Drought conditions disrupt 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 conditions on an interannual scale. We found that the system acts as a substantial carbon sink by absorbing atmospheric CO_2 under wet conditions. In years with prolonged water storage, it is predicted that the lake's CO_2 assimilation capacity can

surpass -0.7 kg C m² annually. Conversely, during extended drought years, a reduction in CO_2 uptake capacity of more than 80% is expected. Regarding CH_4, we measured uptake rates that exceeded those of well-aerated soils such as forest soils or grasslands, reaching values of -0.2 μmol m^{-2} s^{-1}. Additionally, we observed that CH_4 uptake during dry conditions was nearly double that of wet conditions. 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 accounting 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).

Past 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., 2008).

However, more recent works point out that saline lakes have lower partial pressure of CO_2 than freshwater lakes (Wen et al. 2017) and some systems appear to take up CO_2 during the winter (Li et al., 2022) or even annually (Yang et al. 2021) due to physicochemical reactions and increased activity of primary producers. Therefore, more seasonal studies on CO_2 fluxes in saline lakes are needed to understand the conditions when these systems behave as sinks 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 endorheic basins and in the Sahara, Arabia, and 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 Spain's 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. It is worth noting that Fuente de Piedra Lake was designated as a Ramsar site in 1983, ensuring a rich history of monitoring water storage and the various meteorological drivers of CO_2 and CH_4 fluxes. 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 use available records of the time series for the main drivers of fluxes to model the annual net carbon flux of the system in the past. 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 conditions 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 phytoplankton 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 ±0.07 mg C), nitrogen (0.015±0.004 mg N) and the C:N ratio (14.4± 2.3).

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, the 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). These data were recorded on a data logger (CR1000, Campbell Scientific, Logan, UT, USA) 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). 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 flux (G) calculations, including the

energy stored in the soil, 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, 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; Fig S1). The location of the piezometer coincides with the central and deepest part of the lake when there is water. Negative GWL values indicate conditions when the lake is entirely lacking surface water. Positive values measured by the piezometer were used to determine the lake depth. 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 Automatic Gain Control (AGC)

values (AGC value equal to or above 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 came from the terrestrial adjacent environment (251° to 59°) were rejected, representing 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. For night-time, the available data were reduced to 10 and 5% respectively. In order to provide additional information regarding the turbulent flux quality (Moncrieff et al 1997), we calculated the energy balance closure (ratio of the sum of sensible and latent turbulent fluxes, H + LE, to the net radiation minus soil heat flux, $R_n - G$) using all the available data during the drought period. The obtained value. was 76% ($R^2 = 0.64$; n = 3117) and is within the range of most the reported FLUXNET sites (Wilson et al 2022; Stoy et al., 2013)

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- hours, we processed half-hourly CO_2 and CH_4 fluxes collected to construct 24-hour integrated values. It is important to note that gaps in long-term data records are inevitable when using eddy covariance, primarily due to instrument failure and insufficient turbulence (Falge et al., 2001; Baldocchi et al., 2003; Aubinet et al., 2012). Additionally, data coverage is often reduced when wind originates from undesirable sectors, though this does not necessarily compromise measurement quality (Goloub et al., 2023). Despite these limitations, most studies derive their primary results from annual or seasonal CO_2 and CH_4 balances using various gap-filling procedures. In contrast, we exercise greater caution with our limited data coverage, being very restrictive in quantifying daily fluxes. We selected dates with over 50% of the anticipated data points, particularly those with more than 25 valid measurements well-distributed throughout the day, to calculate integrated daily flux. 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. Then, a trapezoidal integration of the values measured every 30 minutes was performed to calculate the daily flux.

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 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 is robust and relevant to the ecological scales being studied.

Finally, the chosen candidate model for predicting the fluxes in the system was fitted using available records for the studied drivers, covering the period from 2001 to the present at Fuente de Piedra Lake. This approach aimed to retrospectively model the fluxes in the system. Detailed instructions on how to run these analyses are 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, except for a brief peak in precipitation and an increase in GWL between August and September 2021 (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 dry conditions, 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.

