



# Breathing Storms: Enhanced Ecosystem Respiration During Storms in a Heterotrophic Headwater Stream

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**Abstract.** Hydrological disturbances following storm events influence the structure and functioning of headwater streams. However, understanding how these disturbances impact critical processes such as stream metabolism is challenging. We assessed the effect of storm events on the resistance and resilience of gross primary production (GPP) and ecosystem respiration (ER) in a heterotrophic headwater stream. We hypothesize stream metabolism will show low resistance to storm events because GPP and ER will be either enhanced by inputs of limited resources (small storms) or hindered by biofilm damage (large storms). We also expected resilience to decrease with the size of the storm event. To test these hypotheses, we hydrologically characterized 53 individual storm events during 4.5 years (period Oct 2018- Feb 2023) and estimated metabolic rates prior, during and after 35 of them. Individual storm events had different magnitude (discharge from 0.6 to 872.4 L s<sup>-1</sup>), duration (from 4 to 32 days) and precipitation intensity (from 1.3 to 31.4 mm h<sup>-1</sup>). Considering all events, GPP and ER averaged 1.7 ± 1.8 and -13.4 ± 7 g O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>, respectively. The two processes showed low resistance to storm events, with magnitudes increasing in 69% and 86% of the cases for GPP and ER, respectively. Changes in GPP were unrelated to any hydrological parameter, while a positive relation with the magnitude of the storm event was found for ER (R<sup>2</sup> = 0.37). Similarly, recovery times were positively related to the size of the event only for ER (R<sup>2</sup> = 0.49), but level-off at ca. 6 days, suggesting that the positive effect of resource inputs on stream metabolic activity limited over time. Our findings support the idea that storm events act as triggers of stream metabolism and highlight how changes in hydrological regimes could impact stream functioning and its role in global biogeochemical cycles.



## 1 Introduction

30 Stream metabolism regulate energy and matter fluxes within running waters, as it includes the processes of carbon fixation (gross primary production, GPP) and mineralisation (ecosystem respiration, ER). GPP and ER are key ecosystem functions as they control organic matter processing, nutrient cycling, greenhouse gas emissions, and aquatic food webs (Roberts et al., 2007). Further, stream metabolism is highly sensitive to both climate and anthropogenic disturbances, making metabolic rates an increasingly valuable tool for understanding aquatic ecosystems functioning and their response to global change  
35 perturbations (Young et al., 2008; Bernhardt et al., 2018; Palmer and Ruhi, 2019).

Stream metabolism is influenced by several abiotic and biotic factors that control its variability over space and time. Light inputs and nutrient concentrations are the main drivers of GPP (Mulholland et al., 2001; Roberts and Mulholland, 2007; Lupon et al., 2016), while ER is usually regulated by temperature (Uehlinger, 2000; Acuña et al., 2004) and organic matter availability (Demars, 2019; Lupon et al., 2023). All these factors are directly or indirectly related to stream hydrology, as increases in  
40 sediment and solute exports during high flows generally alter turbidity, chemistry (Dodds et al., 2002; Webster et al., 2003), and temperature (Butturini and Sabater, 1998) of stream water. Hydrology also controls the interaction between available solutes and stream biofilms, primarily through its control over transient storage (Grimm and Fisher, 1984; Hall et al., 2002), water residence time (Valett et al., 1996), and benthic leaf litter distribution (Mulholland et al., 1985). The influence of hydrology on stream metabolism can be especially pronounced in streams with highly variable hydrological regimes, such as  
45 intermittent rivers. Understanding how stream flow, especially during storm events, influences metabolic activity is critical to assess ecosystem functioning and its response to flow regulation or changing climatic conditions.

In recent years, high-frequency measurements of dissolved oxygen (DO) concentration have been conducted in diverse ecosystems in order to assess the effect of discharge and hydrological disturbance on GPP and ER (i.e., Roberts et al., 2007; Gómez-Gener et al., 2020; O'Donnell and Hotchkiss, 2022). Yet, there is no clear consensus on whether storm events enhance  
50 or diminish metabolic rates, partly because increasing discharge can act either as a “metabolic trigger”, when the supply of limiting resources enhances metabolic rates, or as a “metabolic stopper” when the physical disruptive force of water inhibits metabolic activity. This potential for contrasting responses resonates with the Intermediate Disturbance Hypothesis (Connell, 1978), which postulates that biological activity is higher when the disturbance is intermediate in frequency and intensity. Supporting this idea, previous studies have related elevated metabolic rates during small to medium-size storms to increases  
55 in carbon and nutrient exports from surrounding terrestrial ecosystems (Jowett and Biggs, 1997; Demars, 2019; Lupon et al., 2019; Li et al., 2024). However, this metabolic trigger may eventually reach an asymptote when the supply of resources surpasses the ecosystem's processing capacity (*sensu* River Network Saturation concept; Wollheim et al., 2018). Upon this threshold, one may expect no additional increases in either GPP or ER. Finally, during large storm events, the advective power of water can increase sediment transport and turbidity (Bernhardt et al., 2018), thereby dislodging the substrate and litter from  
60 the streambed (Roberts et al., 2007), decreasing mean water residence time, scouring the benthic biomass (Talbot et al., 2018; O'Donnell and Hotchkiss, 2022), and limiting light availability (Hall et al., 2015). These physical and biological disruptions



may ultimately reduce in-stream processing and promote the pulse and shunt of carbon and nutrients across the entire river network (Raymond et al., 2016).

65 The role of storm events as metabolic triggers or stoppers also depends on the resistance and resilience of stream ecosystems to hydrological disturbances. The resistance to a hydrological disturbance can be defined as the ability of stream ecosystems to uphold metabolic rates unchanged relative to base flow conditions despite increases in discharge. Conversely, either the enhancement or suppression of metabolic activity indicates low resistance to storm perturbations (i.e., Roberts et al., 2007; Uehlinger, 2000; O'Donnell and Hotchkiss, 2022). In turn, the resilience of stream metabolic activity to hydrological events is defined by the time required for either GPP or ER to return to values comparable to those prior to the storm event (Carpenter  
70 et al., 1992; O'Donnell and Hotchkiss, 2022). Hence, streams with high resilience are those from which metabolic rates quickly recover its prior values after the storm event. The duration of this recovery can vary depending on the magnitude of the disturbance, as well as across seasons and on environmental conditions such as light availability and temperature (Roberts et al., 2007).

75 The objective of this study was to assess the response of stream metabolism to storm events of different magnitude, intensity, and duration. To do so, we examined the hydrological characteristics and metabolic response of 53 individual storms in a non-perennial, forested headwater stream showing large temporal variability in discharge (Bernal et al., 2002, 2019). We hypothesized that ER would show low resistance (i.e., abrupt changes) to storm events, by either increasing when intermediate events alleviate resource limitation (metabolic triggers) or decreasing when large events damage biofilm and promote the pulse and shunt of carbon (metabolic stoppers). By contrast, we expected that GPP would generally exhibit high resistance because  
80 it would be limited by light availability in this closed-canopy stream (Fig. 1a). Only during periods of open-canopy (i.e., early spring and late fall), GPP would behave similarly to ER. Further, we hypothesized that stream metabolism would show lower resilience (i.e., longer recovery periods) with increasing magnitude and duration of the storm due to higher metabolic changes and longer periods of land-water connectivity. Yet, we anticipated that recovery time may reach a threshold corresponding to the time required for biofilms to rebuild after large storm disturbances (Fig. 1b).

