Contents lists available at ScienceDirect





Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Multiple drying aspects shape dissolved organic matter composition in intermittent streams



Verónica Granados^{a,1}, Rebeca Arias-Real^{a,b,c,*,1}, Cayetano Gutiérrez-Cánovas^d, Biel Obrador^a, Andrea Butturini^a

^a Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, University of Barcelona, Barcelona, Spain

^b Centre of Molecular and Environmental Biology (CBMA), Department of Biology, University of Minho, Campus of Gualtar, 4710-057 Braga, Portugal

^c Institute of Science and Innovation for Bio-Sustainability (IB-S), University of Minho, Campus of Gualtar, 4710-057 Braga, Portugal

^d Biological Invasions Group, Department of Integrative Ecology, Doñana Biological Station (EBD-CSIC), Av. Américo Vespucio, 26, Isla de la Cartuja, 41092 Seville, Spain

HIGHLIGHTS

GRAPHICAL ABSTRACT

- Drying duration and frequency increase DOC concentration and modify DOM composition.
- Multiple drying aspects are needed to explain DOM composition.
- Drying duration and frequency reduce autochthonous and aromatic compounds.
- Drying frequency and last dry event duration increase humic-like substances.



ABSTRACT

ARTICLE INFO

Editor: Ashantha Goonetilleke

Keywords:

Dissolved organic matter Intermittent rivers and ephemeral streams Dissolved organic carbon Drying aspects Flow intermittence Mediterranean streams Water availability is a fundamental driver of biogeochemical processing in highly dynamic ecosystems such as intermittent rivers and ephemeral streams (IRES), which are recognized as the most common fluvial ecosystem globally. Because of their global extent, IRES have a remarkable contribution to organic matter processing, which is expected to intensify as climate change and water extraction expand IRES extension. Nevertheless, the effect of the complexity of the drying process on river biogeochemistry remains unclear. This study investigated how drying aspects affect the dissolved organic carbon (DOC) concentration and composition in 35 streams along a wide flow-intermittence gradient in the NE Iberian Peninsula. To do that, four drying aspects: annual drying duration, annual frequency, duration of the last drying event, and time since the last drying event were characterized. Results showed that DOC concentration and the contribution of humic-like compounds were positively associated with intensifying drying conditions. In addition, protein-like compounds were positively associated with intensifying drying conditions. In addition, protein-like compounds were positively associated with intensifying drying concentration and the contribution of humic-like compounds were annual drying frequency and the duration of the last drying event jointly explained dissolved organic matter composition. These results suggest that the quantity and composition of dissolved organic matter in streams respond differently to the temporal aspects of the drying process. Our study can help to better anticipate changes in organic matter in the context of climate change.

* Corresponding author at: Department of Evolutionary Biology, Ecology and Environmental Sciences, Faculty of Biology, University of Barcelona, Barcelona, Spain. *E-mail address:* Rebeca.arias.real@ub.edu (R. Arias-Real).

¹ VG and RA-R contributed equally to this manuscript.

http://dx.doi.org/10.1016/j.scitotenv.2022.158376

Received 17 March 2022; Received in revised form 24 August 2022; Accepted 25 August 2022 Available online 29 August 2022 0048-9697/© 2022 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (http://creativecommons.org/licenses/by-nc-nd/4.0/).

1. Introduction

Fluvial ecosystems are hotspots of organic matter processing (Battin et al., 2008; McClain et al., 2003) because they receive large amounts of organic matter from terrestrial ecosystems. It is well established that hydrology has a key role in controlling biogeochemistry in flowing waters (Baek et al., 2019; Fasching et al., 2016; Guarch-Ribot and Butturini, 2016). In particular, recent evidence highlights the impact of flow intermittence on the global carbon cycle (Dewey et al., 2020). Thus intermittent rivers and ephemeral streams are receiving more attention due to their global distribution and expected expansion as a consequence of climate change (Datry et al., 2014, 2018; Granados and Butturini, 2019; Shumilova et al., 2019). However, the complexity of the drying process can give rise to different annual (drying duration and frequency) and previous drying aspects (duration of the last drying event and rewetting) (Arias-Real et al., 2021; Butturini, 2021; Ejarque et al., 2017; Granados and Butturini, 2019). Thus, understanding how these drying aspects influence organic matter dynamics is a fundamental step to better predict how global carbon cycles will respond to global change.

