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Drought disrupts atmospheric carbon uptake in a Mediterranean saline lake

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Abstract: Saline inland lakes play a key role in the global carbon cycle, acting as dynamic zones for atmospheric carbon exchange and storage. Given the global decline of saline lakes and the expected increase of periods of drought in a climate change scenario, changes in their potential capacity to uptake or emit atmospheric carbon are expected. Here, we conducted continuous measurements of CO_2 and CH_4 fluxes at the ecosystem scale in a saline endorheic lake of the Mediterranean region over nearly 2 years. Our focus was on determining net CO_2 and CH_4 exchanges with the atmosphere under both dry and flooded conditions, using the eddy covariance (EC) method. We coupled greenhouse gas flux measurements with water storage and analyzed meteorological variables like air temperature and radiation, known to influence carbon fluxes in lakes. This extensive data integration enabled the projection of the net carbon flux over time, accounting for both dry and wet periods on an interannual scale. We found that the system acts as a significant carbon sink by atmospheric CO_2 uptake in wet conditions, with uptake ceasing in periods of drought. Moreover, increased air temperatures during wet phases slightly decrease the

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CO_2 uptake efficiency. Regarding CH_4, we measured uptake rates that exceeded those of well-aerated soils such as forest soils or grasslands. Additionally, we observed that CH_4 uptake during dry periods was nearly double that of wet periods. However, the absence of continuous data prevented us from correlating CH_4 uptake processes with potential environmental predictors. Our study challenges the widespread notion that wetlands are universally greenhouse gas emitters, highlighting the significant role that endorheic saline lakes can play as natural sink of atmospheric carbon. However, our work also underscores the vulnerability of these ecosystem services in the current climate change scenario, where drought episodes are expected to become more frequent and intense in the coming years.

Keywords: Intermittent saline lake, eddy covariance, greenhouse gas fluxes, ecosystem metabolism, Mediterranean shallow lake

1. Introduction

Saline inland lakes are diverse and play a crucial role in the global carbon cycle, serving as dynamic zones for carbon dioxide exchange with the atmosphere (Li et al. 2022; Liao et al. 2024) and long-term sinks of organic and inorganic carbon (Anderson and Stedmon 2007; Song et al. 2013; Li et al. 2017). In limnology, however, the ecological importance of these systems has only recently been recognized, despite they account for approximately 44% of global lake volume and 23% of lake surface area (Messager et al., 2016). Saline lakes vary in size from ephemeral ponds to extensive deep-water bodies, such as the Caspian Sea (Eugster and Hardie, 1978). These lakes are characterized by salinity levels that exceed 3 parts per thousand and are notably isolated from a direct marine influence (Williams, 2002; Wang et al., 2018). They are found in endorheic (hydrologically landlocked) basins across a wide array of climates, spanning cold to warm/hot arid regions in all continents, including Antarctica (Williams, 2002; Wang et al., 2018). As terminal points in many hydrological networks, they collect not only significant amounts of salts but also nutrients and organic and inorganic carbon (Anderson and Stedmon 2007; Song et al. 2013; Batanero et al. 2017; Li et al. 2017; Liao et al. 2024).

The first estimations about the role of saline lakes on global carbon fluxes suggested that these lakes might function as hotspots for the CO_2 emission (Duarte et al.,

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2008). However, more recent works point out that saline lakes have lower partial pressure of CO_2 (pCO2) than freshwater lakes (Wan et al. 2017) and some systems appear to uptake CO_2 during the winter (Li et al., 2022) or annually (Yang et al. 2021). Therefore, more seasonal studies on CO_2 fluxes in saline lakes are need it to understand the conditions when these systems behave as sink or sources of CO_2.Variations in CO_2 and CH_4 flux estimates across different studies of water bodies are primarily due to the highly variable data obtained from discrete sampling (Li et al. 2022) or because of differences in sampling seasons at the intra-annual scale (Liao et al. 2024). Meanwhile, gathering continuous time series data on CO_2 and CH_4 sequestration and emission fluxes over years is needed for accurate assessment of the net carbon balance in inland water systems (Martínez-García et al. 2024). Nevertheless, long-term, uninterrupted, and direct monitoring of greenhouse gas flux dynamics at the ecosystem level is relatively scarce in aquatic ecosystems, and this is particularly true for saline lakes. To the best of our knowledge, only a couple of studies have reported continuous year-round direct measurements at the ecosystem scale for CO_2 fluxes (Yang et al. 2021; Li et al. 2022). However, saline lakes' characteristics differ with latitude (Hammer 1986) and could have very different behaviors regarding carbon exchanges depending on climate conditions.

The carbon hydrochemistry in permanent saline lakes, especially in mountainous and Arctic latitudes such as the Tibetan Plateau or Svalbard is largely influenced by surface ice formation (Anderson et al., 2004; Rysgaard et al., 2012, 2013; Wu et al., 2014; Yan and Zheng, 2015). In contrast, saline lakes in arid and semi-arid endorheic basins, including Mediterranean climates, are typically shallow, often ephemeral, and/or hypersaline due to evaporation exceeding precipitation (García et al., 1997; Batanero et al. 2017; Saccò et al., 2021). The lower depths and higher surface-to-volume ratio, driven by drought conditions, induce significant physicochemical fluctuations in these saline inland water bodies, spanning from diurnal to interannual scales (Comin et al. 1990; García and Niell 1991; García et al. 1997; Batanero et al. 2017). Consequently, the precipitation regime and subsequent changes in groundwater levels determine the ecology of saline lakes in arid and semi-arid regions. However, research on the interannual variability of carbon fluxes in saline lakes affected by seasonal flooding and drought is lacking. This knowledge gap urgently requires focused research to elucidate the impacts of climatic variability on the carbon dynamics of these ecosystems, which have been identified as particularly vulnerable to climate fluctuations (Tweed et al., 2011). Furthermore, recent studies highlight a global decline in lake water storage in most

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endorheic basins and in the Sahara, Arabia, Southern Europe basin in particular (Wang et al. 2018), a situation expected to worsen with more severe droughts in a climate change scenario, leading to lower water levels and prolonged desiccation periods (Wurtsbaugh et al., 2017; Hassani et al., 2020).