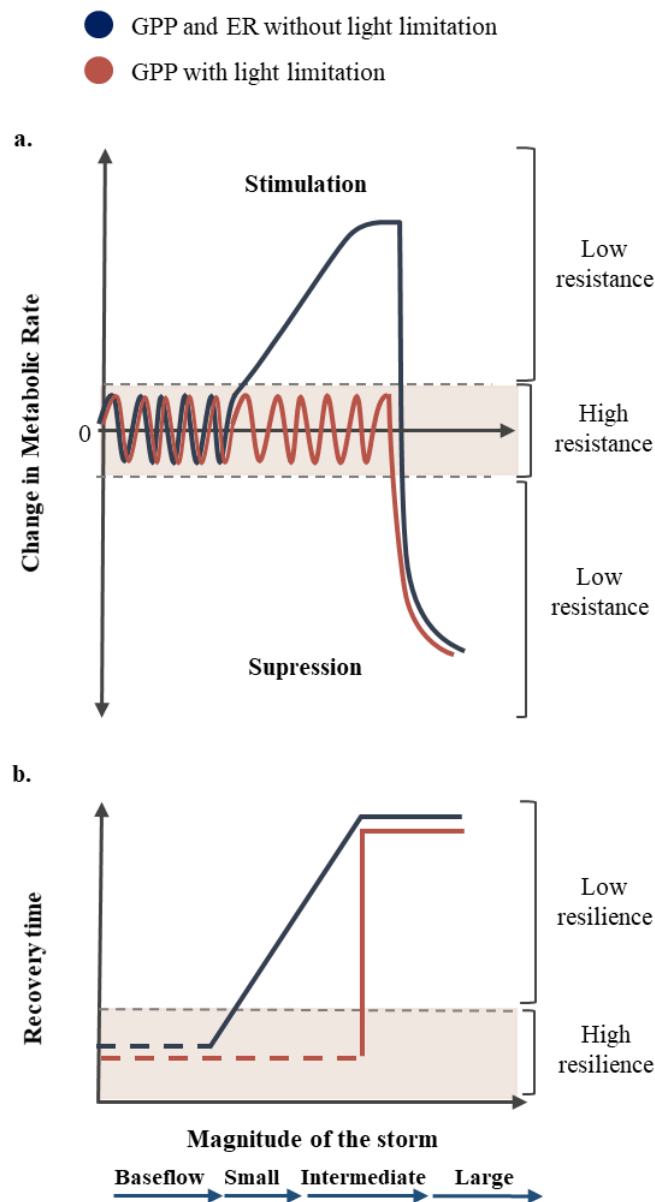


Figure 1: Conceptualization of the impact of storm magnitude on the (a) resistance and (b) resilience of stream metabolic rates. Under no light limitation (dark blue line), stream metabolism has low resistance to hydrological disturbances. It is initially stimulated during low to moderate event magnitude and then suppressed during large events. Further, stream metabolic rates have low resilience to hydrological disturbances, showing prolonged recovery times during larger events until reaching a threshold corresponding to biofilm damage. Under light-limited conditions (orange line), ER has the same behaviour described above, while GPP shows higher resistance and resilience regardless of the magnitude of the disturbance until reaching the threshold of biofilm damage.



## 2 Methods

### 95 2.1 Study Site

The study was conducted in Fuirosos, a three-order stream located in the Montnegre-Corredor Natural Park in Northeast Spain (41° 41' 04.5" N, 2° 34' 46.0" E). The climate is Mediterranean, with warm, dry summers and mild, humid winters. Monthly mean temperatures range from 3°C in January to 24°C in August. Mean annual precipitation is  $658 \pm 216$  mm (mean  $\pm$  standard deviation). Most precipitation falls during spring and autumn, with sporadic storms in summer and winter.

100 The drainage area at the catchment outlet is 18.7 km<sup>2</sup> and the channel width ranges between 3 to 5 meters. The catchment lies on a fine-grained granitoid batholith, resulting in sandy and poorly developed soils. The landscape is predominantly forested, with perennial forests of *Quercus suber*, *Quercus ilex*, *Pinus pinea*, and *Pinus halepensis* covering over 85% of the catchment area. The population density is < 5 inhabitants per km<sup>2</sup>, which can be perceived as minimal with regards to human interference. The stream is flanked at the valley by a well-developed riparian zone occupying 6% of the catchment area. The main riparian  
105 species are *Alnus glutinosa* and *Platanus acerifolia*.

Fuirosos is a non-perennial stream primarily fed by springs and groundwater inputs. As most Mediterranean non-perennial streams, flow regime is extremely erratic (Bernal et al., 2019), with stream discharge ranging from 0 to 3884 L s<sup>-1</sup> and an average water velocity of  $0.11 \pm 0.2$  m s<sup>-1</sup> (period October 2018 to February 2023). The lateral connectivity between the stream and the surrounding riparian zone has also a marked seasonal pattern, as it switches from being a gaining stream during the  
110 wet period (November-April) to a losing stream during the dry season (May-November) (Butturini et al., 2003). Further, stream flow usually ceases for several weeks in summer and resumes during autumn storm events. Isolated pools can persist for several days until the stream dries completely (Butturini et al., 2002). In our study, we only considered storm events that took place during periods with surface flow.

The Fuirosos stream is relatively oligotrophic. Dissolved organic carbon (DOC) concentrations are generally low, averaging  
115 around 4 mg C L<sup>-1</sup>, but they experience a significant rise in autumn, reaching up to 8 mg C L<sup>-1</sup> (Vazquez et al., 2011). Stream nitrate (NO<sub>3</sub><sup>-</sup>) concentration averages  $210 \pm 50$  µg N-NO<sub>3</sub><sup>-</sup> L<sup>-1</sup>, with the highest levels typically observed in winter (Bernal et al., 2005).

### 2.2 Data collection

Meteorological data, including daily precipitation, was obtained from the Dosrius station managed by the Catalan  
120 Meteorological Service and located ca. 15 km southwest of the outlet of Fuirosos (SMC, 2023). The suitability of this station for representing conditions in Fuirosos was carefully evaluated and confirmed in Ledesma et al. (2021).

To estimate stream metabolism, in October 2018 we installed a monitoring station in a stream location draining 9.9 km<sup>2</sup>. The 200-m section upstream of the sampling station is bordered by a well-developed riparian forest. Further, this section is



minimally influenced by tributaries, has a slope of 1.9%, and is representative of the stream hydromorphology featuring small runs, riffles, and a few shallow pools. During the study period, the average water depth was  $7.5 \pm 8$  cm and wetted width was  $2.4 \pm 0.5$  m. The monitoring station was equipped with a suite of sensors that measured both physical (incident light, water temperature, water depth) and chemical (dissolved oxygen) properties at a 10-minute frequency. Incident light (lux) was recorded every 10 minutes using two HOBO UA-002-64 loggers (Onset Corporation) installed in riparian trees near the sampling station. Lux values from the two sensors were averaged, converted to photosynthetic photon flux density (PPFD,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), and aggregated into daily totals. A threshold of  $4 \text{ mol m}^{-2} \text{d}^{-1}$  was considered to be the minimum PPFD required to support stream photoautotrophic activity (Hill et al., 1995). Stream water depth (h, cm) was measured using a HOBO U20-001-04 (Onset Corporation) firmly anchored to the thalweg. Water level measurements were converted to instantaneous stream discharge ( $Q$ ,  $\text{L s}^{-1}$ ) using pre-established rating curves, which were developed from reconstructed sensor stream water levels and field-measured  $Q$  taken ca. biweekly ( $n = 50$ ). Finally, water temperature ( $T$ ,  $^{\circ}\text{C}$ ) and dissolved oxygen concentrations (DO,  $\text{mg L}^{-1}$ ) were measured with a MiniDOT logger (PME, USA) firmly anchored next to the water depth sensor with a perforated plastic pipe as a protective casing. From October 2018 to February 2023, all sensors were checked out every 15-20 days for maintenance and data downloading.

