved according to Eqn (5):

$$\text{Enrichment factor (EF)} = ln\frac{Rx}{R0} / ln\ (f) \quad (5)$$

where EF is the enrichment factor (‰), f is the fraction of CO_2 remaining in the chamber regarding the initial condition, R_x is the isotopic ratio of CO_2 in the chamber at a given time, and R_0 is the isotopic ratio at the initial time. Both R_x and R_0 were obtained from $\delta^{13}C$ and pCO_2 data as explained in Section 2.2, using 5 data points to fit Eq. 5. The enrichment factor of the process removing CO_2 is the slope of the linear relationship (Fig. A1) between the ln of the fraction of CO_2 remaining and the ln of the ratio between the isotopic composition of remaining CO_2 and initial CO_2 (Kendall and McDonnell, 1998).

After solving Keeling plots, we only kept those that showed a significant (alpha=0.05) linear relationship between $\delta^{13}C$ and pCO_2. For Rayleigh plots, we only kept those that showed both a significant (alpha = 0.05) relationship between $ln(R_x/R_0)$ and $ln(f)$, and an intercept not significantly different from zero.

2.6 Numerical simulation of the CO_2 exchanges and isotopic signatures

To better understand the processes behind the observed daily evolution of CO_2 emissions and isotopic signatures during the rewetting experiment, we developed a numerical model fitted to observed data (Fig. A1). Two processes were assumed to control CO_2 dynamics: (i) respiration of sediment organic matter (emitting CO_2 to the chambers) and (ii) an unknown process taking up CO_2. The aims were to determine (1) the magnitude and daily cycle of each process, (2) the $\delta^{13}C$ signature of the respiration source, and (3) the $\delta^{13}C$ enrichment factor of the uptake process. It is important to note that the $\delta^{13}C$ signature and enrichment factor obtained from observations in the field (sections 2.2 and 2.5) may

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be just apparent, resulting from the simultaneous operation of two processes, which would violate the assumptions of Keeling and Rayleigh plots.

In our model both processes were represented as daily sinusoidal waves of CO_2 flux (mmol m^{-2} d^{-1}):

$$CO_2\_flux_{r,u}(time) = a_{r,u} \times \sin[(time - b_{r,u}) / 0.5] + d_{r,u} \quad (6)$$

where *time* is time (minute of day), a the amplitude, d the central value, and b the phase. Subscripts r and u denote respiration and uptake. Respiration was constrained to positive d_r values and uptake to negative d_u, with $a_{r,u} < d_{r,u}$ to avoid zero crossings. The net CO_2 flux (sum of both waves) could alternate between emission and uptake (Fig. A1). The model assumed constant $\delta^{13}C$ values for the respiration source and a fixed enrichment factor for uptake.

A model realization required thus eight parameters: a_r, a_u, d_r, d_u, b_r, b_u, $\delta^{13}C$ for the source of respiration, and the uptake enrichment factor. A model run produced a daily respiration, uptake, and net CO_2 fluxes. Then, we used the daily fluxes and the isotopic behavior of respiration and uptake to simulate 50 one-hour chamber incubations, starting at the same time as the 50 plot measurements in the field. Each of the 50 incubations was evaluated using Keeling or Rayleigh models (depending on flux direction), applying the same quality thresholds as in field experiments (Fig. A1). As in the case of observations, poorly fitted plots were discarded. Note that the combination of two processes in Keeling and Rayleigh plots in simulations imply that $\delta^{13}C$ signature of the respiration and enrichment factor obtained after solving the plots (apparent values) may not necessarily coincide with the parameters used in the model (latent values). Field observations would be comparable with the apparent values obtained with the model.

To identify combinations of the eight parameters that compare well with observations we used the Generalized Likelihood Unbiased Estimator (GLUE) framework (Beven et al., 2000). GLUE randomly sampled parameter combinations from pre-defined ranges, ran the model under those random combinations, and selected the parameter combinations which render simulations consistent with observations ("behavioral" simulations). We generated 250,000 random 8-parameter combinations, simulated emissions and isotopic data for each, and retained those with relative absolute errors < 30% for the following observed quantities in the field: (1) median $\delta^{13}C$ from valid Keeling plots (−39.8 ‰), (2) median Rayleigh fractionation factor (9.54 ‰), (3) minimum $\delta^{13}C$ from Keeling plots (−97 ‰), (4–5) maximum and minimum net CO_2 exchange (225 and −113 mmol m^{-2} d^{-1}), and (6) time of the peak net emission (11:00 h). Only behavioral simulations were retained for further analysis (Fig. A1).

2.7 Statistical analyses

Variation in CO_2 fluxes and sediment properties (gW/gDW (%), aw, conductivity (µS cm^{-1}), soil temperature (ºC), bulk density (g cm^{-3}), AFDW (%) between treatments (dry or rewetted sediments), sampling time and their interactions (treatment and time) was assessed using a linear mixed model (LMM). Treatment, time, and interactions between both factors were considered as fixed effects and replicate sample sites as a random effect. Three-way ANOVAs were conducted to test the significance of the fixed factors and their interactions. Significant differences between factor levels were obtained by using a Student's t-test for treatment and a Tukey HSD multiple comparison

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test for time and interactions of time and treatment. The time before rewetting was not included in the models, as the assignment of sites to rewetted in that sampling was misleading, since the plots were randomly assigned to treatments.

We used artificial neural networks to predict nonlinear relationships between sediment characteristics (temperature, water activity, water content, organic matter content, conductivity, and pH) and CO_2 flux responses. To accomplish this, we built the best-fit artificial neural network to discuss the drivers and their interaction effects on CO_2 fluxes. We built three different models to test three different activation functions (linear, hyperbolic tangent and Gaussian) by applying hyper-parameters including one hidden layer with five neurons per each, and a learning rate of 0.1. The performance of ANN models' results was compared by using the R2 and root-mean-square error (RMSE) values based on the random 3-fold cross-validation. Main and total (main + interaction) effects on the CO_2 flux responses, and variable importance scores of the drivers were obtained from the independent resampling by using Monte Carlo simulations. LMM and the best-fit ANN modeling was performed using JMP Pro 15.1.