In this study, we carried out continuous and interannual measurements of CO_2 and CH_4 fluxes at the ecosystem level in the saline lake Fuente de Piedra using the Eddy Covariance (EC) method. Serving as a model of a Mediterranean shallow saline lake, it is characterized by sporadic episodes of water retention but predominantly dry during the summer. The objectives of our work are a) to quantify carbon exchanges during the dry and the flooded conditions, determining its role as a carbon source or sink, b) to evaluate main drivers promoting carbon exchange behaviors, and finally c) to model the annual net carbon flux of the system as a function of its meteorological drivers. Our research aims to enhance our understanding of the carbon dynamics and the impacts of climate change on the net carbon balance in Mediterranean intermittent endorheic lakes.

2. Material and methods

Study Site

Fuente de Piedra is a shallow and saline lake located in an endorheic basin in the province of Málaga, Andalusia, Spain (37.11 N, -4.77 W, elevation 410 m: **Fig 1**). It spans approximately 17 km^2, measuring 6.8 km in length and 2.5 km in width, with a maximum depth of 1.5 meters. We take advantage of Fuente de Piedra Lake's inclusion in the Ramsar Convention in 1983. This designation ensures a rich history monitoring of water storage and the meteorological drivers discussed in this article. Such a comprehensive dataset allows for the back projection of the net carbon flux of the system over time, incorporating both dry and wet periods at an interannual scale. This lake is recognized as a vital habitat within a protected wetland at various levels—regional (as a natural reserve), European (designated as a special bird protection area), and international (acknowledged as a Ramsar site)—and offers an exemplary nesting ground for the pink flamingo (*Phoenicopterus roseus*), largely due to its shallow waters. Among primary producers, diatoms constitute the largest fraction of primary producers of the phytoplanktpn all through the year, being dominated by *Hantzschia amphioxys*, *Amphora coffeaiformis*, *Stauronensis amphioxys*, *Cocconeis placentula*, *Entomoneis* sp. and several species of *Navicula* and *Nitzchia* sp. (García and Niell, 1993).

Salinity levels in the lake vary significantly, ranging from oligosaline (5 ppt) to hypersaline conditions (> 200 ppt), influenced by the annual hydrological cycle (Batanero et al. 2017). This cycle is delineated into two distinct phases: a pooling phase during autumn and winter (December to March), and an evaporative and drought phase spanning spring and summer (April to November). The lake primarily receives water from groundwater inflow (Rodríguez- Rodríguez et al. 2006), complemented by contributions from two streams (**Fig. 1**) and surface runoff from surrounding farmlands. Notably, the stream entering from the northeast adds nutrients. However, sediment samples distributed across the lake and analyzed through combustion (Heiri et al., 2001) showed it to be homogeneous in organic carbon (0.21 ±0.069 mg C), nitrogen (0.015±0.004 mg N) and the C:N ratio (14.4± 2.26).

Field measurements of greenhouse gas fluxes and meteorological drivers.

We employed the eddy covariance method to quantify the exchanges of CO_2, CH_4, and energy (sensible and latent heat) every 30 min from August 2021 to May 2023. Thus, eddy covariance system was operated for more than 21 months, including two dry periods in summer. An open-path eddy covariance (EC) system was strategically positioned atop a tower, 3.1 meters above ground level, on the western bank of the lake (**Fig.1**). This setup included two open-path infrared gas analyzers: the LI7500 for CO_2 and water vapor, and the LI7700 for CH_4 (LICOR Inc., Lincoln, NE, USA). Wind vector components (u, v, w) and sonic temperature were accurately measured using a sonic anemometer (R.M. Young 81000V, Traverse City, MI, USA). Both instruments recorded the data at a frequency of 10Hz.

In addition to gas measurements, we measured a comprehensive suite of environmental and soil state variables every 10 seconds to capture the conditions over a representative ground surface area and collected every 30 min average by a data logger (CR1000, Campbell Scientific, Logan, UT, USA). A quantum sensor (LI190, Lincoln, NE, USA) was utilized to measure the vertical component of the incoming photosynthetic photon flux density (PPFD) at a height of 2.9 meters. Air temperature (T_a) and relative humidity (RH) were monitored using a thermohygrometer (HMP 45C, Campbell Scientific, Logan, UT, USA). Net radiation (R_n) was quantified by a net radiometer (NR Lite, Kipp and Zonen, Delft, Netherlands). Soil heat flow (G) calculations were facilitated by one heat flux plate (HFP01SC, Hukseflux, Delft, Netherlands) placed at 8 cm depth, complemented by three pairs of soil temperature probes (TCAV, Campbell Scientific,

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Logan, UT, USA) situated at depths of 4 cm and lateral distances of 3.20 m, 6.34 m, and 8.90 m from the tower.

The groundwater level (GWL) was monitored daily using a piezometer situated within a well in the salt flats, approximately 2 kilometres south of the EC tower and on the opposite side of the lake (37.1071° N, -4.7631° W). Furthermore, data on daily precipitation (PPT), air temperature, and incident solar radiation (spanning wavelengths from 350 to 1100 nm) were acquired from a meteorological station located adjacent to Fuente de Piedra Lake, in Sierra Yeguas (37.1383° N, -4.8358°; 467 m.a.s.l.). The tower setup and instruments were maintained (mainly cleaning lenses of the open path sensors) every two weeks.