### 2.3 Storm event characterization

To identify and characterize individual storm events from the hydrograph, we used the method described by Lannergård et al. (2021). Briefly, the start of an event was defined as the moment when daily discharge increased for two consecutive days at a rate exceeding 1.5%. An individual event was considered to end when either a new event began or when the  $Q$  dropped below the level predicted by a first-order baseflow decay function, which was calculated using  $Q$  at the start of the event and assumed to decrease by 0.99% per day. Additionally, if the decay function was met but  $Q$  continued to decrease by more than 0.05%, the event continued until there was no further decrease in  $Q$ . We only kept those events following accumulated precipitation higher than 10 mm, which is the minimum amount of precipitation needed to generate a hydrological response in this stream (Bernal et al., 2002). By following this procedure, we were able to identify 53 individual storm events for the study period (Table S3).

For each individual event, we extracted the following variables: total precipitation ( $P$ , in mm), maximum precipitation intensity ( $PI_{\text{max}}$ , in  $\text{mm h}^{-1}$ ), duration of the storm event ( $D$ , in days), runoff coefficient ( $RC$ , in %), and change in discharge ( $\Delta Q$ , in  $\text{L s}^{-1}$ ). The  $P$ ,  $PI_{\text{max}}$ , and  $D$  provide insights into the size of the event. The  $RC$  was calculated as the ratio of  $Q$  to  $P$  and is sensitive to the antecedent moisture conditions in the catchment (Bernal et al., 2002). Finally, the  $\Delta Q$  is the difference between the peak flow and the average discharge during the three days before the event ( $Q_{\text{prior}}$ ) and indicates the magnitude of the disturbance caused by the storm event.



## 2.4 Metabolism calculations

155 We estimated daily stream metabolic rates during each storm event as well as for the prior and following weeks. GPP and ER (in  $\text{g O}_2 \text{ m}^{-2} \text{ d}^{-1}$ ) were estimated using the Bayesian inverse model *b\_Kb\_oipi\_tr\_plrckm.stan* from the *streamMetabolizer* R package (version: 0.12.1), which incorporates both process and observation errors (Appling et al., 2018) (Appendix 1, Table S1). We assumed that GPP is a linear function of light intensity (Van de Bogert et al., 2007), while ER is constant throughout the day. The model does not account for factors that could increase ER during the day (Hotchkiss and Hall, 2014), such as  
160 photorespiration, which is presumed to be minimal in our forested headwater stream (Parkhill and Gulliver, 1998).

Following the procedure by Bernal et al. (2022), GPP, ER, and the gas transfer coefficient ( $K_{600}$ , in  $\text{d}^{-1}$ ) were fitted daily based on DO dynamics over a 24-hour period starting at 23:00h the previous day. Prior probability distributions for GPP and ER were set based on previously reported values ( $0.5 \pm 10$  and  $-5 \pm 10 \text{ g O}_2 \text{ m}^{-2} \text{ d}^{-1}$  for GPP and ER, respectively) (Acuña et al., 2004; Bernal et al., 2022). Prior probability of  $K_{600}$  was strongly constrained to minimize the problem of equifinality (Appling  
165 et al., 2018). To constrain  $K_{600}$ , we run the Bayesian model using a deterministic, hand-pooled  $K_{600}$  obtained from the relationship between binned Q and the  $K_{600}$  estimated from a series of 11 propane additions using a mixed tracer injection method (Jin et al., 2012) (Fig. S1). Additionally, we verified the feasibility of the modelled  $K_{600}$  using independent  $K_{600}$  predictions from both the night-time regression method (Odum, 1956) and hydraulic geometry (Raymond et al., 2012) (Fig. S2). Only estimates of GPP and ER that passed a quality check and satisfied all the criteria were included. Days with  
170 biologically or physical implausible values (i.e.,  $\text{GPP} < 0$ ,  $\text{ER} > 0$ ,  $K_{600} > 110 \text{ d}^{-1}$ ), poor model convergence (i.e.,  $R\text{-hat} > 1.2$  and number of effective samples  $> 8000$ ), or poor fit to DO data (i.e.,  $R^2 < 0.50$ , root mean square error (RMSE)  $> 0.4$ , mean absolute error (MAE)  $> 0.4$ ) were excluded (Table S2). This procedure allowed us to calculate the metabolic rates for 66% of storm events (35 out of 53 events). Of the 18 excluded events, six lacked complete DO data and 12 did not pass the mentioned quality test. Notably, all days with  $Q > 100 \text{ L s}^{-1}$  failed the quality test, leading to the exclusion of metabolic rate calculations  
175 during large storm events. Consequently, we were unable to test our expectation that metabolic rates would decrease during large storm events.

For each storm event, we assessed the resistance of metabolic activity ( $\Delta\text{MET}$ ) as the relative change in either GPP ( $\Delta\text{GPP}$ ) or ER ( $\Delta\text{ER}$ ) as follows:

$$\Delta\text{MET} = \frac{\text{MET}_{\text{Peak}} - \text{MET}_{\text{Prior}}}{\text{MET}_{\text{Prior}}} \times 100\%,$$

180 where  $\Delta\text{MET}$  is the percentage of change of either GPP or ER, and  $\text{MET}_{\text{Peak}}$  is either the maximum (when there is stimulation) or the minimum (when there is suppression) metabolic rate observed during the event.  $\text{MET}_{\text{Prior}}$  is the average metabolic rate during the three days preceding the event. For  $\text{MET}_{\text{Peak}}$ , we used the maximum (or minimum) metabolic rate rather than the metabolic rate at the peak discharge because there was typically a two-day gap between the discharge and metabolic peaks. We considered that  $\Delta\text{MET}$  values higher than +10% indicate a stimulation of the metabolic process, whereas



185 values of  $\Delta\text{MET}$  values lower than -10% indicate a suppression of metabolic rates. Finally, we considered  $\Delta\text{GPP}$  or  $\Delta\text{ER}$   
values within  $\pm 10\%$  to indicate stable metabolic rates, and hence, high resistance of stream metabolism to storms.

To assess the resilience of metabolic rates, we calculated the recovery time (RT, in days) of GPP and ER for each storm event. Recovery time was determined as the number of days required for either GPP or ER to return to conditions similar to  $\text{MET}_{\text{prior}}$  (i.e., within  $\pm 10\%$ ). When there was insufficient data during the recession limb or when recovery time overlapped with another  
190 event ( $n = 7$ ), we inferred the day when either GPP or ER returned to pre-event values from a linear regression model between time and metabolic rates during the recession limb of the hydrograph.