Richness (i.e., observed ASVs) and Shannon diversity index were calculated to determine alpha diversity on the DNA samples using the package *vegan* v2.6-2 (Oksanen et al., 2020). The differences between species richness and Shannon diversity were compared by a one-way ANOVA (treatment and time independently due to collinearity) using the package *car* v3.1-0 (Fox et al., 2021). For beta diversity, a principal component analysis (PCA) on the Aitchison distance of the centered log ratio vectors of the samples was performed both for DNA and RNA using the package *propr* v4.2.6 (Quinn et al., 2017). A three-way PERMANOVA was performed in *vegan* to test for the effect of type (i.e., DNA or RNA), treatment and time. Pairwise comparisons were subsequently conducted using the package *pairwiseAdonis* v0.4.1 (Martinez Arbizu 2020). Additionally, the correlation of environmental variables with the multivariate space was assessed using *vegan* fitting the environmental vectors onto an ordination of DNA samples. Analyses were conducted using R software v4.2.2 (R Core Team, 2021).

3 Results

3.1 Sediment CO_2 flux and its response to rewetting

The artificial rain treatment affected sediment water content (F-value = 95, df = 1, $p < 0.0001$), water activity (F-value = 811 df = 1, $p < 0.0001$), conductivity (F-value=16, df = 1, $p < 0.0001$) and temperature (F-value = 43, df = 1, $p < 0.0001$), whereas treatment had no effect on sediment bulk density, pH, and organic matter content (Table S1). Rewetting significantly increased water content from 0.10 ± 0.028 (mean ± SE) to 0.20 ± 0.071, and water activity from 0.49 ± 0.19 to 0.82 ± 0.12.

Before the artificial rain experiment, soil CO_2 flux was -35 ± 9.5 mmol CO_2 m^{-2} d^{-1} in the dry sediments' plots (T0 (initial)). During the experiment, daily average CO_2 flux from dry sediment plots varied between -113 and 211, with an average of -4.1±10 mmol m^{-2} d^{-1} (median = -26 mmol m^{-2} d^{-1}) (Fig. 1a). Rewetted plots showed CO_2 fluxes between -105 and 225 mmol m^{-2} d^{-1}, and averaged -16 ± 10 mmol m^{-2} d^{-1} (median = -33 mmol m^{-2} d^{-1}) (Fig. 1a). According to LMM outputs (Table S2), Time and the interaction between Time and Treatment exerted a significant effect (F-value

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= 46; df = 80; $p < 0.0001$; F-value = 6.4; df = 80; $p < 0.0001$, respectively), whereas treatment had a marginal effect on CO_2 fluxes (F-value = 8.8; df = 8; $p = 0.0178$). CO_2 effluxes peaked at midday hours (T6, T30 and T53, i.e. from 11:00h to 12:30h), significantly departing from values during the rest of the day, which showed frequent influx conditions (Table S2).

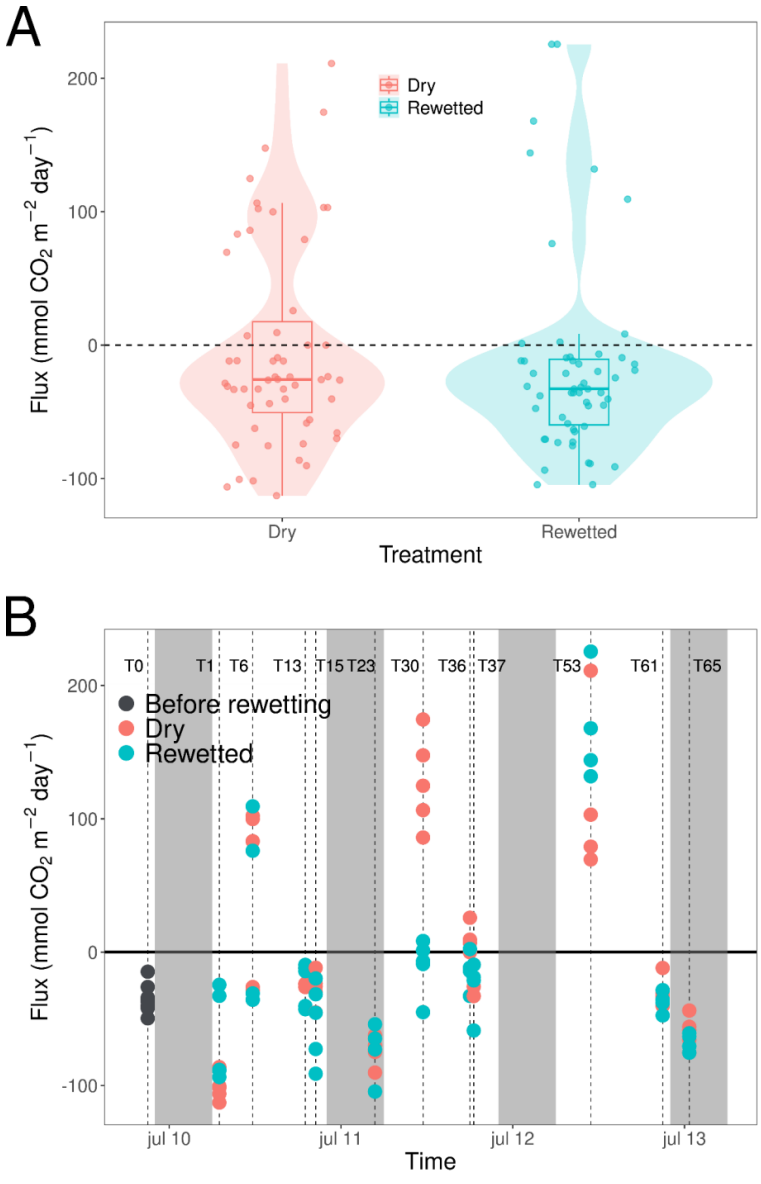

Figure 1: CO_2 fluxes according to Treatment (A), and interaction between Treatment and Time (B). In (B) dashed vertical lines indicate sampling times, labelled from T0 to T65. Dark periods of the day are indicated as a grey area.