Previous studies have found that water availability strongly influence the concentration of dissolved organic carbon (DOC) and the composition of dissolved organic matter (DOM). For instance, drying reflects a reduction of hydrological connectivity with terrestrial ecosystems, which increases the concentrations of autochthonous DOM sources (e.g., protein-like constituents) (Fellman et al., 2011; Siebers et al., 2016; Vázquez et al., 2015; von Schiller et al., 2015). Persistent drying conditions are also associated with a marked increase of DOC concentrations and the prevalence of humic-like compounds (Granados et al., 2020; Harjung et al., 2018, 2019). However, DOM shows a more aromatic and humic-like character during rewetting, although protein-like and microbial-derived sources are also discernible (Inamdar et al., 2011; Shumilova et al., 2019). Although there is evidence showing that both drying and rewetting periods are "hot moments" for DOM production, transformation and transport (Casas-Ruiz et al., 2016; Harjung et al., 2018; Vazquez et al., 2011; von Schiller et al., 2015), it is still unclear how the duration and frequency of these hydrological phases influence DOC concentration and DOM composition.

Despite the progress in the field, previous studies have typically explored drying effects on stream ecosystems by focusing on qualitative hydrological descriptors (perennial vs. intermittent), short-term assessments spanning weeks (pre- and post-drying) or using a single drying descriptor (e.g., drying duration; Arias-Real et al., 2020; Belmar et al., 2019; Reynolds et al., 2015). However, integrating different drying aspects, such as frequency or characteristics of recent drying events, has the potential to better predict organic matter dynamics in intermittent streams.

This study investigated the effects and importance of annual and recent drying aspects on DOM quantity (DOC concentration) and composition (DOM optical qualitative parameters). To do that, 35 Mediterranean streams were selected across a wide flow-intermittence gradient and four drying aspects were characterized: annual drying duration (total number of zeroflow days; ZFT), annual frequency (total number of zero-flow periods; ZFP), the duration of the last drying event (number of zero-flow of the last zero-flow period; ZFL) and the flowing time since the last rewetting event (RE). Next, the effect and importance of these drying aspects on DOC level and DOM composition were investigated, while controlling for other key non-hydrological abiotic factors (water temperature and altitude). According to previous studies (Casas-Ruiz et al., 2016; Granados et al., 2020; Harjung et al., 2018; von Schiller et al., 2015), it is expected that the duration of the last drying event and the time since the last rewetting event will be more important than the annual drying aspects for DOC level and DOM composition.

2. Materials and methods

2.1. Study site

This study was conducted at 35 independent streams located in nine river basins across Catalonia (NE Spain) over a wide flow intermittence gradient (from permanent to ephemeral streams). Stream catchments include natural, semi-natural or extensive agriculture land cover (cereals, olive trees, vineyards; see Appendix A, Table A1 for more details), which resulted in low to moderate nutrient concentrations (median dissolved inorganic nitrogen = 1.44 mg/L, median soluble reactive phosphorous = 0.02 mg/L). The stream order ranges from two to five. Climate is typically Mediterranean, characterized by warm and dry summers and precipitation occurring mainly in autumn and spring. Summer storms can occasionally occur during summer.

2.2. Characterization of drying aspects

To characterize drying aspects, one year before our sampling campaign (on February 2016), temperature and water level data loggers were placed on each streambed, which enabled the inference of water presence and absence (Arias-Real et al., 2021; Gionchetta et al., 2020). The data loggers were recording data at hourly intervals during one year (from February 2016 until February 2017; see Methodological details in Appendix B). Once temperature and water level data were retrieved (that is, on February 2017) four drying aspects were calculated (Fig. 1). First, the annual drying duration was calculated as the total number of dry days (zero-flow total days, ZFT). Second, the drying frequency was calculated as the annual number of dry periods (annual frequency ZFP). Then, the duration of the last dry period was calculated (zero-flow last, ZFL). Finally, the duration of the last rewetting event was calculated (RE, rewetting). Drying aspects exhibited a wide range of variation, ranging from permanent-flow streams with 0 annual dry days to ephemeral streams with >324 annual dry days. Moreover, annual drying frequency ranged from 0 to 8. The duration of the last dry period oscillated from 0 to 294 days, whereas the rewetting duration since the last drying event ranged from 6 to 274 days (Appendix C Table C1).