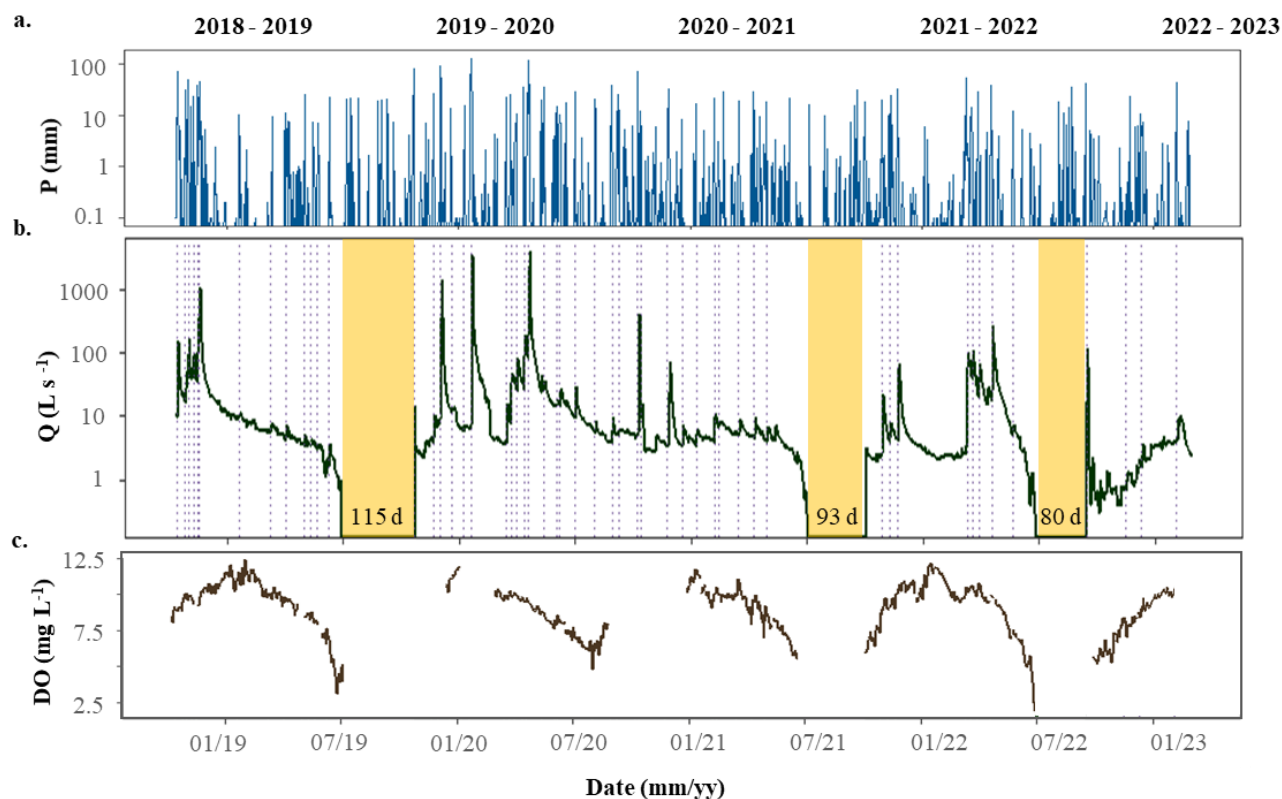
## 2.5 Statistical analysis

We used linear, logarithmic, and exponential regression models to explore the relationships between (i) hydrological descriptors ( $\text{PI}_{\text{max}}$ , D, RC, and  $\Delta\text{Q}$ ), physical parameters (daily PAR and mean daily temperature), and metabolic rates (GPP,  
195 ER) during storm events, (ii) hydrological descriptions and both metabolic resistance (assessed as metabolic change;  $\Delta\text{GPP}$  and  $\Delta\text{ER}$ ) and resilience (assessed as recovery time;  $\text{RT}_{\text{GPP}}$  and  $\text{RT}_{\text{ER}}$ ), and (iii) metabolic resistance and resilience for GPP and ER. The goodness of fit for each regression model was assessed using the coefficient of determination ( $R^2$ ), while the statistical significance of the relationships was evaluated with p-values  $< 0.05$ . All data analyses were conducted using R software (v. 4.3.3).

## 200 3 Results

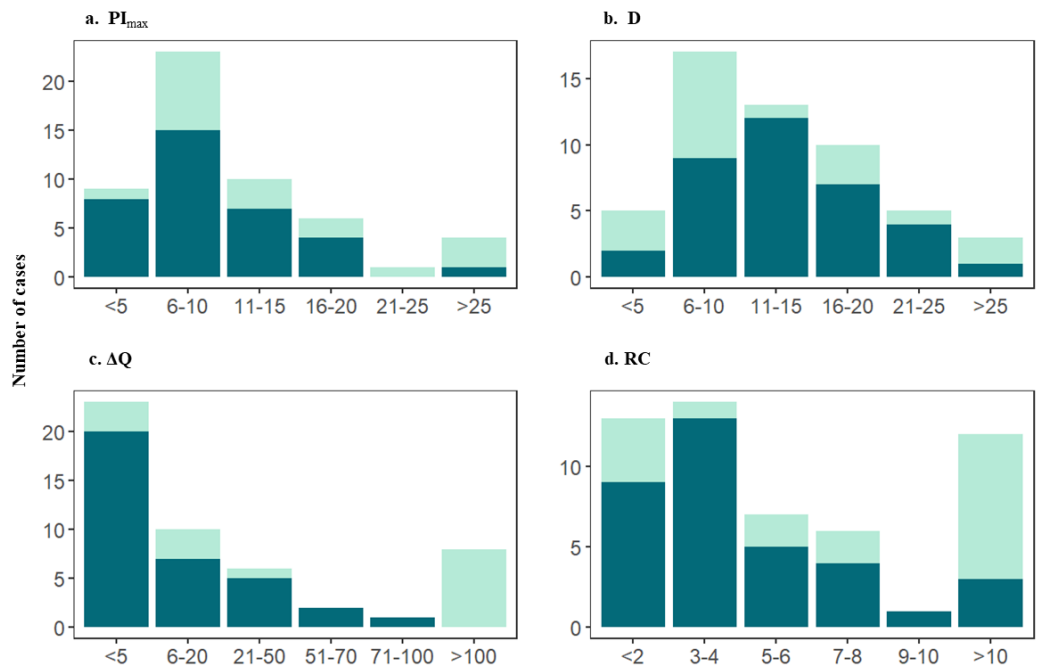
### 3.1 Characterization of storm events

During the study period, both meteorological and hydrological variables varied across seasons and hydrological years (Fig. 2). Annual precipitation ranged from 428 mm in 2019 to 1,172 mm in 2020 and mean annual temperature ranged from 13.8 °C in 2021 to 15.2 °C in 2022. Further, mean daily Q spanned from  $5.67 \pm 21.9 \text{ L s}^{-1}$  (mean  $\pm$  SD) in 2021 to  $59.28 \pm 317.9 \text{ L s}^{-1}$  in  
205 2020. The duration of the summer dry periods was also variable: there were no dry days in 2020, while 2019 had 115 days without water flow (Fig. 2b). The hydrological descriptors (P,  $\text{PI}_{\text{max}}$ , D, RC, and  $\Delta\text{Q}$ ) covered a wide range of values, most of them expanding at least one order of magnitude among individual storm events (light blue bars, Fig. 3). P ranged from 8.6 to 234.9 mm ( $46 \pm 5.7 \text{ mm}$ ),  $\text{PI}_{\text{max}}$  ranged from 1.30 to 31.4 mm h<sup>-1</sup> ( $10.8 \pm 0.98 \text{ mm h}^{-1}$ ), and D ranged from 4 to 32 d ( $13 \pm 7 \text{ d}$ ) (Fig. 3a, b). The magnitude of the storm event also differed widely among events:  $\text{Q}_{\text{prior}}$  ranged from 0.7 to 165 L s<sup>-1</sup> ( $16.5 \pm 3.9 \text{ L s}^{-1}$ ), while  $\Delta\text{Q}$  ranged from 0.6 to 3,501 L s<sup>-1</sup> ( $150 \pm 70 \text{ L s}^{-1}$ ). Finally, RC ranged from 0.22 to 39.44% ( $7.2 \pm 1.9\%$ ) (Fig. 3c, d). Light and water temperature also varied across individual storm events. Daily PAR ranged from 2 to 28.6 mol m<sup>2</sup> d<sup>-1</sup> and was lower than the threshold to support stream photoautotrophic activity for 19 of the 53 cases. Mean daily water temperature varied from 4.3 to 21 °C.