Greenhouse gas flux data processing, quality control and partitioning

Half-hourly means (48 measurements per day), variances, and covariances of greenhouse gas fluxes, adhering to the principles of Reynolds decomposition, were calculated using the EddyPro® 7.0.7 software (Li-Cor), according to international standards and protocols (Sabbatini et al., 2018). The data processing protocol encompassed the following steps: (1) axis rotation for tilt correction using the double rotation method (Wilczak et al., 2001), (2) turbulent fluctuations were calculated using block averaging method, (3) time lag was compensated by covariance maximization with default, (4) Webb–Pearman–Leuning (WPL) correction of air density fluctuation (Webb et al., 1980), (5) despiking and raw data statistical screening (Vickers and Mahrt, 1997) and (6) spectral corrections of high- and low-pass filtering effects. Regarding the latter, high-frequency loss due to path averaging, signal attenuation and sensor separation was compensated according to Moncrieff et al., (1997), whereas low-frequency loss due to finite time averaging length and detrending was corrected according to Moncrieff et al., (2004). Quality check flags were calculated for flux data according to the widely adopted methodology combining two tests: steady state test and the developed turbulent conditions test. Over the study period, we only selected high-quality fluxes (flag value =0) measured when the open-path sensors were totally clean according to their respective AGC values (AGC value equal to 56 for Open path LI-7500A CO_2 /H_2O analyzer and AGC value equal to or higher than 20 for LI-7700.

To quantify the sampling area of flux measurements, a footprint model was estimated using the method by Kljun et al., (2004) (**Fig 1**). Data periods when the wind comes from terrestrial adjacent environment (251° to 59°) were rejected, representing

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between 45% and 70% of the available daytime and night-time data respectively during the dry season (GWL=0), and 30% of the available daytime and night-time data respectively during the wet seasons (GWL>0). Overall, for the nearly 2 years of measurements, 18% and 8% of the potential daytime data were of good quality for CO_2 and CH_4 fluxes respectively. Whereas for night-time the available data were reduced to 10 and 5% respectively. The energy balance closure (ratio of the sum of sensible and latent turbulent fluxes, H + LE, to the net radiation minus soil heat flux, $R_n - G$) was 76% ($R^2 = 0.64$; n = 3117).

Predicting greenhouse gas fluxes as responses to meteorological drivers

We examine the relationship of CO_2 and CH_4 fluxes in response to groundwater level, serving as a proxy for long-term water storage, with air temperature as the main factor regulating respiration in the system, and incident solar radiation modulating the photosynthetic rate. Since these variables were measured every 24-hour, we processed half-hourly CO_2 and CH_4 fluxes collected to construct 24-hour integrated values. We selected dates that contained over 50% of the anticipated data points, particularly those with more than 25 valid measurements distributed during the day, to calculate integrated daily flux. Selecting 26 and Y days for CO_2 and CH_4, respectively, well distributed throughout the measured period (both dry and wet periods). Before integrating daily flux values, we filled gaps in the half-hourly CO_2 and CH_4 flux data using linear interpolation for missing values. This selection criterion aimed to accurately represent the daily pattern in flux measurement distribution.

To analyze the relationship between integrated daily fluxes and their potential environmental predictors, we employed a linear regression combined with a forward model selection technique (Aho et al 2014). This method involved sequentially fitting a series of regression models, each incorporating different combinations of predictors and their interactions. The process began with simple models, each containing only one primary predictor, and gradually increased in complexity to include all possible interactions among predictors. We then used the Akaike Information Criterion (AIC) to evaluate and identify the most effective model from the set. The model with the lowest AIC was selected as the best fit, indicating it provides the most useful balance between model complexity and explanatory power. After selecting the model, we examined the influence of the predictors by analyzing the slope β coefficients at a significance level of

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alpha = 0.05, using a 95% confidence interval to determine if these coefficients were significantly different from zero.

Additionally, while ground water level (GWL) was measured daily, our model selection process also aimed to identify which daily measurements of air temperature and incident solar radiation (mean, minimum, or maximum) were the best predictors. This method ensured that the chosen model was robust and relevant to the ecological scales being studied. Detailed instructions on how to run these analyses are detailed in the R script available in DRYAD (see details in the *data accessibility statement* section).

3. Results

Time series of greenhouse gas emissions and meteorological drivers

At Fuente de Piedra Lake, we observed significant seasonal variations in meteorological conditions, as illustrated in **Fig 2A**. Air temperature (T_a) and incident solar radiation exhibited consistent trends throughout the study period, with mean daily values of 17 ± 7 °C for T_a and 18 ± 8 MJ m^{-2} d^{-1} for incident solar radiation. In contrast, these two environmental variables generally followed asynchronous patterns with groundwater level (GWL) and precipitation events (**Fig 2A** and **B**). Particularly during the summer months (July, August, September), the highest daily air temperature values coincided with GWLs beneath the surface and a lack of precipitation. Also, during the "dry" periods, a salt crust several centimeters thick developed on the sediment (see Figure 3B). For instance, the minimum T_a recorded was 2 °C in January 2023 corresponding with a period of frequent precipitation and GWL above the surface. Conversely, the maximum T_a of 34 °C occurred in August 2021, during a period when the GWL was 24 cm below the surface.