2.3. Dissolved organic carbon and optical measurements

Water samples for DOC and DOM analysis were collected just after the rainy season (on February 2017) to ensure that all streams were in flowing phase. Water samples were filtered using precombusted (450 °C) glass fiber filters (Whatman GF/F, 0.7 μ m pore size) followed by nylon filters with a 0.22- μ m pore. The filtered samples were placed in precombusted amber glass bottles previously washed with diluted acid. Samples were kept cooled in dark conditions, being immediately transported to the laboratory, where they were stored at 4 °C until analysis.

DOC concentration was analyzed by oxidative combustion infrared analysis on a Shimadzu TOC-VS (Shimadzu Corporation, Kyoto, Japan) on preacidified samples (HCl, final sample pH = 2-3). DOM composition was characterized using spectroscopic methods. Absorbance spectra for the DOM were obtained using a UV1700 PharmaSpec spectrophotometer (Shimadzu) and a 1-cm quartz cell. Absorbance data were obtained in the double-beam mode, with the wavelength scanned from 200 to 800 nm, using deionized water as the blank. Excitation-Emission matrices (EEM) were generated with an RF-5301 PC spectrofluorometer (Shimadzu). Spectra were obtained over (excitation-emission) wavelengths of 240-420 nm and 280-690 nm. EEMs were standardized with the method by Goletz et al. (2011), using the Mathematica software (Wolfram Research). The same method was used to correct the inner filter effects on the absorbance data (Lakowicz, 2006). To correct the wavelength-dependent inefficiencies of the detection system, the method of Gardecki and Maroncelli (1998) for emission measurements and the method of Lakowicz (2006) for excitation correction were applied. Daily measurements of the area under the Raman peak of Milli-Q water blanks were used to normalize the data from each day of analysis with the spectrofluorometer (Lawaetz and Stedmon, 2009).

DOM optical indices included three chromophoric indices and three fluorophoric indices. The chromophoric indices were: (a) the specific ultra-violet absorbance at 254 nm (SUVA254), (b) the ratio of absorbance at 250 nm to that at 365 nm (E2:E3) and (c) the spectral slope ratio (Sr). The three fluorophoric indices considered were: (a) the humification



Fig. 1. Characterization of drying aspects. F corresponds to flowing conditions, ZF to zero-flow conditions. ZFT is the annual number of days with zero flow, ZFP is the annual number of zero-flow periods, ZFL is the number of zero-flow days during the last drying event, and RE is the number of days since the last drying event.

index (HIX), (b) the fluorescence index (FI) and (c) the biological index (BIX). These optical indices are able to capture different components of the DOM composition (Hansen et al., 2016), including aromaticity

(SUVA₂₅₄), humic-like substances (HIX), autochthonous DOM sources and protein-like substances (FI, BIX) and molecular weight (E2:E3 and Sr) (see Table 1 for more details).

Table 1

Description of the DOM optical qualitative indices.

-			
Index	Calculation	Interpretation	Reference
SUVA ₂₅₄ Specific ultra-violet absorbance at 254 nm	The absorption coefficient at 254 nm is normalized by the DOC concentration.	Higher values of SUVA $_{254}$ are typically related to greater aromaticity.	(Weishaar et al., 2003)
HIX Humification index	The area under the emission spectra at 435–480 nm divided by the peak area at 310–345 nm from the spectra at an excitation wavelength of 254 nm.	HIX indicates the extent of humification by quantifying the shift in the emission spectra towards longer wavelengths due to lower H: C ratios. HIX values range from 0 to 1. Higher values indicate a greater degree of DOM humification.	(Ohno, 2002)
FI Fluorescence index	The ratio of emission intensity at 470 nm to that at 520 nm emitted at an excitation wavelength of 370 nm.	The FI is a proxy of the DOM origin. High values suggest the prevalence of labile, algal-, or microbial-like sources (i.e., stream-produced DOM).	(Cory and McKnight, 2005)
BIX Biological index	The BIX is calculated at an excitation wavelength of 310 nm as the fluorescence intensity ratio emitted at 380 nm to that emitted at 430 nm.	High BIX values (>1) suggest the presence of autochthonous and fresh DOM. Values of 0.6–0.7 indicate low or zero autochthonous DOM production.	(Huguet et al., 2009)
E2:E3	The ratio of absorbance at 250 nm to that at 365 nm.	$E_2:E_3$ provides information about the DOM molecular size. This index is inversely related with molecular weight.	(De Haan and De Boer, 1987)
Sr Slope ratio	Dimensionless parameter. The ratio of the logarithmically transformed absorbance spectra slope at 275–295 nm ($S_{275-295}$) to that estimated at 350–400 nm ($S_{350-400}$).	The Sr integrates shifts in the molecular size of DOM. High values of this index indicate an increase in the proportion of the small DOM molecular fraction.	(Helms et al., 2008)