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3.2 Drivers of CO_2 fluxes

3.2.1 Sediment properties

The ANN was built with 5 hyperbolic tangent activation functions (Fig. S2). The model was selected according to the random 3-fold cross-validation (n training: 80, n validation:40) and had a prediction power of 83% for sediment CO_2 fluxes (R2: 0.82; RMSE: 30 mmol m^{-2} d^{-1}). According to the Monte Carlo resampling simulations, the most important driver was sediment temperature followed by water activity (Fig. 2b). Sediment temperature had a positive effect on sediments CO_2 fluxes, whereas it was negative for water activity (Fig. S3). Accordingly, a sediment temperature above 24 °C and a water activity below 0.6 favored CO_2 indicating an important synergistic effect of water activity and temperature on CO_2 fluxes (Fig. 2a).

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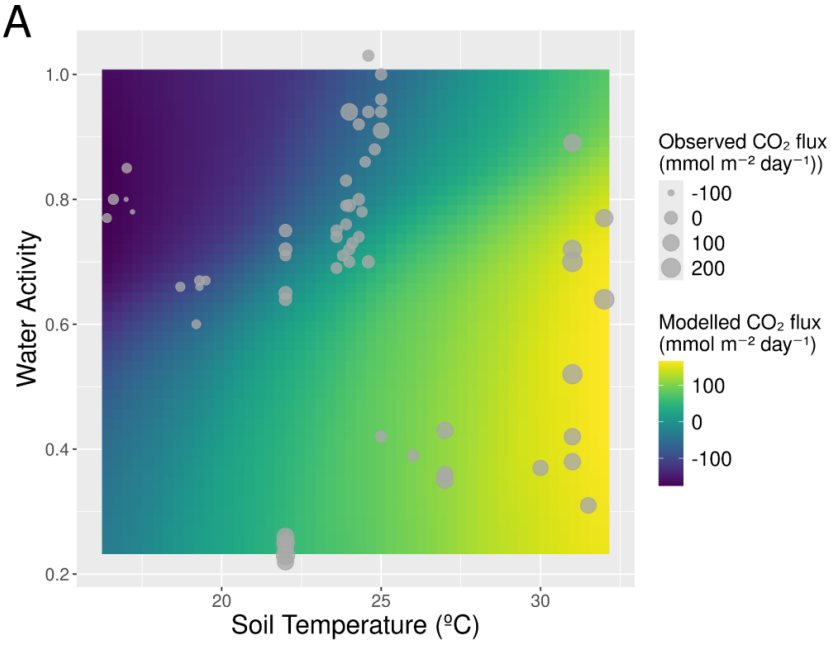

B

Variable	Main effect	Total effect
Soil temperature	0.381	0.603
Water activity	0.245	0.470
Water content	0.039	0.133
AFDW	0.043	0.102
pH	0.021	0.063
Conductivity	0.019	0.047

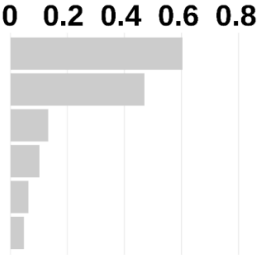

Figure 2: Response of CO_2 fluxes (mmol CO_2 m^{-2} d^{-1}) to the interaction between soil temperature and water activity based on best-fit ANN and Monte Carlo resampling analysis. A) Surface plot of the modelled CO_2 flux (color) and the corresponding observations (dots). Size of dots corresponds to the value of observed flux. **B)** The Monte Carlo-driven variable importance scores of the predictors in terms of their Main (alone) and Total (Main + Interaction) effects on the CO_2 fluxes.

3.2.2 Bacterial community composition

After denoising the sequence dataset (29 DNA and 18 cDNA sediment samples), we obtained 3,816,007 reads with a sample depth ranging from 1,617 to 211,150 reads per sample. A total of 6,499 ASVs were recovered (5,861 from DNA and 2,512 from cDNA). After filtering by abundance and prevalence (see Methods), 986 ASVs were retained for further analyses (982 from 29 DNA samples and 804 from 12 cDNA samples).

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At the order level, DNA samples were dominated by sequences affiliated to orders Cyanobacteriales (9.2% in dry and 8.1% in rewetted samples), Rhodobacterales (6.0% and 5.9% in dry and rewetted, respectively), Sphingomonadales (Dry: 6.0%, Rewetted: 7.0%), Rubrobacterales (Dry: 5.4%, Rewetted: 5.7%) and Cytophagales (Dry: 5.3%, Rewetted: 6.5%) (Fig. S4). The remaining 68% was distributed among more than 100 bacterial orders at lower relative abundances. In cDNA libraries, sediments were dominated by Cyanobacteriales in a higher proportion (Dry: 42%, Rewetted: 35%), Rubrobacterales (Dry: 7.2%, Rewetted: 5.8%), Phormidesmiales (Dry: 6.0% and Rewetted: 5.9%) and Rhodobacterales (Dry: 5.2 and Rewetted: 6.7%). We also detected over 100 orders at low proportions (Fig. S4).

For DNA, bacterial richness and alpha-diversity showed higher values in the Rewetted samples (median: 5.5 and 585, respectively) than in the Dry ones (median: 4.3 and 373, respectively) (one-way ANOVAs, F-value = 10 $p < 0.01$ and F-value = 25 $p < 0.001$, respectively) (Fig. 3). No significant differences were found between sampling times ($p > 0.05$). For cDNA, no significant differences were observed for treatment or time ($p > 0.05$).

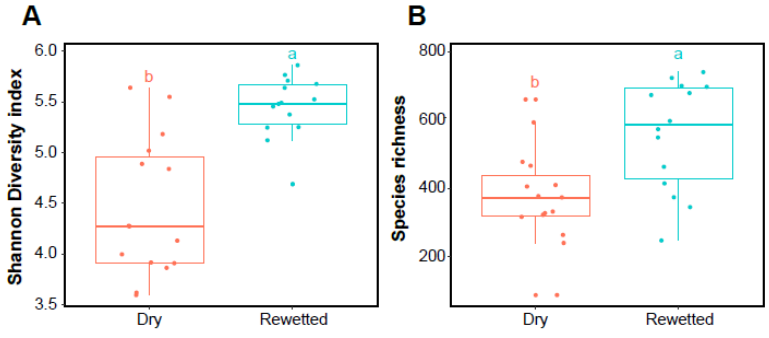

Figure 3: Shannon diversity (A) and species richness (B) of the composition of bulk (i.e., DNA libraries) sediment bacterial communities.