We observed a strong correspondence between water storage in Fuente de Piedra Lake and its capacity to assimilate atmospheric CO_2. The CO_2 flux patterns can be categorized into two distinct lake states: a flooded lake (groundwater level >0 cm, indicated from purple to blue colour in **Fig 2C and D**) and a dry lake (groundwater level <0 cm, shown from orange to yellow colour). During periods of flooding, the lake acted as a CO_2 sink, with fluxes ranging from 0 to -30 µmol m^{-2} s^{-1}. The CO_2 assimilation capacity increases with groundwater level and incident solar radiation, particularly from January to June. Notably, the flooded periods in the two years of the study showed marked differences in groundwater level. In 2022, we recorded the highest CO_2 uptake of 30 µmol m^{-2} s^{-1} in May, when the groundwater level was at its peak, 40 cm above the surface. The

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peak CO_2 uptake in 2023 was approximately half of what was observed in 2022. Although this peak occurred in March rather than May, it followed a similar trend to the ground water level (GWL), which was also about half of the peak level observed in 2022 (~20 cm above the surface). In contrast, under dry conditions, Fuente de Piedra Lake cesses the CO_2 uptake, occasionally transitioning to minor CO_2 emissions. Notice that during extreme rainfall pulses within dry periods, when Fuente de Piedra Lake remained relatively dry with the groundwater level below the surface, we observed notable net CO_2 emissions. For example, a heavy rainfall event in September 2021 (36 mm day^{-1}) resulted in CO_2 emissions reaching up to 10 µmol m^{-2} s^{-1}, with a high elevation of the groundwater level above the surface (from -20 to near 20 cm). Also, in October of both 2021 and 2022, subsequent rainfall events (12 mm day^{-1} and 22 mm day^{-1}, respectively) corresponded with CO_2 emissions of 7 µmol m^{-2} s^{-1} and 5.5 µmol m^{-2} s^{-1}, respectively. In these cases, emissions occurred under negative GWL conditions.

In the case of CH_4, flux was relatively stable throughout the whole study period, generally acting as a sink, with values fluctuating between -0.2 and 0.1 µmol m^{-2} s^{-1} (**Fig 2D**). Furthermore, no clear relationship was observed between CH_4 fluxes, and the meteorological variables examined.

Fluxes of CO_2 and CH_4 at a daily scale

When examining the daily scale during wet periods, it becomes evident that CO_2 assimilation predominantly takes place during daylight hours, specifically between 9 am and 2 pm (local time) (**Fig. 3**). It should be noted that the few emission values observed within this time frame correspond to the emission occurrences described earlier for the dry season, which promptly followed rainfall events. In the case of the dry period, it is noteworthy that a salt crust forms over the lake, leading to a near cessation of CO_2 fluxes. In the case of CH_4, there is also a discernible increase in assimilation fluxes between 9 am and 2 pm. This observed pattern is consistent in both wet and dry conditions.

Model predictions of 24-hour integrated flux values in the study system

A clear pattern in CH_4 flux was not detected during the study period. Likewise, no clear relationship with the environmental predictors studied could be identified. Additionally, measurements obtained from the EC tower resulted in a substantial number of gaps in the CH_4 time series, making it impossible to establish a predictive model for these fluxes. On

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the contrary, we were able to adjust a robust regression model for CO_2 integrated daily flux. A total of 26 daily integrated CO_2 flux values were obtained for the sampling period, analyzing those dates when more than 25 valid measurements were available. After AIC model selection routine, the candidate predictive model for daily integrated CO_2 flux was determined to include groundwater level, maximum daily air temperature, and mean incident solar radiation. Additionally, the model incorporated interactions between groundwater level and maximum daily air temperature, as well as between groundwater level and incident solar radiation (Summary Table of the model is available in the Supplementary Material). Indeed, fitted statistical capacity of the model has a relatively high explanatory capability (Adjusted R^2 =0.72).

The model confirmed a positive effect of groundwater level on enhancing CO_2 assimilation in the system (**Fig 4A**; β_{GWL} = -0.115, 95% CI = -0.214 to -0.016; note that assimilation corresponds with negative values of the CO_2 flux). While the isolated impact of air temperature increase on CO_2 assimilation could not be determined (β_{Ta} = +0.07, 95%CI = -0.053 to +0.192), the model identified an antagonistic interaction between air temperature and groundwater level ($\beta_{GWL\times Ta}$ = +0.010, 95%CI = +0.005 to +0.015). As air temperature increases, the positive effect of GWL on CO_2 asimilation diminishes (**Fig 4B**). Conversely, mean daily incident solar radiation was found to promote CO_2 assimilation (β_{Rad} = -0.12, 95%CI = -0.21 to -0.03), with a pronounced synergy between mean daily incident solar radiation and the presence of water ($\beta_{GWL\times Rad}$ = 95%CI = -0.0116 to -0.003), notably enhancing the capacity for CO_2 assimilation (**Fig 4C**).

Using time series data for groundwater level, daily maximum air temperature, and mean daily incident solar radiation at Fuente de Piedra Lake, we generated retrospective predictions of CO_2 assimilation capacity in the system dating back to 2001 (**Fig 4D**). The model predictions closely aligned with the observed values for the study period when using the time series data for the predictors, supporting the robust predictive ability of our model (Suplementary Material; **Fig S1**). Our estimates indicate a pronounced fluctuation in CO_2 assimilation capacity according to hydrological variations. In years with higher groundwater level and prolonged water storage the model predicted an exceptionally high capacity for atmospheric CO_2 assimilation of the lake, with annual values surpassing 0.7 Kg C m^2 $year^{-1}$ (e.g., in 2011, 2012, 2014, 2020). In contrast, during years marked by extended droughts, a substantial reduction in CO_2 assimilation capacity was modeled. These drought periods, characterized by dry conditions, resulted in a reduction of the

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assimilation capacity to less than a third of the levels recorded in wet years (e.g., from 2006 to 2010).