After the study period, we were able to collect 4,128 measurements for CO_2 fluxes and 2,425 measurements for CH_4 fluxes, which were relatively well-distributed over the study period. 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 flooding conditions, 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 conditions 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} and an averaged value of -3.11 μmol m^{-2} s^{-1} during May, when the groundwater level was at its peak, 40 cm above the surface. This period was also characterized by high variability in CO_2 flux, occasionally showing peaks of CO_2 outgassing approaching 20 μmol m^{-2} s^{-1}. The 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) resulting in averaged CO_2 uptake values of -3.66 μmol m^{-2} s^{-1}. In contrast, under dry conditions, Fuente de Piedra Lake ceases CO_2 uptake, occasionally transitioning to minor CO_2 emissions. Notice that during extreme rainfall pulses within dry conditions, 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, the 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} and an average of -0.05 μmol m^{-2} s^{-1} for the study period (**Fig 2D**). Furthermore, the measured CH_4 fluxes did not seem to align clearly with the meteorological variables examined (**Fig S1**).

Fluxes of CO_2 and CH_4 at a daily scale

When examining the daily scale during wet conditions, it becomes evident that CO_2 assimilation predominantly takes place during daylight hours, specifically between 9 a.m. and 2 p.m. (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 dry condition, 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 a.m. and 2 p.m. This observed pattern is consistent in both wet and dry conditions.

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

No evident relationship between CH_4 flux and the environmental predictors studied was found during the study period. 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 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, the fitted statistical model has a relatively high explanatory capability (Adjusted R^2 =0.73).

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 (Supplementary Material; **Fig S2**). 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, with predicted reductions exceeding 80% compared to wetter years (Fig. 4D). These drought periods, resulted in a reduction of the 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 on permanent saline lakes of the Tibetan plateau (Li et al. 2022), we demonstrate that a model Mediterranean shallow saline lake serves as a substantial carbon sink, absorbing atmospheric CO_2 when flooded. In particularly wet years, expected uptake values can exceed -1.2 kg C m^{-2} $year^{-1}$. Sporadic instances were

368 also observed where the system acted as a CO_2 emitter, resulting from rewetting events
369 that followed rainfall during dry conditions. Conversely, CO_2 uptake ceases during dry
370 conditions, reducing the system's capacity in dry years to below -0.2 kg C m^{-2} $year^{-1}$.
371 Longitudinal time series analysis reveals that prolonged droughts indeed hinder the ability
372 of the system to assimilate atmospheric CO_2 due to the lack of water, but we also observed
373 that an increase in air temperature during wet conditions moderates the CO_2 net
374 assimilation capacity, a process likely related to the reduction of gas water solubility with
375 temperature. This underscores the pronounced impact of seasonal and interannual
376 variability, ultimately dictated by drought and rainfall patterns, on the ability of the
377 studied system to sequester atmospheric carbon. Moreover, this pattern also displayed
378 considerable variability at the daily scale, closely correlating with fluctuations in incident
379 solar radiation over daily cycles. In this regard, the CO_2 assimilation capacity of the
380 system peaked during those hours of maximum incident solar radiation. While
381 measurement of CO_2 (and CH_4) fluxes at multiple scales is challenging and requires
382 specialized equipment (i.e. eddy covariance sensors), our research proposes an alternative
383 proxy. By integrating data from environmental predictors at various scales we have been
384 able to reconstruct the behavior of CO_2 exchanges between Fuente de Piedra Lake and
385 the atmosphere. In essence, we estimate CO_2 flux through the continuous measuring of
386 accessible environmental variables, namely, the amount of water, air temperature, and
387 incident solar radiation.
388 In shallow, well-mixed, and oxygenated systems like Fuente de Piedra Lake, the
389 photosynthetic capacity of the phytoplankton community is closely linked to the water
390 column height (i.e. groundwater level; Batanero et al. 2017), promoting CO_2 assimilation
391 as the extent of the habitat for these communities expands (Wetzel, 2001). Related to the
392 aforementioned, a significant synergy exists between water storage in the ecosystem and
393 incident radiation, serving as a proxy for the photosynthetically active radiation upon
394 which photosynthesis depends. This interaction occurs on both a daily scale, associated
395 with variations in light intensity following day-night cycles, and an annual seasonal scale,
396 largely determined by changes in daylight hours throughout the year. Notably, during the
397 night, the net exchange of CO_2 between the water and the atmosphere in Fuente de Piedra
398 Lake is negligible. This could be attributed to the absence of photosynthesis during
399 nighttime. Additionally, the high salinity inherent to these environments constrains
400 methanogenesis, which is the least energy-efficient carbon mineralization process in the
401 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 conditions, despite the high content of dissolved organic carbon ranging between 1.00 and 13.59 mmol C L^{-1} (Batanero et al., 2017).