Regarding beta diversity, the PCA explained 27.1% of the variance (Fig. S5) and revealed that bacterial composition of bulk (*i.e.*, DNA) and potentially active (*i.e.*, cDNA) communities was significantly different (three-way PERMANOVA, df = 1, F = 2.7, $p < 0.001$). Differences were also found by the interactions of type and treatment (df = 1, F = 2.023, $p = 0.008$) and by treatment alone (three-way PERMANOVA, df = 1, F = 2.7, $p < 0.001$). Particularly, differences were found between DNA and cDNA within each treatment and between treatments for DNA, but no treatment effect was observed for cDNA (Table S3).

Among the community members, CO_2 fixation could be performed by members of the Cyanobacteria (oxygenic photosynthesis), as well as by ammonia-oxidizing archaea, both also identified as active members of the sediment microbial community (*i.e.*, cDNA). Besides, Campylobacterota (chemolithotrophic sulfide oxidation) and the Halobacterota (archaea) were also identified in the bulk community (*i.e.*, DNA libraries). However, we did not find any correlation between the CO_2 fluxes and these ASVs except for some members of cyanobacteria (in cDNA libraries) with a positive relationship. No relationship was found for DNA. Beyond the potential main contributors to

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CO_2 emissions, Thermoanaerobaculales appeared positively related to CO_2 emission and conductivity (Fig. 4). Analyzing community composition separately for DNA (Fig. S6; PCA explained variance of 28.1%), we observed that the interaction between treatment and time had a significant effect on the community composition. CO_2 fluxes, conductivity, water activity and soil temperature were significantly associated with the bulk microbial community (DNA). For instance, at midday (T30), the bacterial composition of the bulk communities was positively correlated with CO_2 fluxes and conductivity, whereas was negatively correlated with water activity. This result was somehow counterintuitive (*i.e.*, higher CO_2 fluxes in sediments dominated by Cyanobacteria).

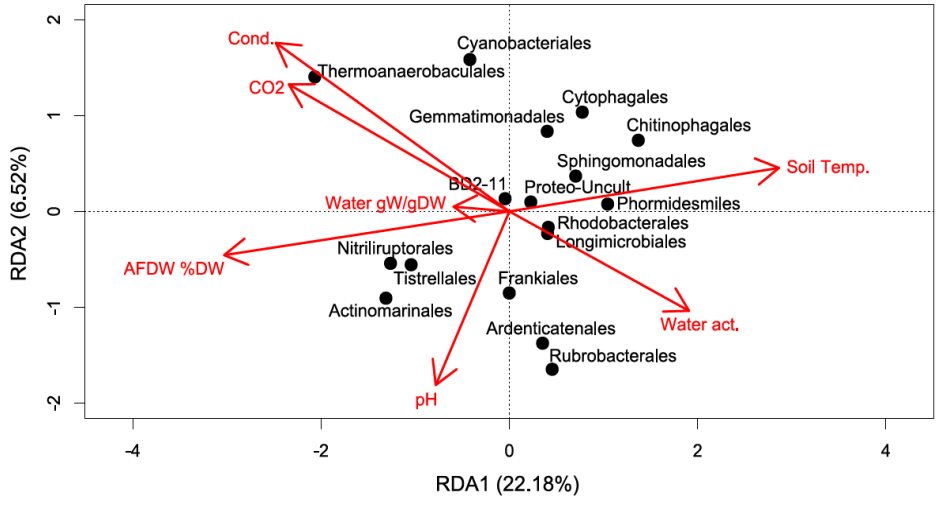

Figure 4: Compositional redundancy analysis (RDA), based on Aitchison distance, of sediment microbial community composition. Environmental variables correspond to sediment conductivity (Cond.), CO_2 flux (CO2), sediment water content (Water gW/gDW), ash free dry weight (AFDW %DW), sediment pH (pH), water activity (Water act.) and sediment temperature (Soil Temp.).

3.3 Sources of CO_2 fluxes and isotopic fractionation

The median pCO_2 change during Keeling plots was 59 µatm, ranging from 10 to 174 µatm in 12 out of 50 flux measurements, when positive efflux of CO_2 was measured. In the remaining 38 experiments, we observed CO_2 influx (Rayleigh plots), with a median pCO_2 change of -87 µatm, ranging from -8 to -413 µatm. Among the 12 positive flux measurements, only 6 were successfully fitted to a Keeling plot. In the case of the remaining 38 influx data, only 19 delivered usable results for solving a Rayleigh plot. Thus, almost half of the experiments did not result in a fitted plot due to insufficient statistical quality. Those unsuccessful plots were scattered in all samplings, with no discernible temporal or circadian cycle, or relationship to treatment.

Among the 19 successfully fitted Rayleigh plots, estimates suggest that there was a mechanism responsible for the CO_2 uptake with an *EF* of 10‰, although there is substantial scattering within the measurements, which ranged

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between 5.2‰ and 24.3‰. On the other hand, valid Keeling plots delivered an average value of -21.6‰, but there were also some marginally low values between -51‰ and -97‰ (not shown in the plots). This prompted us to look at our results critically and evaluate whether the high rate of unsuccessful experiments and unusual values and substantial scatter was a consequence of uncontrolled errors in the field or laboratory, or an implication of a genuine complex underlying CO_2 flux dynamic.

3.4 Results from the numerical experiment

Out of the 250,000 simulations based on the combinations of the 8 parameters, 88 simulations were identified as behavioral. The ensemble of all behavioral simulations suggested a conspicuous dial respiration cycle, while the uptake process is more constant throughout the day (Fig. 5). The net result implied switching between periods of net emissions and periods of net uptake, as observed in the field.