4. Discussion

In agreement with previous research in permanent saline lakes of the Tibetan plateau (Li et al. 2022), we show that a model Mediterranean shallow saline lake acts as a significant carbon sink through the uptake of atmospheric CO_2 when flooded. Conversely, CO_2 assimilation ceases during dry periods. Longitudinal time series analysis reveals that prolonged droughts indeed hinder the ability of the system to assimilate atmospheric CO_2 due to the lack of water, but we also observed that an increase in air temperature during wet periods moderates the CO_2 net assimilation capacity, a process likely related to the reduction of gas water solubility with temperature. This underscores the pronounced impact of seasonal and interannual variability, ultimately dictated by drought and rainfall patterns, on the ability of the studied system to sequester atmospheric carbon. Moreover, this pattern also displayed considerable variability at the daily scale, closely correlating with fluctuations in incident solar radiation over daily cycles. In this regard, the CO_2 assimilation capacity of the system peaked during those hours of maximum incident solar radiation. While measurement of CO_2 (and CH_4) fluxes at multiple scales is challenging and requires specialized equipment (i.e. eddy covariance sensors), our research proposes an alternative proxy. By integrating data from environmental predictors at various scales, we have achieved highly accurate predictions of CO_2 exchanges between Fuente de Piedra Lake and the atmosphere. In essence, we estimate CO_2 flux through the continuous measuring of accessible environmental variables, namely, the amount of water, air temperature, and incident solar radiation.

In shallow, well-mixed, and oxygenated systems like Fuente de Piedra Lake, the photosynthetic capacity of the phytoplankton community is closely linked to the water column height (i.e. groundwater level) (Batanero et al. 2017), promoting CO_2 assimilation as the extent of the habitat for these communities expands (Wetzel, 2001). Related to the aforementioned, a significant synergy exists between water storagein the ecosystem and incident radiation, serving as a proxy for the photosynthetically active radiation upon which photosynthesis depends. This interaction occurs on both a daily scale, associated with variations in light intensity following day-night cycles, and an annual seasonal scale, largely determined by changes in daylight hours throughout the year. Notably, during the

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night, the net exchange of CO_2 between the water and the atmosphere in Fuente de Piedra Lake is negligible. This could be attributed to the absence of photosynthesis during nighttime. Additionally, the high salinity inherent to these environments constrains methanogenesis, which is the least energy-efficient carbon mineralization process in the redox sequence (reviewed in Soued et al., 2024). Considering the above, it appears to offer a plausible explanation for why microbial respiration does not surpass inorganic carbon assimilation through photosynthesis in systems like Fuente de Piedra Lake during wet periods, despite the high content of dissolved organic carbon (Batanero et al., 2017).

What is more, despite the lack of CH_4 flux data, our results position Fuente de Piedra lake as a CH_4 sink. Vast approximation estimates determined that Fuente de Piedra could uptake on average 1.83 mg C m^{-2} day^{-1} and 3.70 mg C m^{-2} day^{-1} during the wet and the dry period respectively (Suplementary Material; **Fig S2**). Such values are even higher than those measured in typical well aerated soils such us soil forest or grasslands, with average rates of 0.4-1.26 mg C m^{-2} day^{-1} (Murguia-Flores et al., 2021; Perez-Quezada et al., 2021). The double value of uptake during the dry periods compared to the wet ones appear to be consistent with some proposed mechanisms promoting CH_4 reductionaccording to the existing literature, since the increase of temperature together with gas diffusivity due to loss of water, may increase methane oxydation in a similar way to terrestrial ecosystems (Chen et al., 2010; Rafalska et al 2023). However, caution is needed when interpreting our results, as the dynamics of methane fluxes could become very complex in an intermittent system like Fuente de Piedra. On the one hand, just as methanogenic activity is inhibited by salinity (Herbert et al., 2015), methanotrophic activity has also been observed to be significantly reduced by salinity in terrestrial systems (Ho et al., 2018). However, methane oxydation processes associated with aquatic prokaryotes may be more resistant to salinity (Khmelenina et al., 2010; Deng et al. 2017), especially if the variation is gradual (Osudar et al., 2017). Thus, further measurements and analysis are needed to estimate the role of methane oxydation and the relevance of saline intermitent lakes as CH_4 sinks in a climate change scenario.

Drought periods are accompanied by an increase in air temperature, with the high air temperatures recorded immediately before the system completely dries out. We have found that this rise in air temperature leads to a reduction of the system's capacity to assimilate CO_2, even during wet conditions. A direct consequence of climatic warming is the reduction of gas solubility accentuated in saline wetlands (Batanero et al. 2022) . In addition, increase in temperature can enhance microbial metabolic rates and therefore, biomass-specific CO_2 production (Smith et al. 2019). Given that endorheic saline lakes are fueled by significant amounts of organic matter (Li et al., 2017; Batanero et al., 2017; Song et al., 2013), it is unsurprising that warming leads to a decrease in net primary production in the system as a result of enhanced microbial respiration, and consequently, a reduction in CO_2 assimilation capacity. In addition, carbon emissions in inland waters could increase with warming, independently of organic carbon inputs, simply because the apparent activation energy is predicted to be higher for respiration than photosynthesis (Yvon-Durocher et al. 2010; Yvon-Durocher et al. 2012). Finally, it has been recognized that photosynthesis is often the first process to be affected by environmental stressors, with photosynthetic capacity diminishing prior to other cellular functions (Feller, 2016; Cardona et al., 2018). Specifically, carbon assimilation through the Calvin–Benson cycle exhibits particular vulnerability to both drought and elevated temperatures, occurring even when photosynthetic electron transport continues to operate effectively (Sharkey, 2005). On the whole, we show the profound synergy between global warming and intensifying drought severity and frequency, disrupting the CO_2 assimilation capacity of Mediterranean saline lakes and leading to negative feedback loops.