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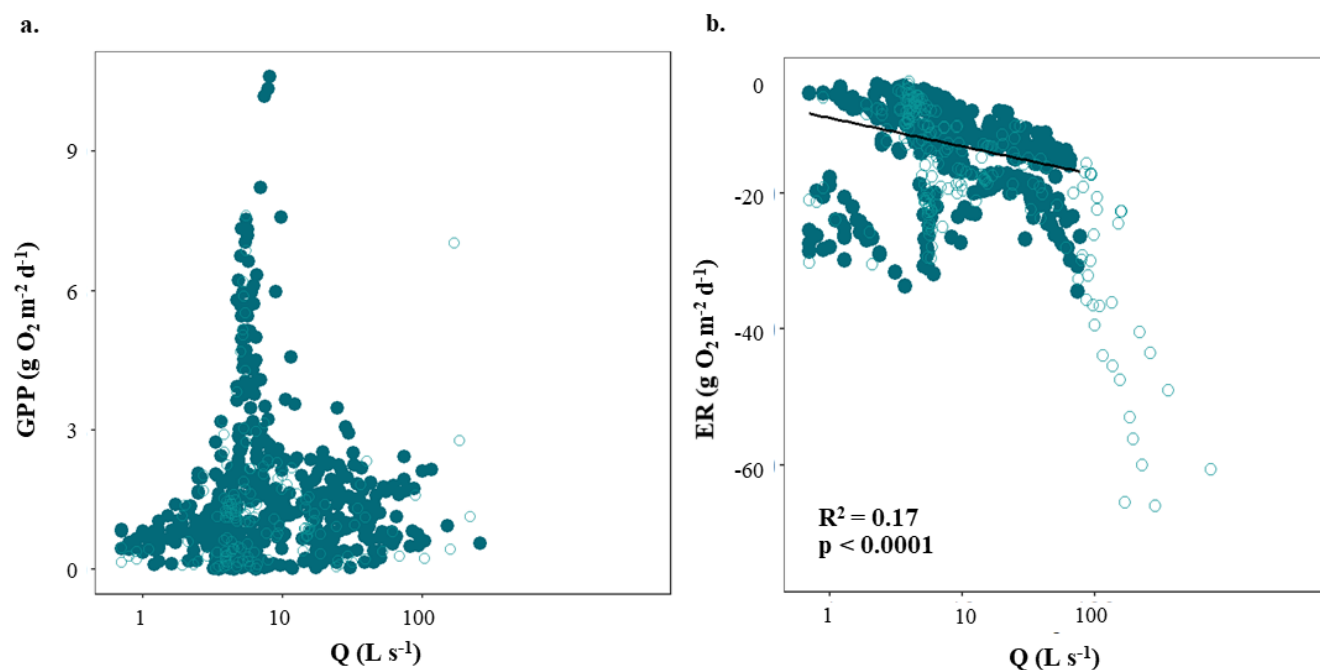
**Figure 2: Temporal variation of a) daily precipitation ( $P$ ), b) mean daily discharge ( $Q$ ), and c) mean daily dissolved oxygen concentrations ( $DO$ ) at the Fuirosos stream from October 2018 to February 2023. Dashed vertical lines represent each of the 53 identified storm events.**



**Figure 3. Histograms showing the distribution of (a) maximum precipitation intensity ( $PI_{max}$ ) (b) duration of storm event (D), (c) change in discharge ( $\Delta Q$ ), and (d) runoff coefficient (RC) for the 53 identified storm events (light and dark blue) as well as for the 35 events for which we could calculate metabolic rates (dark blue).**

### 3.2 Metabolic rates during storm events

From the 53 storm events identified, we were able to calculate metabolic rates for 35 events that expanded across most of the range covered by hydrological and environmental descriptors (dark blue bars, Fig. 3). During these storm events, GPP ranged from 0.005 to 10.6 g O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup> ( $1.7 \pm 1.8$  g O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) and did not relate to either Q (Fig. 4a) or daily PAR (in both cases;  $p > 0.05$ ). Rates of ER were 9 times higher than GPP, ranging from -4.3 to -36.4 g O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup> ( $-13.4 \pm 7$  g O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>). ER was positively related to Q (linear regression,  $R^2 = 0.17$ ,  $p < 0.0001$ ) (Fig. 4b). There was no relationship between ER and stream water temperature ( $p > 0.05$ ).



**Figure 4. Relationship between mean daily discharge (Q) and a) gross primary production (GPP) and b) ecosystem respiration (ER) for each day across all individual storm events. The colour coding indicates whether the estimated metabolic rates passed (closed circles) or did not pass (open circles) the quality test as defined in the methods. Linear regression was made only with the days that passed the quality test.**

### 3.3 Response of metabolic rates to the storm events

Stream metabolic rates changed in response to the storm events, but the proportion of cases showing stimulation, suppression, or no change differed between GPP and ER. Stimulation was observed during 69% and 86% of the cases (24 and 30 out of 35 cases) for GPP and ER, respectively, whereas suppression was observed more often for GPP (9 out of 35 cases) than for ER (1 out of 35 cases) (Table 1). Only 6% of the events (2 out of 35) showed no change in GPP, while no changes in ER occurred in 11% of the events (4 out of 35) (Table 1).



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**Table 1. Mean metabolic rates, resistance, and resilience of gross primary productivity (GPP) and ecosystem respiration (ER) for each storm event. GPP and ER rates are expressed as mean  $\pm$  S.D. Resistance is expressed as the maximum percentage of change in metabolic rates relative to prior conditions ( $\Delta$ GPP and  $\Delta$ ER). Zero values (i.e., no change) indicate changes smaller than 10% and are interpreted as high resistance. Resilience is expressed as the time needed for GPP or ER to recover pre-event values ( $RT_{GPP}$  and  $RT_{ER}$ ). Events marked with asterisks indicate inferred recovery times derived from linear regression overlapping with another event.**