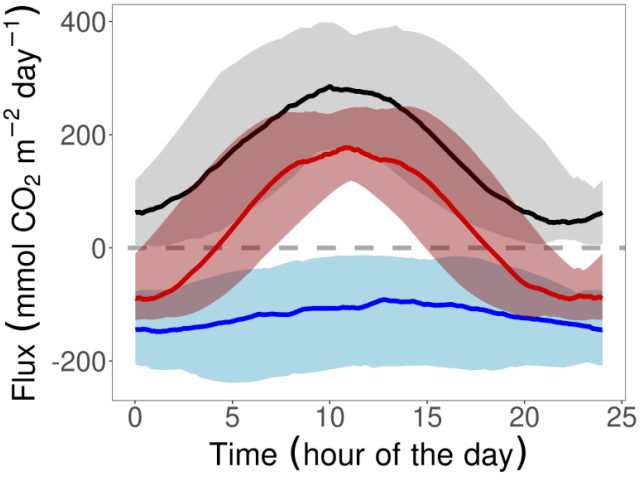

Figure 5: CO_2 exchanges from respiration (gray), uptake process (blue), and the net result (red) resulting from behavioral simulation during the numerical experiment. The bold lines are the 0.5 percentiles, and the shades are 95% bounds.

The distribution of parameters obtained with the GLUE methodology (that is, the "latent" values of the parameters, Fig. 6) suggested that the median value for $\delta^{13}C$ of the source of respiration was around -26.5‰, whereas the median enrichment factor was +3.5‰. These two processes, when combined to solve for Keeling plots, resulted in a distribution of apparent values for the isotopic signature of respiration that compared well with the results obtained when using field data (Fig 6a). The same was also the case for the comparison of the apparent Enrichment Factors obtained from simulations and field data (Fig. 6b). It must be stressed that the apparent results from solving Keeling or Rayleigh plots with the numerical experiments showed excursions to unrealistic values, which were similar to those obtained when using observations (Fig. 6). Furthermore, around 90% of the modelled Rayleigh plots and 20% of the Keeling plots did not pass the quality thresholds. We know that these modelled odd values and unsuccessful plots

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were the result of breaching the only-one-process assumption, and thus cannot be considered as meaningful. This reinforced our conclusion that values obtained from field data can only be considered as apparent values, and must be treated with caution. This also suggested that our results in the field were compatible with the existence of two processes acting on the net emissions in different directions. Also, the high number of unsuccessful plots obtained with field observations was thus probably related to the existence of two processes affecting CO_2 exchange, and not the result of uncontrolled errors in the field or lab.

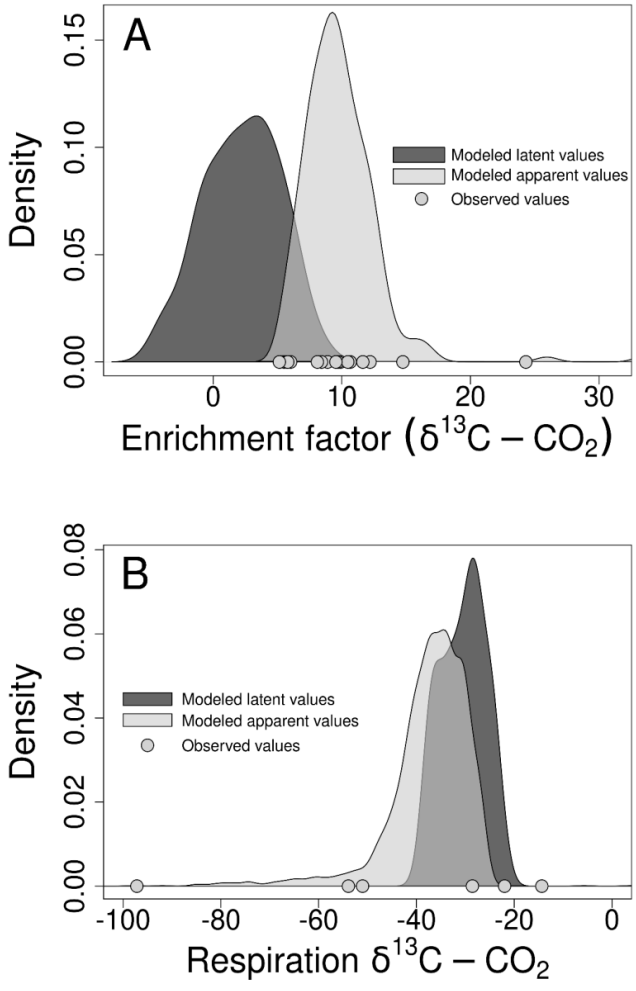

Figure 6: A) Comparison of the apparent (light gray) and latent (dark gray) distributions for $\delta^{13}C$ of the source of respiration, calculated with Keeling plots solved from behavioral simulations. Observations are indicated as light gray dots. **B)** Comparison of the apparent (light gray) and latent (dark gray) distributions for the enrichment factor of the uptake process solved with Rayleigh plots from behavioral simulations. Observations are indicated as light gray dots.

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4 Discussion

4.1 Dry sediment CO_2 fluxes in response to rewetting and their main drivers

Long-term dried sediments in Gallocanta acted as a net sink for CO_2, independently of the treatment applied. Similarly negative mean daily fluxes (mean ± SD = −136 ± 28 mmol CO_2 m^{-2} d^{-1}) were observed in a laboratory-scale incubation study using reservoir sediments exposed to the atmosphere for two years (Light et al., 2019). In both dry and rewetted plots, we detected a clear circadian cycle of CO_2 fluxes, with the highest emissions occurring at midday and negative fluxes during the afternoon, night, and early morning. The mean midday CO_2 fluxes were lower than those reported for temporarily dry sediments from reservoirs (Amani et al., 2022: 296 ± 75 mmol m^{-2} d^{-1}), lakes (Ertürk Arı et al., 2021: 242 ± 404 mmol m^{-2} d^{-1}), and streambeds (Gómez-Gener et al., 2016: 781 ± 390 mmol m^{-2} d^{-1}), but comparable to those from temporary ponds (Catalan et al., 2014: 121 ± 138 mmol m^{-2} d^{-1}). Circadian cycles of CO_2 fluxes characterized by midday emissions and nighttime uptake have also been reported in arid soils (Xie et al., 2009; Yates et al., 2012; Ma et al., 2013) and in dry river sediments (Koschorreck et al., 2022).