5. Conclusion

While the desiccation of saline lakes is not novel, with researchers highlighting the concerning increase in dry periods within many of these ecosystems over recent decades (Williams 1993; Gross 2017; Wurtsbaugh et al. 2017; Wang et al. 2018), our study underscores the significant implications this has for the ecosystem services they support. Our retrospective predictions show that in wet years, the system could exhibit a high CO_2 assimilation rate. For instance, between 2010 and 2015, we estimated that Fuente de Piedra Lake had an average assimilation rate of 0.83 (SD = ±0.27) kg C m^{-2} year $^{-1}$, comparable to the net assimilation observed in evergreen or deciduous forest systems (Pastorello et al., 2020). This result challenges the generalised belief that inland waters primarily act as sources of greenhouse gases (Raymond et al. 2013). Conversely, the system undergoes significant reductions in its annual atmospheric CO_2 sequestration capacity during dry periods. For instance, under severe drought conditions as observed in Fuente de Piedra from 2005 to 2009, the annual CO_2 sequestration is estimated to have fallen to less than a quarter of what was observed in more humid periods. Climate change projections, including even the most optimistic scenarios, forecast an increase in both the frequency and duration of heatwaves and droughts in the coming years (Trenberth 2011, Perkins-Kirkpatrick 2020). This implies that saline lake ecosystems in arid and semi-arid endorheic basins will remain dry for longer periods, or may even vanish, resulting in the loss of a significant carbon sequestration pathway. Importantly, the disappearance of saline lakes due to water scarcity has been largely attributed to anthropogenic water overuse (i.e., agriculture) rather than to macroclimatic phenomena (Wurtsbaugh et al. 2017). This seems to be the case of Fuente de Piedra Lake, as the catchment area is dominated by agricultural land. Thus, a proper water management during drought periods seems to be the most plausible solution to preserve the ecosystem services provided by Mediterranean saline lakes.

Author contribution

PS-O and IR conceived the study; all authors contributed to the installation and maintenance of the eddy covariance tower; IA led the fieldwork and the processing of the samples with the help of the rest of the authors; IP-M carried out the analyses and the preparation of the results; IA, IP-M, and PS-O conducted the preparation of the first draft of the work; all authors participated in the drafting of the final draft.

Data accessibility statement

The R script used to conduct the data analysis and the datasets are available at the Dryad Digital Repository: https://datadryad.org/stash/share/qEpPRJopVR132UszL3bnaxoZh07ADL0E5LpVL6xCSZA

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Competing interests

The authors declare that they have no conflict of interest.

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FIGURES

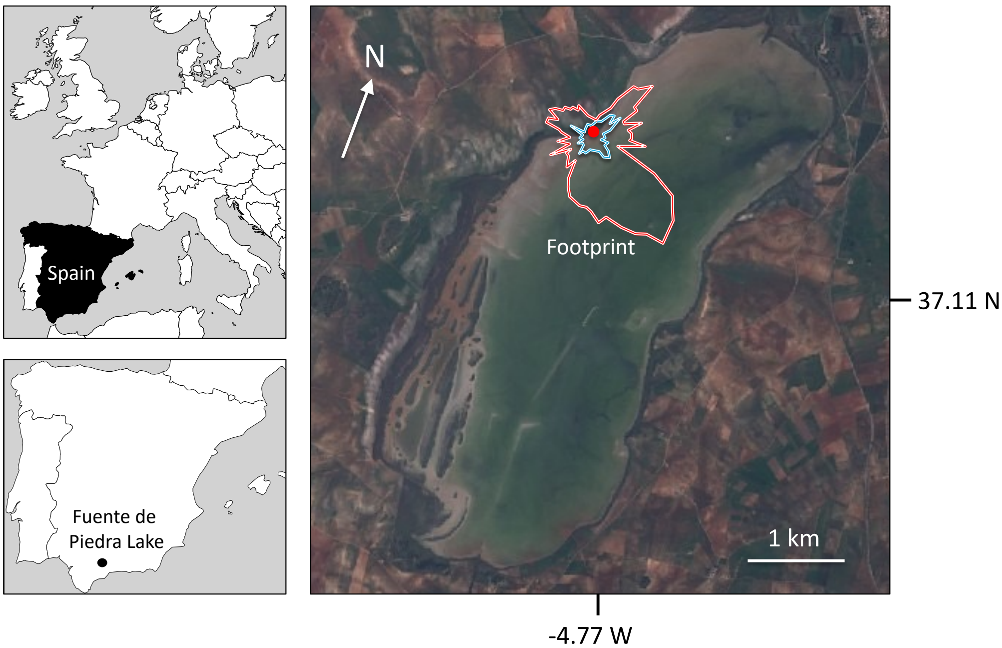

Fig 1. Location of the Fuente de Piedra Lake (province of Málaga, South of Spain). Dot inside polygon in right panel shows the location of the eddy covariance tower. The areas within the footprint contributing the 90% to measured fluxes are delimited inside polygons for daytime (blue) and nighttime (red).