| Event | GPP                      | ER                       | $\Delta$ GPP | $RT_{GPP}$ | $\Delta$ ER | $RT_{ER}$ |
|-------|--------------------------|--------------------------|--------------|------------|-------------|-----------|
|       | $g\ O_2\ m^{-2}\ d^{-1}$ | $g\ O_2\ m^{-2}\ d^{-1}$ | %            | d          | %           | d         |
| 2     | $0.5 \pm 0.3$            | $-12.8 \pm 1.6$          | + 100.8      | 2          | + 24.4      | 4         |
| 4     | $0.7 \pm 0.1$            | $-14.5 \pm 1.9$          | + 29         | 2          | + 33.1      | 4         |
| 7     | $1.2 \pm 0.1$            | $-10.4 \pm 1.2$          | 0            | 0          | + 10.4      | 1         |
| 8     | $1.6 \pm 0.3$            | $-6.74 \pm 0.6$          | + 20.9       | 1          | + 16.2      | 1         |
| 9     | $1.6 \pm 0.5$            | $-7.51 \pm 2.1$          | + 26.5       | 2          | + 37.2      | 2         |
| 10    | $1.3 \pm 0.5$            | $-7.44 \pm 1.5$          | + 67.9       | 4          | + 62.3      | 3         |
| 11    | $0.8 \pm 0.1$            | $-6.86 \pm 0.7$          | + 17.9       | 1          | + 32.5      | 1         |
| 12    | $1.1 \pm 0.4$            | $-6.96 \pm 1.2$          | + 62.4       | 1          | + 23.6      | 1         |
| 13    | $0.7 \pm 0.6$            | $-7.64 \pm 0.6$          | + 22.5       | 1          | + 13.3      | 1         |
| 20    | $1.8 \pm 0.5$            | $-17.2 \pm 5.1$          | -76.1        | 2          | + 86.9      | 3*        |
| 21    | $1.8 \pm 0.2$            | $-21.5 \pm 2.2$          | -14.8        | 2          | + 66.6      | 6*        |
| 22    | $1.5 \pm 0.2$            | $-23 \pm 4.1$            | 0            | 0          | + 68.5      | 5         |
| 25    | $0.9 \pm 0.2$            | $-13.4 \pm 1$            | + 91         | 3          | 0           | 0         |
| 26    | $1.1 \pm 0.7$            | $-18.2 \pm 1$            | + 48.3       | 2          | 0           | 0         |
| 27    | $1.5 \pm 0.3$            | $-18.5 \pm 1$            | + 38.9       | 1          | 0           | 0         |
| 28    | $2.4 \pm 1.4$            | $-21.9 \pm 2.8$          | + 67.1       | 2          | + 60.6      | 3         |
| 29    | $4.3 \pm 2.3$            | $-24.9 \pm 4$            | -73.1        | 2          | + 30.6      | 1         |
| 30    | $5.9 \pm 2.1$            | $-28.9 \pm 1.7$          | + 15.2       | 2          | + 18.3      | 2         |
| 34    | $0.3 \pm 0.2$            | $-12.9 \pm 7.4$          | + 35.8       | 2          | + 85        | 6         |
| 35    | $0.3 \pm 0.1$            | $-10.5 \pm 1.5$          | + 85.2       | 5          | + 43.5      | 4         |
| 36    | $0.5 \pm 0.2$            | $-5.83 \pm 0.4$          | -87.3        | 1          | + 20.9      | 2         |
| 37    | $1.5 \pm 0.5$            | $-11.9 \pm 1.3$          | + 26.6       | 1          | + 70.5      | 2*        |
| 38    | $3.5 \pm 1.1$            | $-12.9 \pm 1.1$          | + 141.7      | 8          | + 29.2      | 2         |
| 39    | $6.3 \pm 2$              | $-12.5 \pm 1.6$          | + 130.3      | 9          | + 36.8      | 4         |
| 40    | $2.7 \pm 0.4$            | $-12.2 \pm 2.2$          | + 29.7       | 1          | + 37.4      | 2         |
| 41    | $1.6 \pm 0.6$            | $-11.1 \pm 0.9$          | -56.2        | 2          | 0           | 0         |
| 42    | $0.1 \pm 0.1$            | $-9.7 \pm 3.7$           | + 28.1       | 1          | + 51.2      | 4         |
| 43    | $0.1 \pm 0$              | $-7.39 \pm 1$            | -16.1        | 2          | + 33.3      | 4         |
| 44    | $0.1 \pm 0$              | $-6.14 \pm 2.9$          | -95.9        | 4          | + 39.6      | 5         |
| 45    | $1.4 \pm 1.2$            | $-23.5 \pm 5.6$          | -67.8        | 6*         | + 106       | 6*        |
| 47    | $2.3 \pm 0.6$            | $-16.3 \pm 4.5$          | -21.3        | 2          | + 91.3      | 6         |
| 49    | $0.6 \pm 0.7$            | $-12.4 \pm 1.7$          | + 110.8      | 1          | + 34        | 1         |
| 51    | $0.6 \pm 0.2$            | $-24.7 \pm 3.5$          | + 36.8       | 2          | -29.4       | 4         |
| 52    | $0.8 \pm 0.2$            | $-28.5 \pm 3.4$          | + 76.6       | 4*         | + 47.6      | 4*        |
| 53    | $0.9 \pm 0.1$            | $-6.4 \pm 1.3$           | + 53         | 4          | + 51.4      | 5         |

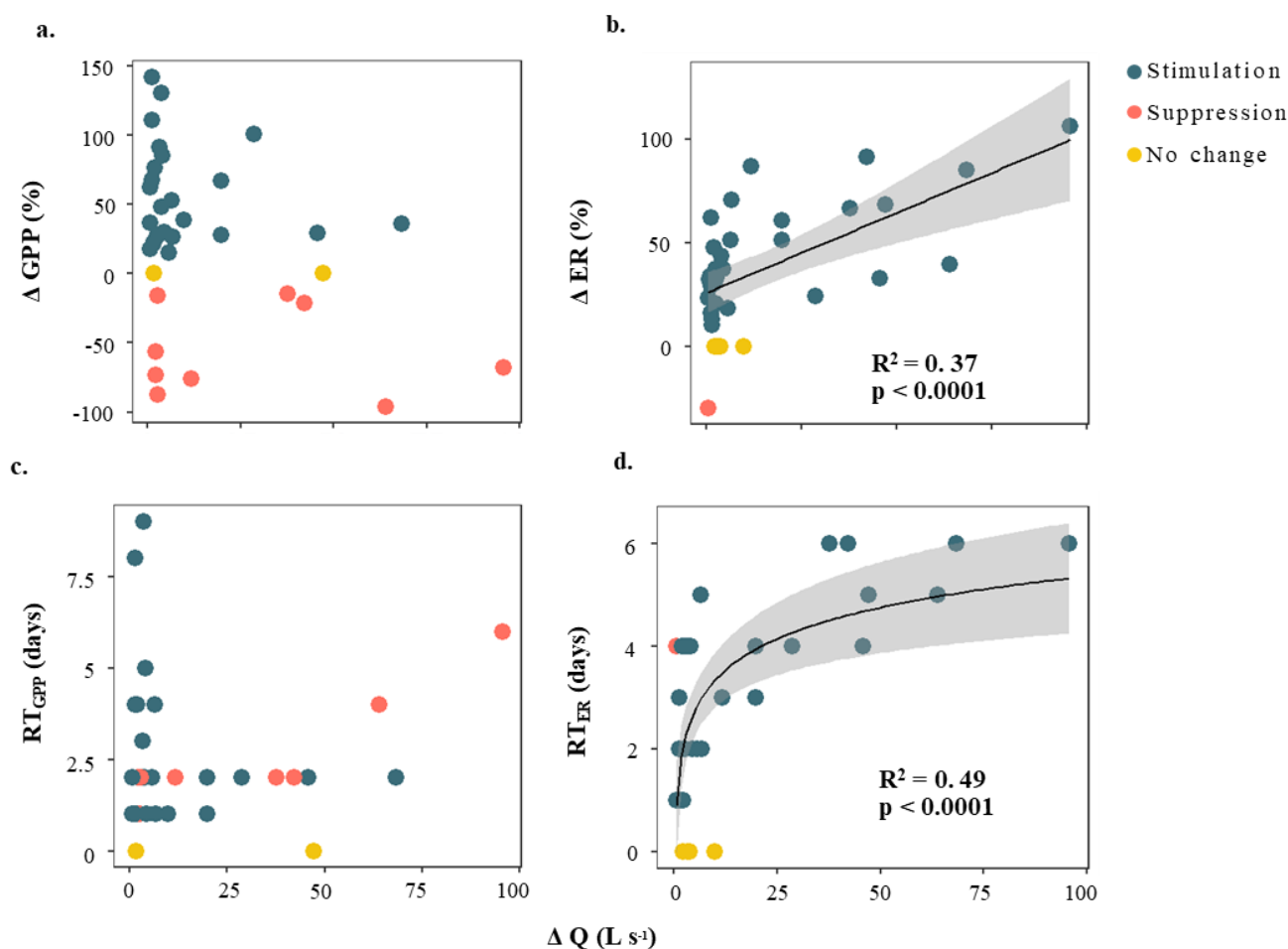
255

The change in metabolic rates ( $\Delta$ GPP and  $\Delta$ ER) ranged from -95.9% to +141.7% for GPP, and from -29.4% to +106% for ER, respectively (Table 1). Values of  $\Delta$ GPP were not related to any hydrological descriptor (i.e., D,  $PI_{max}$ ,  $\Delta$ Q,  $Q_{prior}$  or RC; in all cases  $p > 0.05$  for either linear, logarithmic, or exponential relationship). By contrast,  $\Delta$ ER showed a positive linear relationship with  $\Delta$ Q ( $R^2 = 0.37$ ,  $p < 0.0001$ ) (Fig. 5b). All cases showing suppression or no change in ER ( $\Delta$ ER  $\leq 0$ ) were associated with small  $\Delta$ Q ( $< 10\ L\ s^{-1}$ ), while ER stimulation ( $\Delta$ ER  $> 0$ ) occurred over a broader range of  $\Delta$ Q (from  $0.6\ L\ s^{-1}$  to  $95.6\ L\ s^{-1}$ ).