A sudden increase in CO_2 flux following rewetting, commonly known as the *Birch effect* (Birch, 1958), was expected. Instead, the rewetted plots generally acted as CO_2 sinks during most sampling events. The Birch effect, driven by a sudden rise in water availability, typically enhances microbial activity or physically displaces trapped gases (Coulson et al., 2002; Arce et al., 2021). In our experiment, however, water availability was sufficient to sustain microbial activity throughout the entire period (i.e. water activity remained above 0.7; Gómez et al., 2021), yet not only was a Birch effect absent, but higher CO_2 effluxes were observed at lower water activity levels (Fig. S3). Rewetting through artificial rainfall may reduce the magnitude of CO_2 release from dried sediments and arid soils. Rainwater can block sediment pores during precipitation events, impeding gas escape from deeper layers (Koschorreck et al., 2022). Additionally, CO_2 may dissolve in the increased pore water following rainfall and become diluted within the sediment matrix, thereby dampening rapid CO_2 exchange with the atmosphere (Looman et al., 2017; Arce et al., 2018).

Interestingly, higher CO_2 emissions were recorded under high temperature when water activity was lowest (Fig. 2). Both water activity and temperature emerged as the main controls of CO_2 fluxes. While the positive relationship with temperature was anticipated, the negative relationship with water activity contrasts with previous findings in dry sediments, where temperature had no effect under low water content (Keller et al., 2020). Although a positive temperature–CO_2 relationship is often interpreted as evidence of respiration-driven fluxes (Koschorreck et al., 2022), a threshold of water availability below which this relationship disappears has also been widely documented (Kannenberg et al., 2024). Higher soil moisture has been shown to enhance carbon sequestration in dryland vegetation and in areas experiencing water limitation after rainfall, primarily through increases in net ecosystem productivity (Hao et al., 2025). In bare, dry sediments, however, this mechanism is unlikely to operate; therefore, other biogenic and physical processes likely contribute to post-rainfall CO_2 fluxes, as root respiration and plant fixation effects were excluded from this study.

4.2. Microbial response to rewetting

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Drying and rewetting events can exert a significant effect on microbial diversity and function due to the different abilities of microbes to adapt to extreme conditions (Sabater et al., 2016; Arce et al.; 2018; Coulson et al., 2022). In the present study, the bacterial richness and alpha-diversity of the bulk microbial community (i.e., DNA) were significantly higher in rewetted than in dry sediments. Consistent with these findings, higher diversity was previously observed in rewetted sediments of intermittent streams in comparison to dry ones (Coulson et al.; 2022). Although the rapidly increasing water activity with rewetting can cause cell bursting and death due to osmotic shock (Schimelet al., 2007; Borken and Matzner, 2009), community survivors are expected to benefit from available substrates and water (Fierer and Schimel, 2003).

Regarding beta diversity, the structure of bulk communities (i.e., DNA) and their potentially active fractions (i.e., cDNA) clustered apart, agreeing with results from previous studies (Aanderud et al. 2016). However, for cDNA, no differences were observed either in terms of treatment or time, implying that our rewetting experiment had no effect on the bacterial alpha diversity (i.e., did not trigger a response of the microbial community). Assuming, however, that the low number of cDNA valid samples may influence the results, we further assessed the effect of the interaction between treatment & time (Fig. S6), and potential environmental drivers on the composition of bulk communities (Fig. 4). Microbial communities were differentiated across time, and diversity was mainly regulated by water activity, conductivity, and temperature. Conductivity and water activity provide favorable conditions for water-soluble ions that can be used as electron acceptors in microbial respiration according to their oxidation-reduction potential (i.e.- O_2, NO_3^-, Fe^{2+}, SO_4^{2-}), resulting in changes in the dominant metabolic processes and the bacterial groups involved. The order Cyanobacteriales dominated the community both in the dry and the rewetted sediments, and were also the most abundant taxa in cDNA datasets. In calcareous streams of Mediterranean climates, cyanobacteria are able to develop a high resistance to environmental extremes through the formation of stromatolytic-like forms (Sabater, 2000). Cyanobacteria peaked at central day hours (T30; Fig. S6), coinciding with the highest CO_2 emissions. Although rewetting might have altered community composition, this response cannot be directly linked to CO_2 emissions, as cyanobacteria are generally associated with negative CO_2 fluxes due to photosynthetic CO_2 fixation. Under intense light conditions, the production of ROS might inhibit cyanobacterial growth (Welkine et al. 2018), which could explain higher CO2 emissions in their presence, but then, we would expect to see their influence also during night-time, which was not the case. Thus, our community analysis revealed an effect of rewetting on microbial community composition but did not explain the observed CO_2 flux pattern.

4.3. Potential processes driving CO_2 fluxes

The circadian cycle of CO_2 efflux and influx observed in long-term dried sediments likely represents the net outcome of two contrasting processes, biotic and abiotic in nature. Here, we assess the evidence supporting each mechanism and their relative contributions to the net flux direction. CO_2 effluxes are generally associated with respiration. Species composition differed significantly between treatments in our experiment, with higher diversity observed under rewetting conditions. The order *Thermoanaerobaculales*, which includes strictly anaerobic and thermophilic chemoorganotrophs (Losey et al., 2012), showed a strong positive association with CO_2 efflux in the Gallocanta

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sediments. This pattern suggests that CO_2 production may largely stem from organic matter fermentation occurring under high-temperature and anoxic microenvironments typical of gypsum-rich sediment pores (Casero et al. 2021).