2.4. Data analysis

First, Pearson correlations were used to understand the covariation between DOC and DOM optical indices over the drying gradients. Next, the effect and importance of the drying aspects (ZFT, ZFP, ZFL and RE) on DOC concentration and DOM optical indices were estimated using linear regression models and a multi-model inference approach (Burnham and Anderson, 2002; Grueber et al., 2011). Altitude and water temperature were also included as predictors to account for the non-hydrological variation in our models. See Appendix D, Table D1 for more details on model construction.

To do so, the explanatory capacity of 12 multiple-regression models were evaluated, considering all possible combinations of predictors, excluding those with high collinearity (i.e., $r \le |0.70|$ or the variance inflation factor ≤ 2). Models that simultaneously included ZFT and ZFL were discarded because they showed high collinearity (r = 0.78; see Appendix E, Table E1 and E2 for more details). Afterwards, for each response variable, all 12 models were ranked using the values of the Akaike information criterion for small sample sizes (AICc), retaining those showing a Δ AICc < 2 with respect to the model ranked first (Zuur et al., 2009). The explained variance (\mathbb{R}^2) and Akaike weights were also calculated to determine the explanatory power and relative likelihood of each model being the best model. MuMIM R package was used to obtain AICc, Akaike weights and explained variance (Bartoń, 2016).

A variance partitioning analysis was used to evaluate the effects of drying aspects and non-hydrological abiotic factors on DOC concentration and DOM optical indices (Hoffman and Schadt, 2016). For all models, residual plots were visually checked to verify model assumptions. Before analysis, to reduce distribution skewness, a log-transformation for DOC, HIX, SUVA254 and Sr a square-root transformation for E2:E3, ZFL, ZFP and ZFT, and a fourth-root transformation for RE were performed. Finally, to produce standardized and comparable model coefficients, predictors were standardized to a comparable scale (mean = 0, SD = 1). All statistical analyses were performed in R 3.5.1 (R Development Core Team, 2011).

3. Results

3.1. Variation of dissolved organic matter quantity and composition over the drying gradient

DOC concentration and DOM optical indices (see Table 1) showed high variability across the studied streams. DOC concentrations ranged from 0.7 to 14.6 mg C·L⁻¹, the SUVA₂₅₄ varied from 1.83 to 8.59 L mg C⁻¹ m⁻¹, the HIX values fluctuated from 0.49 to 0.94, the FI ranged from 1.47 to 1.92, the BIX varied from 0.73 to 3.91 (see Table 1 for a full description of DOM optical indices). DOC was positively correlated with the HIX ($r_P = 0.62$) and E2:E3 ($r_P = 0.48$) and negatively associated with the SUVA254 ($r_P = -0.22$), FI ($r_P = -0.41$), BIX ($r_P = -0.67$) and Sr ($r_P = -0.44$).

3.2. Effects of drying aspects on dissolved organic matter quantity and composition

Two contrasting patterns in response to annual and recent drying aspects were identified. The first group of variables, including DOC concentration, and the HIX and $E_2:E_3$, tended to increase with the annual drying duration and frequency. DOC concentration increased with both annual drying duration and frequency (Fig. 2), whereas the HIX and $E_2:E_3$ showed a positive response to annual drying frequency and the duration of the last drying event (Fig. 3). However, rewetting duration showed a positive effect on the $E_2:E_3$, negative effect on the HIX and no effect on the DOC concentration. On the contrary, the second group of variables, including the SUVA₂₅₄, FI, BIX and Sr indices decreased with drying conditions to different degrees. The SUVA₂₅₄ and Sr also decreased with the annual drying frequency and the duration of the last drying event. The BIX and FI responded positively to rewetting duration, whereas the Sr showed a negative response (Fig. 3). Water temperature and altitude had an overall positive effect on



Fig. 2. Mean standardized effects of drying aspects on DOC concentration. ZFT: annual drying duration; ZFP: annual drying frequency; ZFL: duration of the last drying event; RE: the number of rewetting days since the last drying event.

DOC, and the SUVA $_{254}$ and FI and an overall negative effect on the HIX and E2:E3 (Appendix F, Table 1). Altitude had an overall positive effect on the Sr.