What is more, despite the limited CH_4 flux data, our results position Fuente de Piedra Lake as a CH_4 sink. Rough estimates determined that Fuente de Piedra could take up on average 1.83 mg C m^{-2} day^{-1} and 3.70 mg C m^{-2} day^{-1} during wet and the dry conditions respectively (Supplementary Material; **Fig S3**). Such values are even higher than those measured in typical well aerated soils as in forests 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). Twice the value of uptake during dry conditions compared to wet ones appear to be consistent with some proposed mechanisms promoting CH_4 reduction according 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 conditions 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, an 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.

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 trend 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} $year^{-1}$, within the same range as the net assimilation observed in evergreen or deciduous forest systems worldwide (Pastorello et al., 2020) and marine salt marshes (Mayen et al. 2024). Considering the 13.6 km^2 area of Fuente de Piedra and assuming a constant flux across the lake surface when flooded, we could estimate around 11 tons of carbon sequestered during a wet and fully flooded year. Although this upscaling exercise is crude, it highlights that Mediterranean shallow saline lakes could be a substantial carbon sink and underline the potential keeping them inundated with water during their conservation policies. Therefore, further studies across different Mediterranean shallow saline lakes are necessary to refine these estimates and enhance our understanding of their role in the global scale carbon budget.

5. Conclusion

Our 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 conditions. 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 conditions. 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 system management during drought conditions 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

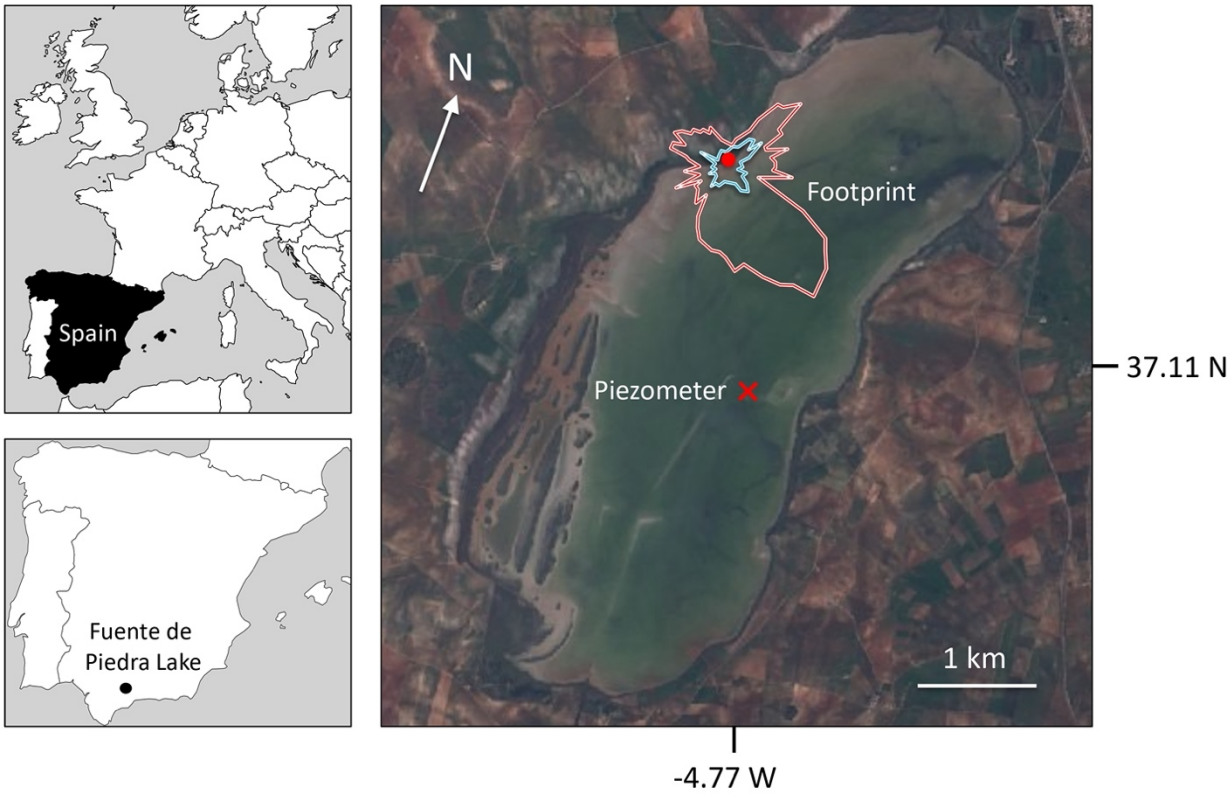

Fig 1. Location of the Fuente de Piedra Lake (province of Málaga, South of Spain). Dot inside polygon in right panel shows the location of the eddy covariance tower. The areas within the footprint contributing the 90% to measured fluxes are delimited inside polygons for daytime (blue) and nighttime (red). The cross indicates the location of the piezometer used for measuring groundwater level. Source image: Sentinel-2. Wet image was taken on 17-02-2021.