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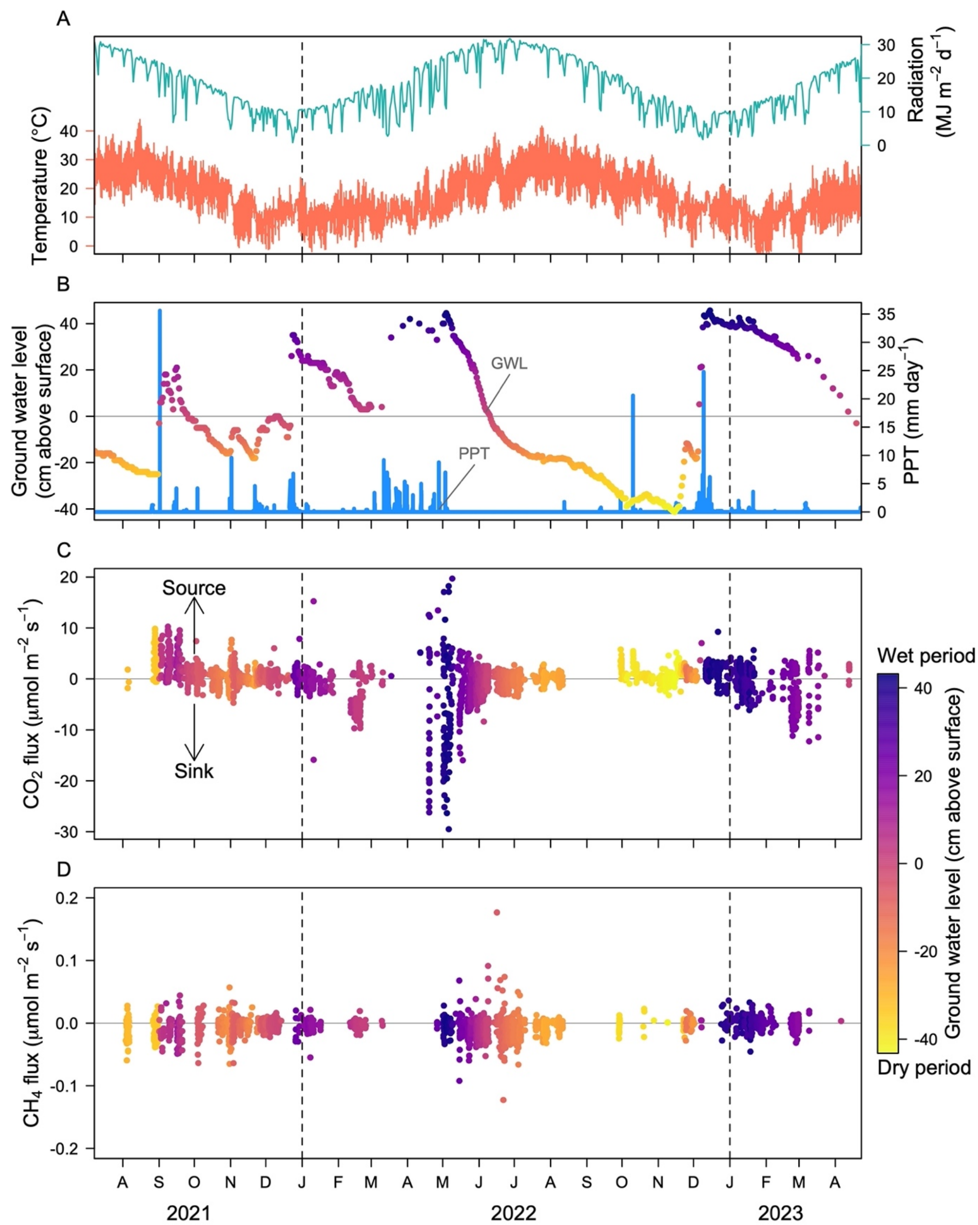

Fig 2. Time series of (A) air temperature and incident solar radiation, (B) groundwater level and precipitation (PPT), (C) CO_2 and (D) CH_4 flux, collected at Fuente de Piedra Lake during 2021, 2022, and 2023.

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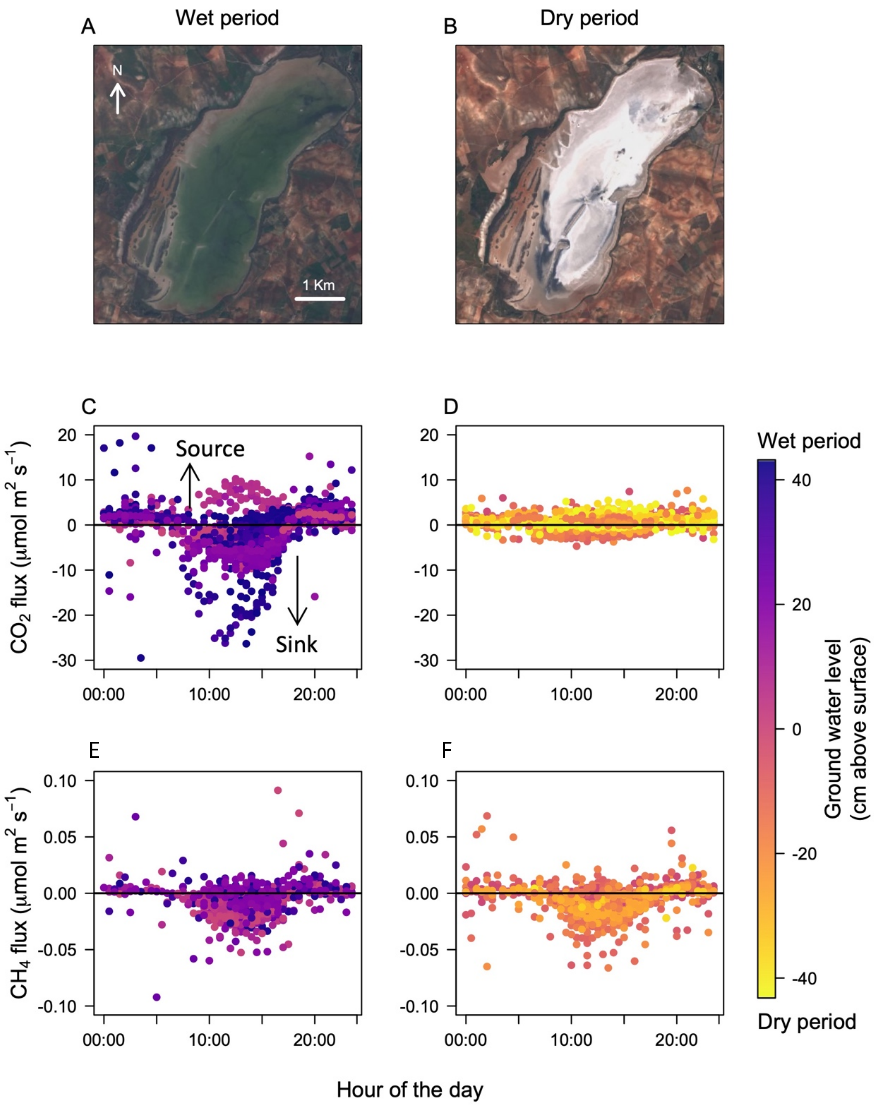