3.3. Importance of drying aspects on dissolved organic matter quantity and composition

Annual drying duration was the best predictor of DOC concentration (mean explained variance: 42.9 %), whereas DOM composition was explained by a combination of multiple drying aspects (Fig. 4). Annual drying duration showed a limited capacity to predict variations in DOM composition (mean explained variance: 5.9%) compared to annual drying frequency (mean explained variance: 13.1 %) and the duration of the last drying event (mean explained variance: 9.2 %). Annual drying frequency was the best predictor of the E2:E3 (mean explained variance: 36.5 %), HIX (mean explained variance: 20.9 %) and Sr (mean explained variance: 14.8 %). The duration of the last drying event also explained the E2:E3 (mean explained variance: 33.7 %) and Sr (mean explained variance: 12.5 %). Rewetting duration showed a certain explanatory capacity for the BIX (mean explained variance: 8.7 %) and HIX (mean explained variance: 7.9 %). Water temperature was generally relevant for DOC and DOM indices (mean explained variance: 7.2 %, range: 1.3-17.9 %), but altitude had a weak predictive capacity (mean explained variance: 1.1 %, range: 0.0-3.2 %). Water temperature was particularly important for the SUVA₂₅₄ (mean explained variance: 17.9 %) and FI (mean explained variance: 14.9 %).

4. Discussion

This study demonstrated that preceding drying increased DOC concentration and modified DOM composition during the flowing phase. In addition, DOC concentration was mainly explained by annual drying duration, whereas DOM composition was better predicted by multiple drying aspects than by a single drying descriptor. Specifically, annual drying frequency, the duration of the last drying event and the time since the last drying event jointly explained changes in DOM composition. These findings suggest that the quantity and composition of DOM in streams respond differently to the temporal components of the drying process.

4.1. Effects of drying aspects on dissolved organic matter quantity and composition

The results of this study align with previous evidence showing that drying events tend to increase DOC concentration (Granados et al., 2020; Harjung et al., 2018; Vazquez et al., 2011; von Schiller et al., 2015). This pattern

Science of the Total Environment 852 (2022) 158376



Fig. 3. Mean standardized effects of drying aspects on DOM optical indices. ZFT: annual drying duration; ZFP: annual drying frequency; ZFL: duration of the last drying event; RE: the number of rewetting days since the last drying event.



Fig. 4. Mean importance of the drying aspects on DOC and DOM patterns. ZFT: annual drying duration; ZFP: annual drying frequency; ZFL: duration of the last drying event; RE: the number of rewetting days since the last drying event.

can be explained by the reduced capacity of intermittent and ephemeral streams to degrade organic matter (Abril et al., 2016; Arias-Real et al., 2020). Channel desiccation slows down microbial activity (Gionchetta et al., 2020) and reduces microbial diversity (Febria et al., 2012), which jointly can limit the degradation of certain organic compounds (e.g., drying events inhibit lignocellulolytic enzyme activities; Arias-Real et al., 2018; Bärlocher, 2016; Mas-Martí et al., 2015). For example, the contrasting correlation of labile (the BIX and FI) and humic-like substances (the HIX) with DOC seems to support these processes, where the more reactive substances are replaced by refractory organic compounds as drying intensifies (Granados et al., 2020). In addition to desiccation, hydrological contraction and fragmentation leading to isolated pools, can also reduce DOM degradation (Catalán et al., 2017; Gómez-Gener et al., 2016). Collectively, the annual and recent aspects of the hydrological fragmentation and drying phases appear as critical factors determining dissolved organic matter concentration and composition.

The main novelty of the present study was in finding that DOM composition during the flowing phase was better explained by a wider range of drying aspects than previously thought. Thus, in addition to annual drying duration, annual drying frequency, the duration of the last dry period and the time since the last dry period explained changes in DOM composition. Furthermore, DOM constituents changed over this drying gradient towards a progressive reduction in the amount of protein-like, autochthonous and aromatic compounds, and an increase in humic-like substances.