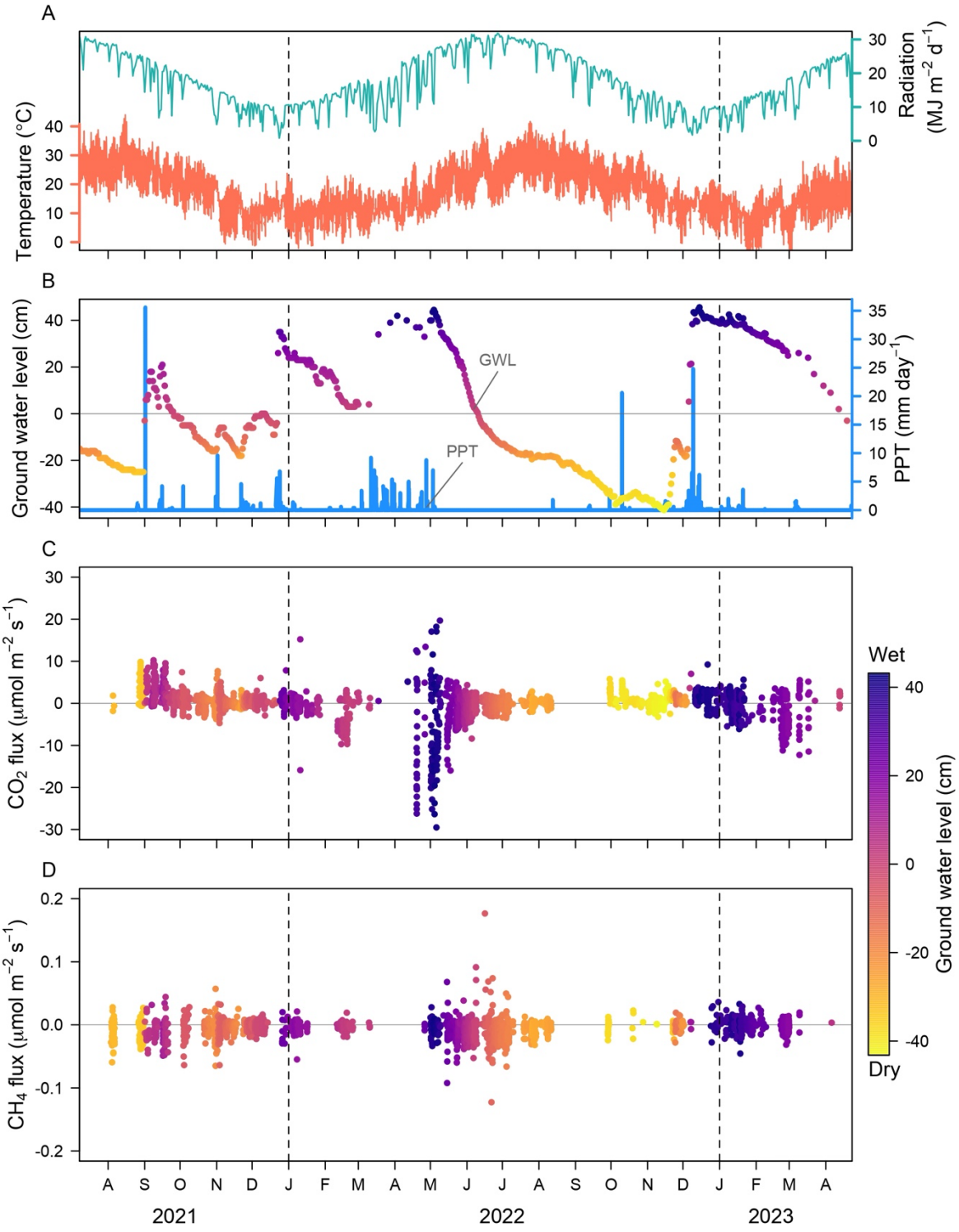

Fig 2. Time series of (A) air temperature and incident solar radiation, (B) groundwater level and precipitation (PPT), (C) CO_2 and (D) CH_4 flux, collected at Fuente de Piedra Lake during 2021, 2022, and 2023.