Our Keeling plot analyses support biotic control of CO_2 efflux. The median $\delta^{13}C–CO_2$ value (–26.5‰) aligns with typical signatures of microbial respiration in soils (–25 to –27‰; Cerling et al., 1991; Kuzyakov, 2006). The absence of a respiration increase following rewetting may reflect the scarcity of reduced organic substrates after long-term desiccation. Extended photocatalytic degradation of surface organic matter likely transformed labile compounds into recalcitrant forms unavailable for microbial metabolism (Gomez-Gener et al., 2016). In contrast, CO_2 uptake in dry river sediments has been attributed to daytime photosynthetic activity continuing within opaque chambers (Koschorreck et al., 2022). However, this cannot explain our observations, as CO_2 uptake occurred during nighttime and no vegetation was present. Chemoautotrophic organisms may instead account for part of the CO_2 influx (Menéndez-Serra et al., 2019), particularly under conditions of elevated temperature and water activity (> 0.6). We identified several bacterial and archaeal taxa with the potential to fix CO_2 using inorganic reduced compounds as energy and electron sources. Among these, *Campylobacterota* (sulfur-oxidizing chemolithotrophs) and ammonia-oxidizing archaea are recognized CO_2 fixers; however, neither group showed a significant correlation with measured CO_2 fluxes. Members of the order *Campylobacterales* have previously been detected in inundated Gallocanta sediments (Menéndez-Serra et al., 2019), suggesting a possible role in coupling carbon and sulfur cycles through dark CO_2 fixation, using reduced sulfur species (e.g., sulfide) as energy and electron donors under microaerophilic conditions. Other phyla previously associated with dark carbon fixation, including *Desulfobacterota*, *Gemmatimonadota*, and *Nitrospirota* (Grüterich et al., 2024), were also detected but showed no apparent relationship with CO_2 fluxes or rewetting treatment (Fig. 4). Therefore, although a minor microbial contribution to CO_2 influx via photosynthetic or dark fixation cannot be ruled out, it appears to be of limited significance in Gallocanta long-term dry sediments.

Several abiotic mechanisms can contribute to the observed CO_2 influx in the long-term dry sediments of Gallocanta: 1) carbonate dissolution promoted by pH shifts (Parsons et al., 2004) that would consume CO_2 from the pore water; 2) temperature mediated changes in the solubility of CO_2 in the sediment pore water (Parsons et al., 2004; Soper et al., 2017), as observed in arid soils (Ma et al., 2013; Fa et al., 2016) and deserts (Wang et al., 2020); and 3) changes in sediment water content promoted by water vapor adsorption (Bekin et al., 2025) leading to changes in solubilized CO_2 (i.e., increased water content leads to influx of CO_2). Although we cannot differentiate between these processes in absence of pore water analysis, the results of our numerical experiment provide evidence that CO_2 influx is promoted by a relatively constant abiotic process. The median enrichment factor found during CO_2 influx situations was +3.5‰. This value suggests that the process behind CO_2 influx is fractionating towards ^{13}C, which would be very unlikely if the process was of biological origin (Preuß et al., 1989 Michener and Lajtha, 2007), such as dark CO_2 fixation (-10‰ to -40‰). Moreover, the observed median enrichment factor and its variability would be compatible with the fractionation occurring when gaseous CO_2 is solubilized in water containing carbonates (Myrttinen et al., 2012, Mook et al., 1974).

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Despite the lack of detailed information on the abiotic carbon processes in dry sediments, Light et al. (2019) observed a net CO_2 influx during the prolonged incubation of drying reservoir sediment samples due to the calcium carbonate weathering. Besides, there may be some additional geochemical processes in sediments, such as $CaMg(CO_3)_2$ dissolution [$CaMg(CO_3)_2 + 2CO_2 + 2H_2O \leftrightarrow Ca^{2+} + Mg^{2+} + 4HCO_3^-$] and albite-to-kaolinite transformations [$2NaAlSi_3O_8 + 2CO_2 + 3H_2O \leftrightarrow 2HCO_3^- + Al_2Si_2O_5(OH)_4 + 4SiO_2 + 2Na^+$] which should be considered as minor mechanisms on CO_2 uptake (Zilberbrand, 1999).

Based on our hypothesis, abiotic mechanisms would have a significant influence on total fluxes in situations where biotic processes are not dominant, which goes against common assumptions. Our study shows that fluxes are largely driven by abiotic mechanisms in early morning, afternoon, and night hours when the sediment temperature drops below 20 °C, as revealed by both Keeling plots and numerical analyses. This phenomenon has not yet been described in dry lake sediments, nor has the effect of daily variation of the environmental factors on long-term dry inland waters sediments' CO_2 fluxes. However, similar to our study, CO_2 fluxes attributed to abiotic factors have been reported in some land types with extreme soil environment conditions (arid, saline, and/or alkaline soils). Similarly, Wang et al. (2020) conducted a controlled experiment by sterilizing the soil samples to remove the biotic factors from the equation and then distinguished that CO_2 fluxes from saline and alkaline soils were related to abiotic mechanisms such as carbonate weathering and CO_2 dissolution. Biotic and abiotic fluxes occurred at almost the same magnitude but in opposite directions (influx and efflux), making the total daily net flux almost neutral (Wang et al. 2020). Similar to our results, they indicated that the abiotic CO_2 flux from the soil concealed the temperature-related biotic respiration and its daily variations in the arid alkaline soil.

In extreme environments, CO_2 exchange is influenced by abiotic factors that are controlled by the combined effects of temperature and soil water content. These abiotic factors interact with biological controls (Ball et al., 2009). In alkaline sediments, such as those studied in Gallocanta, the interaction between CO_2 and the carbonate system may be more pronounced than in other ecosystems. This interaction causes the long-term dry sediments of Gallocanta to alternate between two processes: CO_2 absorption (abiotic) and emission (biotic).