Reductions in protein-like and autochthonous organic compounds can be linked to two different processes. First, drying can limit algal and heterotrophic microbial production during the dry phases. This can occur as a result of desiccation processes that slow down the metabolic activity of aquatic organisms (Gionchetta et al., 2020; Graça et al., 2022) or due to cascading effects disrupting species interactions and synergisms (Arias-Real et al., 2022). Second, after rewetting, the organic carbon pool of IRES might loss the most-reactive components due to the intense carbon degradation during this hydrological phase (Inamdar et al., 2011; Shumilova et al., 2019; von Schiller et al., 2019). Flash storms can lead to an episodic but rapid recovery of microbial activity, even during the dry phase, which might further accelerate the consumption of the most labile DOM (Amalfitano et al., 2008; Inamdar et al., 2011; Marxen et al., 2010). However, these patterns contrast with the early steps of stagnation, where hydrological contraction and fragmentation increase protein-like and autochthonous DOM (Casas-Ruiz et al., 2016; Vazquez et al., 2011; von Schiller et al., 2015). These contrasting patterns between hydrological phases suggest that intermittent streams experience abrupt changes in organic matter quantity and composition over the hydrological cycle, potentially influencing microbial biodiversity and associated functions.

Reduced aromaticity in response to the duration of the last drying event might be linked to the reduced surface runoff and thus terrestrial organic matter inputs during drying events. Yet episodic storms can increase DOM aromaticity through an increase in terrestrial carbon inputs (Inamdar et al., 2011). However, models showed a limited capacity to explain changes in the SUVA₂₅₄, calling for caution to verify these expectations.

The observed increase in humic-like substances over the drying gradient can be related to the accumulation of refractory DOM constituents as water renewal decreases (Casas-Ruiz et al., 2017; Catalán et al., 2016). During the first moments of the hydrological contraction and fragmentation, humiclike compounds increase abruptly (Granados et al., 2020). In addition, after flow resumption, humic-like substances tend to persist over the river continuum because of their refractory composition (Catalán et al., 2017). In this study, the large inputs of terrestrial organic matter during autumn and winter preceding data collection, could have further favored the persistence of humic-like substances in the streams with lower water renewal (i.e., the most intermittent and ephemeral streams).

4.2. Importance of drying aspects on dissolved organic matter quantity and composition

The results of this study underscore the importance of considering additional drying aspects beyond annual drying duration to better understand the biogeochemistry of IRES. Annual drying frequency and the duration of the last drying events emerge as complementary drivers of DOC and DOM composition, potentially reflecting a wider array of hydrological, geochemical and biological processes (Gómez-Gener et al., 2021). Unexpectedly, the time since the beginning of the last rewetting had a low explanatory capacity of DOC and DOM composition. Previous studies have highlighted the importance of this hydrological phase in organic matter processing (Shumilova et al., 2019; von Schiller et al., 2019). For example, in small intermittent streams, rewetting causes a large input of allochthonous compounds followed by a delayed microbial carbon processing of 2-3 days (Guarch-Ribot and Butturini, 2016; Vazquez et al., 2011; von Schiller et al., 2015). However, because of the timing of our study (February 2017), this study was unable to capture this short-term, episodic processes, suggesting that this drying aspect needs to be refined to be useful. Future studies should determine a more suitable timing to capture how the duration and frequencies of short-term rewetting processes influence the spatial distribution of DOC and DOM. In addition to drying aspects, water temperature contributed to explain variations in DOM composition, whereas altitude had a limited capacity to explain organic carbon concentration and composition. In this study, warmer waters were linked to more labile and aromatic organic compounds and less humified DOM constituents. A potential explanation is that warmer waters are related to reduced riparian cover and increased instream autotrophic and microbial productivity, which results in a higher production of protein-like compounds (Adams et al., 2010; Morin et al., 1999). These findings match previous results showing that climatic variables, such as temperature and precipitation, control organic matter processing at large scales (Catalán et al., 2018; Picazo et al., 2020; von Schiller et al., 2019).

4.3. Implications for global biogeochemical cycles

The results of this study suggest that watercourses are expected to show increased DOC concentration and altered DOM composition in response to climatically-driven increases of drying duration and frequency (Döll and Schmied, 2012; Koutroulis et al., 2019; Messager et al., 2021). Accordingly, this can lead to an increased flux of DOC to oceans due to the reduced processing over drainage networks only if the discharge does not decrease as well, with implications for coastal ecosystems and the global carbon cycle (Aufdenkampe et al., 2011; Battin et al., 2009). In this sense, increasing drying conditions might turn intermittent rivers and ephemeral streams into more passive carbon conduits than perennial watercourses (Casas-Ruiz et al., 2020; Cole et al., 2007). Thus, this study can be helpful to better understand how future spatial changes in drying conditions can influence global carbon dynamics and budgets.