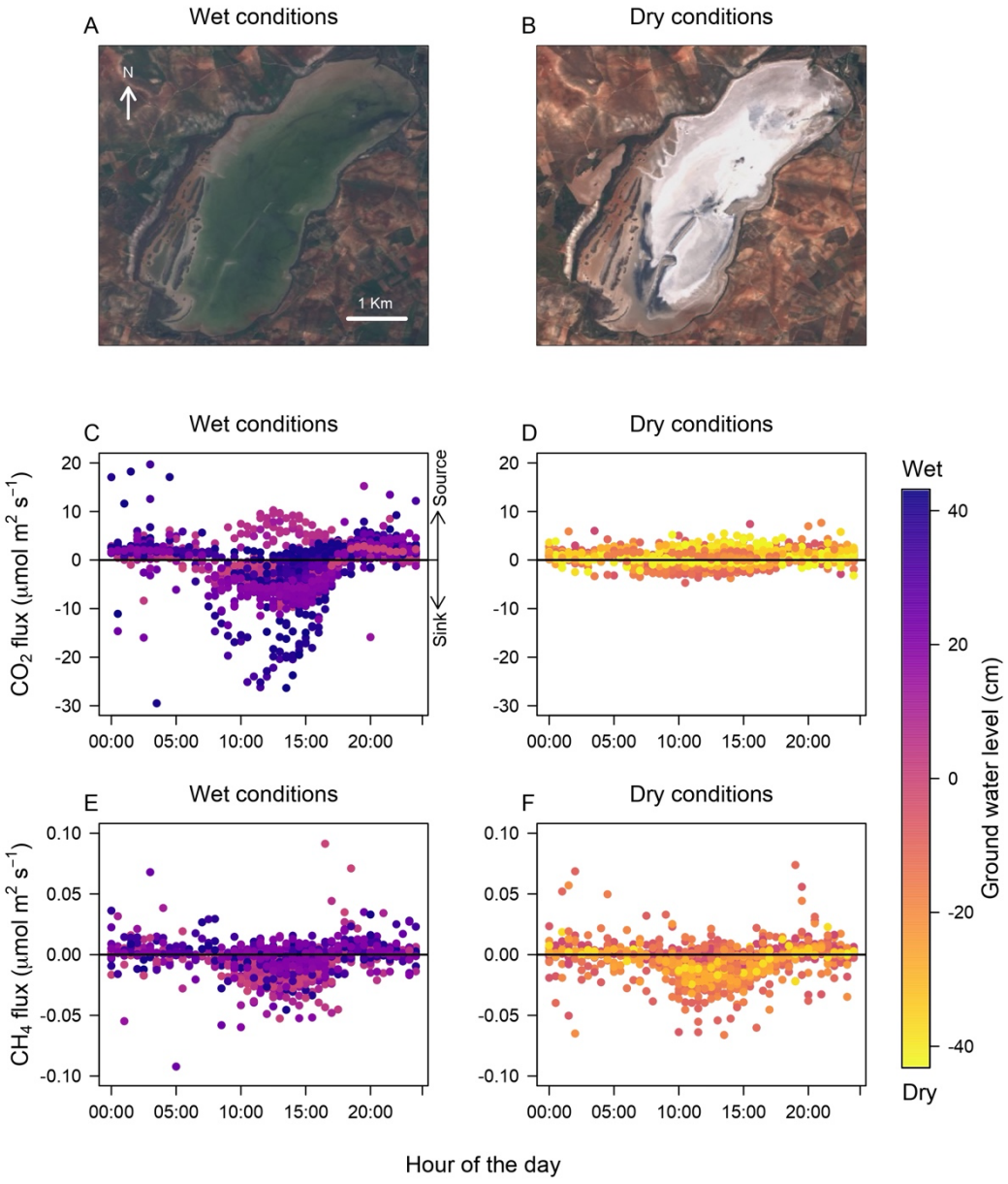

Fig 3. Aerial photos of Fuente de Piedra Lake during a period of maximum water availability (wet, **A**) and during a typical dry episode (**B**). Note that for some period during the dry episodes, a salt crust forms covering practically the entire extent of the lake. The figure shows the daily pattern of CO_2 and CH_4 fluxes during wet conditions (**C** and **E** respectively) and dry conditions (**D** and **F** respectively). Water availability is measured in terms of groundwater level. Source image: Sentinel-2. Wet image was taken on 17-02-2021 and dry image was taken on 13-5-2021.