Conclusion

We conducted a field experiment to investigate the effect of rewetting on CO_2 fluxes in long-term dried sediments of Lake Gallocanta. Contrary to what was expected, rewetting of long-term dry lake sediments showed minimal impact on CO_2 fluxes, which instead exhibited a conspicuous diel pattern of efflux and influx. Water activity and its synergistic interaction with temperature played a key role in regulating the CO_2 fluxes. Our numerical experiment revealed two processes: i) a biotic respiration varying with the circadian cycle, and ii) an abiotic uptake process more constant throughout the day, resulting in periodically switching between a net emission and a net uptake. Many lakes around the world are drying (Wurtsbaugh et al., 2017; Yao et al., 2023), thus it is key to understand the idiosyncrasy of systems that dry as their role on CO2 emissions may be extremely contrasted, ranging from higher emissions than in inundated conditions to uptake as reported here. Our findings, not just contribute to a better understanding of CO_2

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flux dynamics in dry aquatic ecosystems, but highlight the relevance of measuring gross fluxes of CO2 that reveal biotic and abiotic processes governing net CO_2 fluxes in dry sediments in order to have a more accurate approach to sedimentary carbon fixation and losses.

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Appendix A

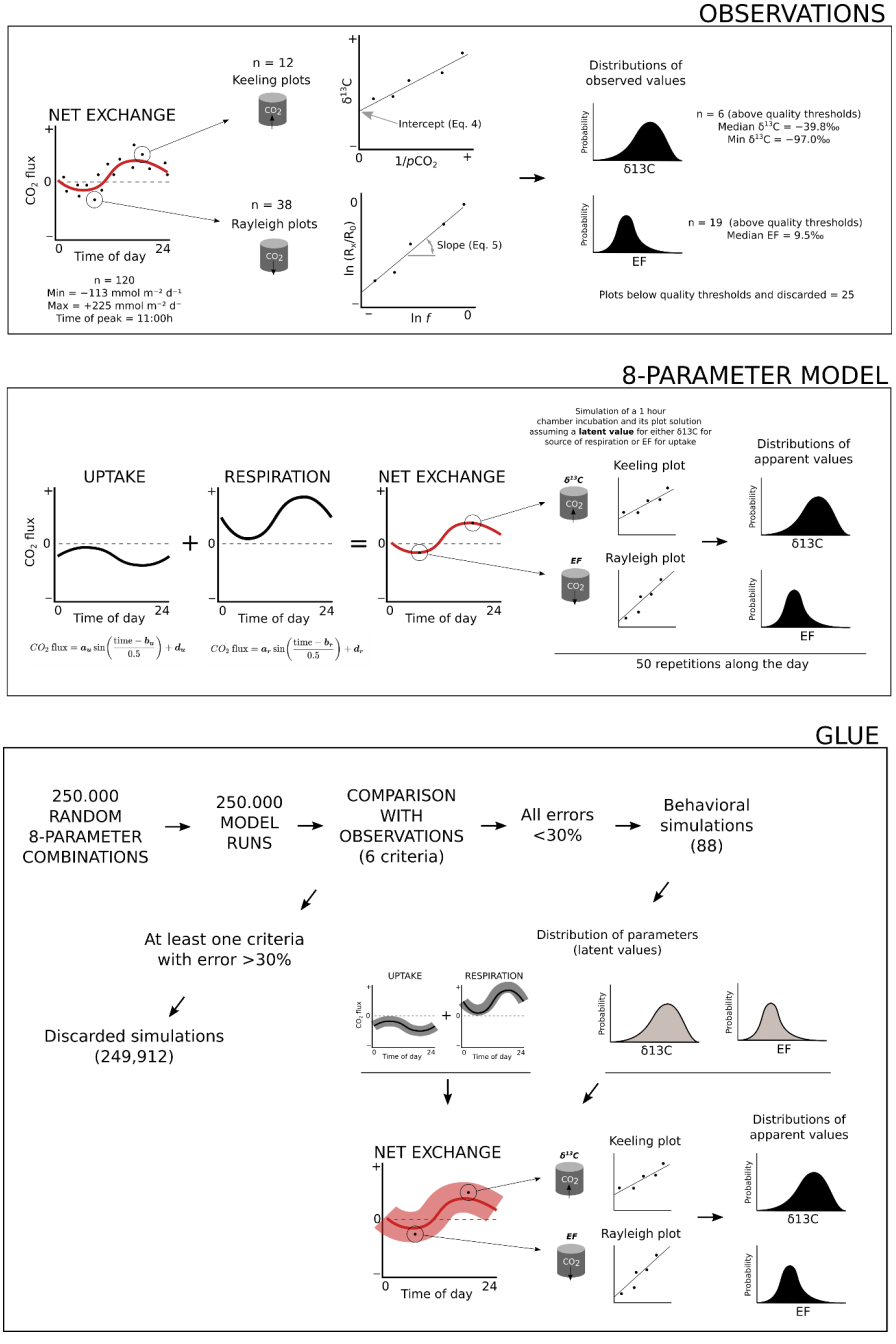

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Figure A1: Numerical simulation used to disentangle the contribution of respiration and an unidentified uptake process to net CO_2 exchanges and isotopic signatures. The model is based on our observations in the field, including net emissions and Keeling and Rayleigh plots (top box). We simulate those observations assuming two processes following a circadian cycle and a value for the isotopic signature of respiration and an enrichment factor of the uptake process (latent values). From this, we solve Keeling and Rayleigh plots as during sampling in the field (middle box). To identify values for the 8 parameters of the model that would deliver results comparable to observations, we applied the GLUE framework, to obtain a distribution of the 8 parameters (latent values) and a resulting ensemble of net CO_2 exchange and apparent isotopic signatures (bottom box).

Code and data availability

Data and full R code for this paper will be available in Zenodo. Raw sequence data were deposited in NCBI SRA under the project ID PRJNA1090308.

Author contributions

According to CRediT contributor roles taxonomy. Conceptualization: RM, DT, NC; Data curation: PEA, RM, NC; Formal Analysis: PEA, RM, OSS, CMB, NC; Investigation: RM, SP, BO, EMO, JJMP, TCO, MK, NC; Methodology: PEA, RM, DT, CMB, JP, NC; Project administration: RM, NC; Software: OSS, CMB, RM; Validation: PEA, RM, DT, NC; Visualization: PEA, RM, OSS, NC; Supervision: RM; Writing – Original draft: PEA, RM, DT, NC; Writing – reviewing and editing: all authors.

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