5. Conclusions

The comprehensive characterization of the drying process in Mediterranean streams allowed to evaluate the effect and importance of multiple drying aspects on DOM quantity and composition. This study showed that single indicator of drying (annual drying duration) captured variations in DOC but did not fully capture changes in DOM composition. This highlights the need to integrate additional drying aspects, such as drying annual frequency and the duration of the last drying event, in biogeochemical studies. This study also indicated that increasing drying severity and frequency resulting from climate change can further increase DOC concentration and alter DOM composition. Collectively, these findings can help to better understand the role of drying events in organic matter processing and to anticipate the consequences of climate change.

CRediT authorship contribution statement

Verónica Granados: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. Rebeca Arias-Real: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. Cayetano Gutiérrez-Cánovas: Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing – review & editing. Biel Obrador: Conceptualization, Data curation, Investigation, Methodology, Validation, Visualization, Writing – review & editing. Biel Obrador: Conceptualization, Data curation, Investigation, Methodology, Validation, Visualization, Writing – review & editing. Andrea Butturini: Conceptualization, Data curation, Investigation, Methodology, Validation, Visualization, Data curation, Investigation, Methodology, Validation, Writing – review & editing.

Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare no conflict of interest.

Acknowledgements

We would like to thank Prof. Ashantha Goonetilleke and four anonymous reviewers for constructive suggestions on earlier versions of the manuscript. This research was funded by the Spanish Ministry of Education and Science (MEC) (CGL2014-5876-C3-R), the European Union 7th Framework Programme (No. 603629-ENV-2013-6.2.1-Globaqua) and DRYHARHSAL (RTI2018-097950-B-C21) by MCIN/AEI/10.13039/501100011033. AB and BO are members of the research group ForeStream (2014SGR949). CG-C was supported by a "Juan de la Cierva – Incorporación" contract from the Spanish Ministry of Science and Innovation (MICINN, IJC2018-036642-I). RA-R held a post-doctoral grant "Margarita Salas" from the Spanish Ministry of Universities and the Next Generation EU — Recovery, Transformation and Resilience Plan.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.scitotenv.2022.158376.