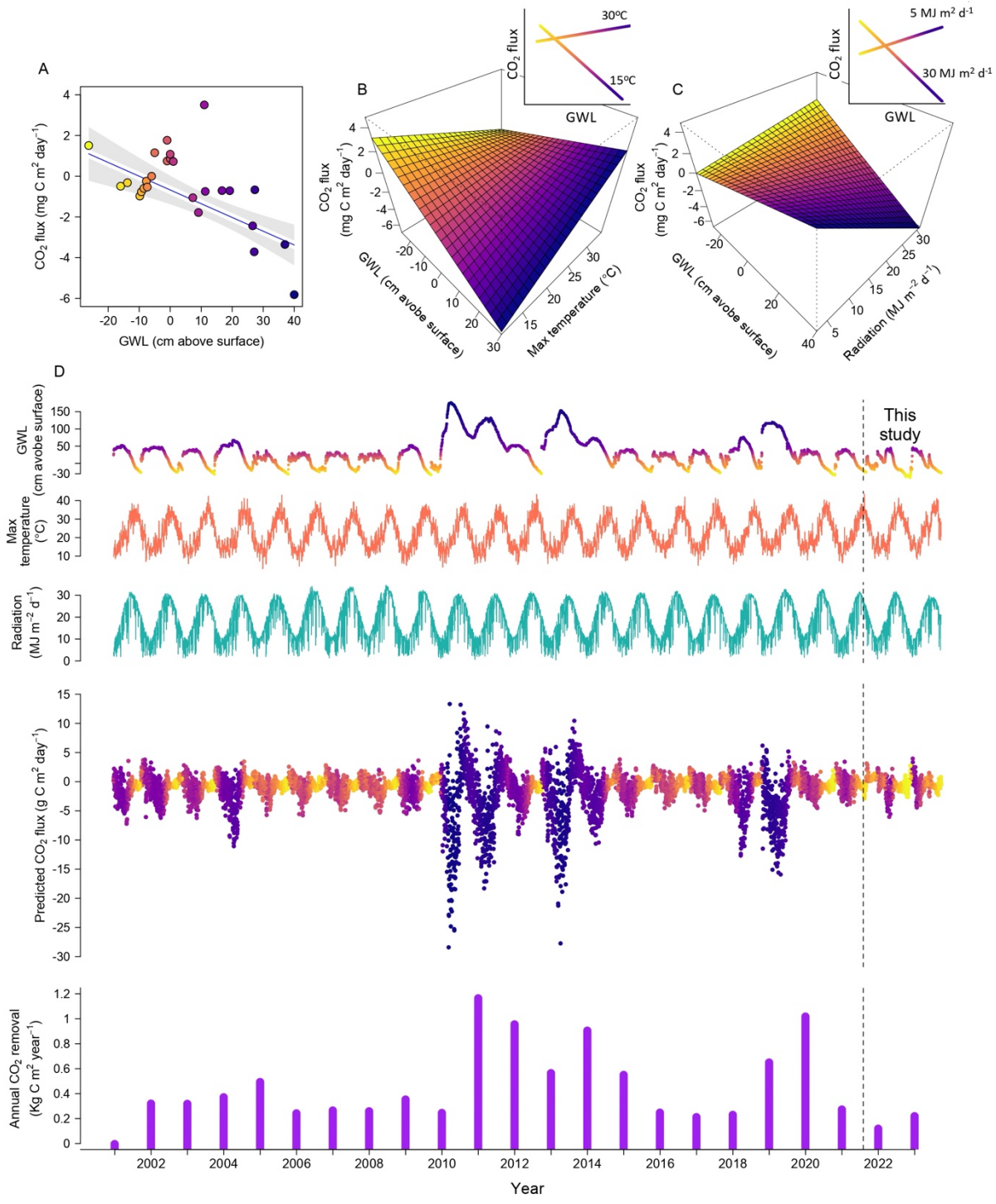

Fig 4. Prediction of CO_2 flux as a response to groundwater level with a slope of -0.115 (**A**), the interaction between groundwater level and daily maximum temperature (**B**), and the interaction between groundwater level and incident solar radiation (**C**). Model has an R^2 of 0.73. Using existing 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**).