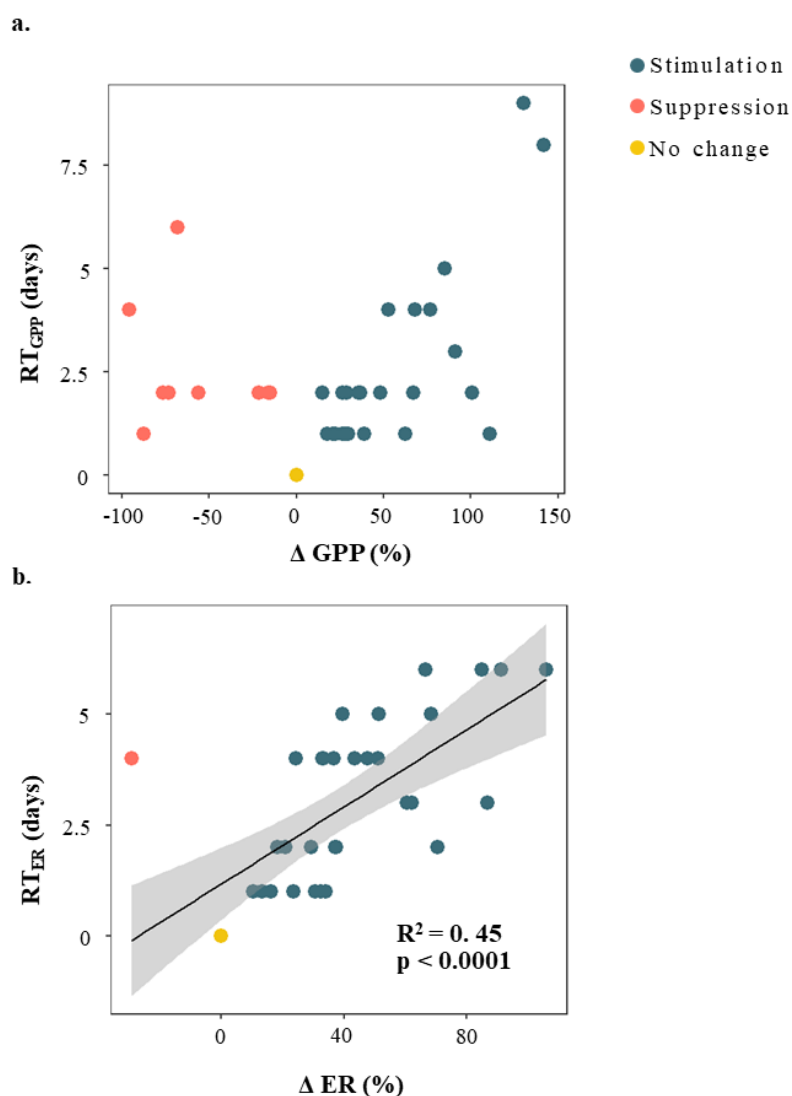
260



The recovery time (RT) was similarly fast for both metabolic rates,  $2.6 \pm 2$  days and  $3 \pm 2$  days for GPP and ER, respectively (Table 1); and there was no relationship between the  $RT_{GPP}$  and  $RT_{ER}$  ( $p > 0.05$ ). As observed for the resistance parameters,  $RT_{GPP}$  and  $RT_{ER}$  were not related to either D,  $PI_{max}$ , or RC (in all cases, linear or non-linear regression,  $p > 0.05$ ). Further, there was no relation between  $RT_{GPP}$  and  $\Delta Q$  (Fig. 5c), while  $RT_{ER}$  showed a positive logarithmic relationship with  $\Delta Q$ , up to a threshold of 6 days ( $R^2 = 0.49$ ,  $p < 0.0001$ ) (Fig. 5d). There was no relationship between  $\Delta GPP$  and  $RT_{GPP}$  (linear or non-linear regression,  $p > 0.05$ ), yet there was a tendency for stimulation to take longer periods of recovery time than suppression. By contrast, there was a moderate and positive linear relationship between  $\Delta ER$  and  $RT_{ER}$  ( $R^2 = 0.45$ ,  $p < 0.0001$ ) (Fig. 6).



**Figure 5.** Relationship between the change in discharge (difference in mean daily discharge between base flow and peak flow) and, in panel a) and b), the change in metabolic rate, used as a proxy for resistance, for  $\Delta GPP$  and  $\Delta ER$  respectively. In panels c) and d) the relationship with the recovery time in days, was used as a proxy for resilience, for  $RT_{GPP}$  and  $RT_{ER}$  respectively. The colour coding indicates whether the metabolic activity experienced stimulation (blue), suppression (red), or no significant change (yellow) in response to the storm event.



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**Figure 6. Relationship between the resistance and resilience of stream metabolism to hydrological perturbations for a) gross primary production (GPP) and b) ecosystem respiration (ER) for individual storm events. The colour coding indicates whether the metabolic activity experienced stimulation (blue), suppression (red), or no change (yellow) in response to the storm event.**

#### 4 Discussion

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In this study, we monitored the hydrology and metabolic activity across 35 individual storm events to understand how biota respond to hydrological perturbations in a highly oligotrophic, heterotrophic, non-perennial headwater stream. The magnitude, intensity and duration of storm events showed substantial variability, with all hydrological descriptors fluctuating over an order



of magnitude. For example, the increase in discharge ( $\Delta Q$ ) during the storm events ranged from 0.6 to 872.4 L s<sup>-1</sup>, capturing a broad spectrum of flow hydrographs. Similarly, RC values varied from 0.2% to 39%, which likely relates to large variability in antecedent soil moisture, land-water hydrological connectivity, and the associated solute supply from terrestrial ecosystems.

Our results showed no significant relationship between GPP and either discharge or light irradiation. On average, GPP was relatively low ( $1.7 \pm 1.8$  g O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>), with values falling at the lower end of the range reported for similarly sized streams (from 0.10 to 22 g O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) (Roberts and Mulholland 2007; Hall et al. 2016; Savoy et al. 2019). Yet, our estimates are within the range previously reported in this stream (from 0.05 to 1.9 g O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>; Acuña et al. 2004, Bernal et al. 2022). Compared to GPP, estimates of ER during the study period were an order of magnitude higher ( $-13.4 \pm 7$  g O<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>) and similar to previous studies (Acuña et al. 2004), highlighting the heterotrophic nature of this stream. ER was not related to water temperature, a major driver of metabolic activity, likely because it consistently remained above the threshold for sustaining biological activity (>4° C, De Nicola, 1996) or because other factors act as primary controls of in-stream heterotrophic activity. In this sense, ER was positively related to stream discharge, which aligns with previous studies pointing out that hydrology is a key driver of stream heterotrophic activity (Roberts et al., 2007; Hall et al., 2017). High flows can enhance heterotrophic activity by promoting the interaction of water with hyporheic sediments, by supplying soil heterotrophic bacteria (Roberts et al., 2007; Li et al., 2021), and more importantly, by delivering limiting nutrients and organic matter subsidies to the stream (Hinton et al., 1997; Demars, 2019; Lupon et al. 2023). In Fuirosos, this later explanation is supported by the overall increase in dissolved inorganic nitrogen (DIN) observed during storm flows (Bernal et al., 2002; 2005), which can decrease stream water C:N ratios and meet heterotrophic microbial stoichiometric needs as observed in other Mediterranean streams (Ledesma et al. 2022). This stimulation response of ER is likely enhanced in highly oligotrophic streams such as Fuirosos, typically exhibiting low DIN concentrations (< 0.6 mg NL<sup>-1</sup>) as well as limited in-stream N uptake rates during base flow conditions (Bernal et al., 2005; Peipoch et al., 2016; Peñarroya et al., 2022).