Fig 3. Aerial photos of Fuente de Piedra Lake during a period of maximum water availability (wet period, **A**) and during a typical dry episode (**B**). Note that for some period during the dry episodes, a salt crust forms covering practically the entire extent of the lake. The figure shows the daily pattern of CO_2 and CH_4 fluxes during the wet period (**C** and **E** respectively) and the dry period (**D** and **F** respectively). Water availability is measured in terms of groundwater level.

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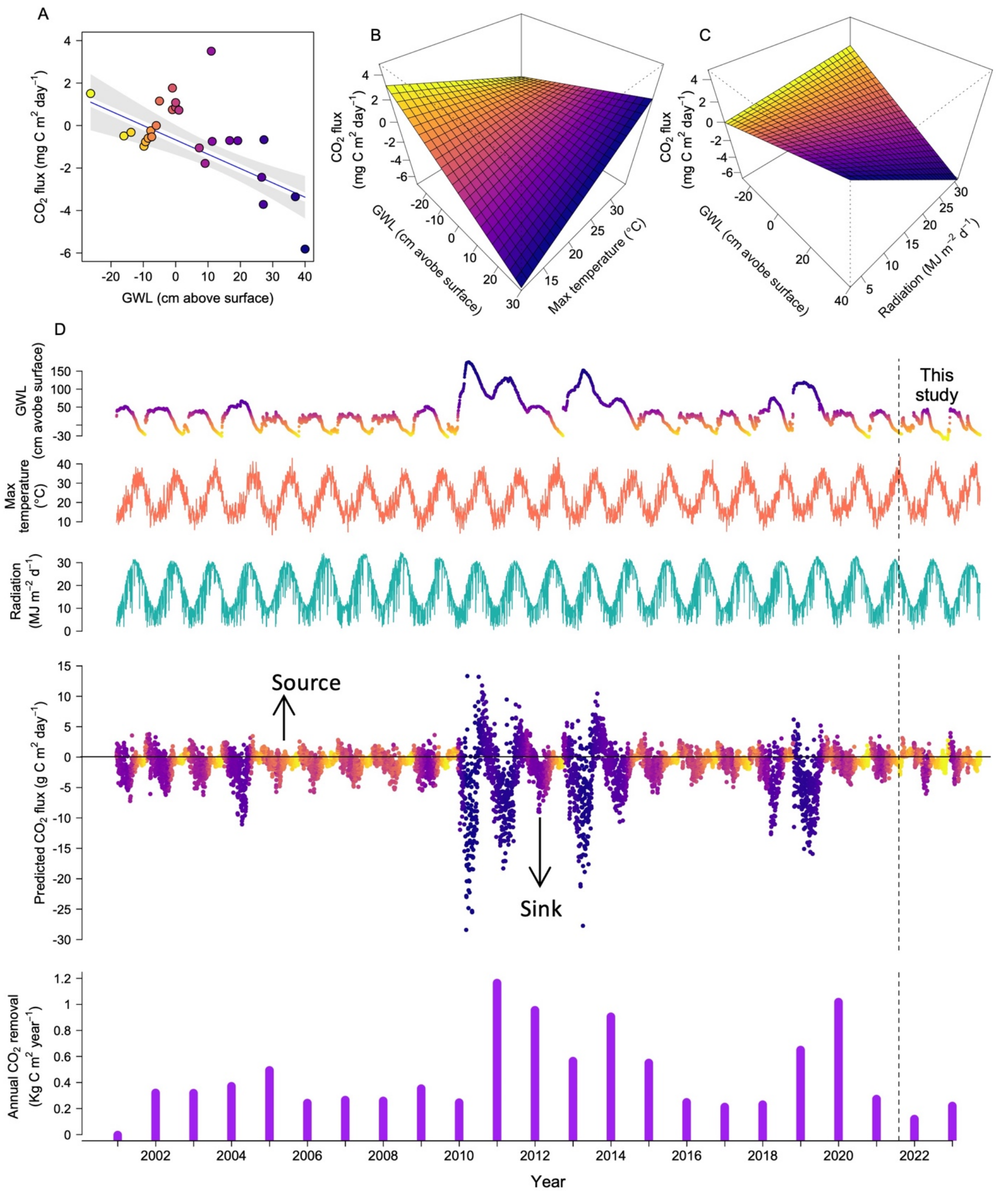

Fig 4. Prediction of CO_2 flux as a response to groundwater level (**A**), the interaction between groundwater level and daily maximum temperature (**B**), and the interaction between groundwater level and incident solar radiation (**C**). Using existing time series for the model predictors, it has been possible to reconstruct the estimated CO_2 fluxes, as well as the annual cumulative value of CO_2 removal since 2001 for Fuente de Piedra Lake (**D**).