During individual storm events, both GPP and ER exhibited low resistance, regardless of the magnitude of the storm. Low resistance in GPP was observed in 94% of storm events, with rates changing between -95.9 and 141.7%. Interestingly, 69% of the storm events led to GPP stimulation, suggesting that hydrological disturbances might act as metabolic triggers for photoautotrophic activity. These findings agree with previous studies, which attributed this stimulation to a "cleaning effect" of the streambed induced by high flows, when benthic leaf litter and fine particulate organic matter are scored downstream, potentially enhancing light inputs and photosynthetic efficiency (e.g., Roberts et al., 2007; Demars 2019). However, and contrary to our expectations, GPP stimulation was not associated with the storm magnitude. This result could be explained by the small photoautotrophic activity measured in this heterotrophic stream, which led to marginal increases in GPP during individual storm events.

We also observed that storms act as triggers for heterotrophic metabolism, as 86% of events showed increases in ER rates compared to base flow conditions. The significant relation between  $\Delta Q$  and  $\Delta ER$  further suggests that greater solute flux



315 mobilized during storms amplified stream metabolic activity. As seen in previous studies, in Fuirosos, storm events can  
increase DOC and NO<sub>3</sub> concentrations by 35% and 28%, respectively, further supporting the idea that floods act as subsidies  
for heterotrophic microbial activity (Butturini et al., 2008). Moreover, the low hydrological connectivity of intermittent  
streams, driven by periodic disconnection from potential sources (e.g., riparian soils), reduces nutrient inputs from terrestrial  
ecosystems and exacerbates resource limitation (Bernal et al., 2013), likely explaining the low resistance and high stimulation  
320 of ER observed during storms. Conversely, our results suggest a minor effect of antecedent moisture conditions on ER,  
probably because we were only able to estimate metabolic rates under low RC values (in all cases, RC < 15%). Moreover, ER  
generally peaked 1–2 days after the discharge peak, which is consistent with prior studies showing that the highest metabolic  
and nutrient uptake rates usually occur during the beginning of the recession limb of the hydrograph (Roberts et al., 2007;  
Seybold and McGlynn, 2017). This delay may reflect either a physiological response (i.e., the time required for biofilms to  
325 respond to increased resource availability) or a hydrological response (i.e., the lag in the arrival of limiting nutrients from  
catchment sources). Aside from  $\Delta Q$ , we found no relation between changes in metabolic rates (i.e.,  $\Delta GPP$  and  $\Delta ER$ ) and storm  
duration or intensity. This finding could be explained by the intricate water flow paths and erratic hydrological response to  
precipitation events exhibited by this intermittent stream (Butturini et al., 2002). Overall, our findings highlight the complexity  
of biotic responses to hydrological perturbations, which cannot be easily linked to specific storm characteristics such as  
330 duration, intensity, or antecedent moisture conditions.

Notably, only one storm event resulted in ER suppression, which contrasts with previous studies reporting almost no change  
or mostly suppression of ER during storm events (Reisinger et al., 2017; O'Donnell and Hotchkiss, 2022). O'Donnell and  
Hotchkiss (2022) explored different magnitudes of storm events, though in a suburban stream with no nutrient limitation, while  
Reisinger et al. (2017) focused on extreme events that had a destructive effect on stream biofilm. The increase in sediment  
335 transport and turbidity (Bernhardt et al., 2018) as well as the reduction in water residence time (Fisher and Grimm, 1988;  
Uehlinger, 1991) can also contribute to decreased stream metabolic activity during large storm events. Unfortunately, in  
Fuirosos, none of the days with discharge exceeding 100 L s<sup>-1</sup> passed quality checks for metabolic estimates, so large storm  
events could not be included in our analysis. Future studies should aim to overcome the logistical and computational challenges  
of calculating metabolism during extreme discharges to better predict the metabolic responses to such disturbances.

340 Our results also show that metabolic rates have high resilience to hydrological perturbations, as the average recovery time  
(RT) for GPP and ER after a storm were ca. 3 days. Similar metabolic recovery times (ca. 5 days) were observed in other USA  
and European headwater streams (e.g., Roberts et al., 2007; O'Connor et al., 2012; Griffiths et al., 2013). For GPP, resilience  
was not influenced by any hydrological descriptor, suggesting that recovery patterns might be related to other environmental  
drivers. For instance, previous studies have suggested that the recovery time of GPP varies with seasonal patterns of light  
345 availability (Uehlinger and Naegeli, 1998; Connell, 1978; Acuña et al., 2004; O'Donnell and Hotchkiss, 2022). For ER,  
recovery times increased proportionally with the storm magnitude ( $\Delta Q$ ) and the degree of stimulation ( $\Delta ER$ ), emphasizing a



link between the resistance and resilience of stream biota to hydrological perturbations. Interestingly, we observed a threshold for ER recovery times at ca. 6 days (Fig. 5a), a period clearly shorter than the mean duration of storm events in this stream ( $13 \pm 7$  days). This result can be explained either by the duration of the washing of nutrients and organic matter from terrestrial sources to the stream (Jowett and Biggs, 1997; Butturini et al., 2005; Demars, 2019), or the dilution of those resources by other catchment water sources contributing to stream runoff later on (Bernal et al., 2006). Overall, our findings suggest that metabolic rates, particularly ER, are susceptible to fluctuations in resource availability, especially in oligotrophic headwater streams.

## 5 Conclusion

This study reveals that the dynamic response of stream metabolism to storm disturbances is a key element for understanding ecosystem functioning in the context of global change. By assessing the effects of storms of varying magnitude, duration, and intensity, we gained valuable insights into how hydrological perturbations shape key metabolic processes in heterotrophic headwater streams. Our results highlight the low resistance and resilience of ER, which consistently showed significant increases during storm events and required up to 6 days to recover to base flow conditions, particularly in cases with greater discharge. These findings highlight the importance of terrestrial-aquatic linkages in replenishing limiting resources in oligotrophic systems, where nutrient and organic matter inputs are crucial for sustaining metabolic activity. In this context, non-perennial oligotrophic streams experience “breathing storms”, where disturbances act as triggers of heterotrophic metabolism and fundamentally alter the role of streams in carbon dioxide emissions and the global carbon cycle. To better understand the consequences and underlying mechanisms of these metabolic pulses, future studies should focus on analysing the variability of water chemistry and dissolved organic matter composition during storms to pinpoint the specific limiting resources driving these changes. Additionally, it is crucial to consider the stoichiometric balance of nutrients and organic matter during floods, as this balance governs the metabolic response of heterotrophic systems. Overall, our findings have significant implications for the carbon budgets of headwater catchments, suggesting that shifts in hydrological regimes due to climate change could alter carbon cycling.

## Data availability

The data that support the findings of this study will be openly available in a public repository (HydroShare) that issues datasets with DOIs if the paper is accepted.



## Author contributions

Conceptualisation: CJ, AL, SB. Field work and laboratory analysis: CJ, AL, XP, SB. Data analysis: CJ, EL, JLJL, GRR. Preparation of figures and tables: CJ. Data interpretation: CJ, AL, EL, XP, JLJL, GRR, SB. Writing first draft: CJ. Writing  
375 final draft: CJ, AL, EL, XP, JLJL, GRR, SB.

## Competing interests

The authors declare that this research was conducted in the absence of any commercial or financial relationships that could be construed as potential conflicts of interest.

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