References

- Abril, M., Muñoz, I., Menéndez, M., 2016. Heterogeneity in leaf litter decomposition in a temporary Mediterranean stream during flow fragmentation. Sci. Total Environ. 553, 330–339. https://doi.org/10.1016/j.scitotenv.2016.02.082.
- Adams, H.E., Crump, B.C., Kling, G.W., 2010. Temperature controls on aquatic bacterial production and community dynamics in arctic lakes and streams. Environ. Microbiol. 12, 1319–1333. https://doi.org/10.1111/j.1462-2920.2010.02176.x.
- Amalfitano, S., Fazi, S., Zoppini, A., Barra Caracciolo, A., Grenni, P., Puddu, A., 2008. Responses of benthic bacteria to experimental drying in sediments from Mediterranean temporary rivers. Microb. Ecol. 55, 270–279. https://doi.org/10.1007/s00248-007-9274-6.
- Arias-Real, R., Menéndez, M., Abril, M., Oliva, F., Muñoz, I., 2018. Quality and quantity of leaf litter: both are important for feeding preferences and growth of an aquatic shredder. PLoS One 13 (12), e0208272. https://doi.org/10.1371/journal.pone.0208272.
- Arias-Real, R., Gutiérrez-Cánovas, C., Menéndez, M., Granados, V., Muñoz, I., 2021. Diversity mediates the responses of invertebrate density to duration and frequency of rivers' annual drying regime. Oikos 130, 2148–2160. https://doi.org/10.1111/oik.08718.
- Arias-Real, R., Gutiérrez-Cánovas, C., Muñoz, I., Pascoal, C., Menéndez, M., 2022. Fungal biodiversity mediates the effects of drying on freshwater ecosystem functioning. Ecosystems 25, 780–794. https://doi.org/10.1007/s10021-021-00683-z.
- Arias-Real, R., Muñoz, I., Gutierrez-Cánovas, C., Granados, V., Lopez-Laseras, P., Menéndez, M., 2020. Subsurface zones in intermittent streams are hotspots of microbial decomposition during the non-flow period. Sci. Total Environ. 703, 135485. https://doi.org/10. 1016/j.scitotenv.2019.135485.
- Aufdenkampe, A.K., Mayorga, E., Raymond, P.A., Melack, J.M., Doney, S.C., Alin, S.R., Aalto, R.E., Yoo, K., 2011. Riverine coupling of biogeochemical cycles between land, oceans, and atmosphere. Front. Ecol. Environ. 9, 53–60. https://doi.org/10.1890/100014.
- Baek, S., Lee, H., Park, J., Cho, K.H., 2019. Investigating influence of hydrological regime on organic matters characteristic in a Korean watershed. Water https://doi.org/10.3390/ w11030512.
- Bärlocher, F., 2016. Aquatic hyphomycetes in a changing environment. Fungal Ecol. 19, 14–27. https://doi.org/10.1016/j.funeco.2015.05.005.
- Bartoń, K., 2016. MuMIn: Multi-model Inference. R Package Version1.15.6.
- Battin, T.J., Kaplan, L.A., Findlay, S., Hopkinson, C.S., Marti, E., Packman, A.I., Newbold, J.D., Sabater, F., 2008. Biophysical controls on organic carbon fluxes in fluvial networks. Nat. Geosci. 1, 95–100. https://doi.org/10.1038/ngeo101.
- Battin, T.J., Luyssaert, S., Kaplan, L.A., Aufdenkampe, A.K., Richter, A., Tranvik, L.J., 2009. The boundless carbon cycle. Nat. Geosci. 2, 598–600. https://doi.org/10.1038/ngeo618.
- Belmar, O., Bruno, D., Guareschi, S., Mellado-Díaz, A., Millán, A., Velasco, J., 2019. Functional responses of aquatic macroinvertebrates to flow regulation are shaped by natural flow intermittence in Mediterranean streams. Freshw. Biol. 64, 1064–1077. https://doi. org/10.1111/fwb.13289.
- Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. Ecological Modelling, 2nd ed Springer, New York https://doi.org/10.1016/j.ecolmodel.2003.11.004.
- Butturini, A., 2021. Fuirosos stream (NE Iberian Peninsula): for how much longer? Limnetica 40, 205–222. https://doi.org/10.23818/limn.40.14.
- Casas-Ruiz, J.P., Catalán, N., Gómez-Gener, L., von Schiller, D., Obrador, B., Kothawala, D.N., López, P., Sabater, S., Marcé, R., 2017. A tale of pipes and reactors: controls on the instream dynamics of dissolved organic matter in rivers. Limnol. Oceanogr. 62, S85–S94. https://doi.org/10.1002/lno.10471.
- Casas-Ruiz, J.P., Spencer, R.G.M., Guillemette, F., von Schiller, D., Obrador, B., Podgorski, D.C., Kellerman, A.M., Hartmann, J., Gómez-Gener, L., Sabater, S., Marcé, R., 2020. Delineating the continuum of dissolved organic matter in temperate river networks. Glob. Biogeochem. Cycles 34, e2019GB006495. https://doi.org/10.1029/2019GB006495.
- Casas-Ruiz, J.P., Tittel, J., von Schiller, D., Catalán, N., Obrador, B., Gómez-Gener, L., Zwirnmann, E., Sabater, S., Marcé, R., 2016. Drought-induced discontinuities in the source and degradation of dissolved organic matter in a Mediterranean river. Biogeochemistry 127, 125–139. https://doi.org/10.1007/s10533-015-0173-5.

- Catalán, N., Casas-Ruiz, J.P., Arce, M.I., Abril, M., Bravo, A.G., del Campo, R., Estévez, E., Freixa, A., Giménez-Grau, P., González-Ferreras, A.M., Gómez-Gener, L., Lupon, A., Martínez, A., Palacin-Lizarbe, C., Poblador, S., Rasines-Ladero, R., Reyes, M., Rodríguez-Castillo, T., Rodríguez-Lozano, P., Sanpera-Calbet, I., Tornero, I., Pastor, A., 2018. Behind the scenes: mechanisms regulating climatic patterns of dissolved organic carbon uptake in headwater streams. Glob. Biogeochem. Cycles 32, 1528–1541. https://doi.org/10.1029/2018GB005919.
- Catalán, N., Casas-Ruiz, J.P., von Schiller, D., Proia, L., Obrador, B., Zwirnmann, E., Marcé, R., 2017. Biodegradation kinetics of dissolved organic matter chromatographic fractions in an intermittent river. J. Geophys. Res. Biogeosci. 122, 131–144. https://doi.org/10. 1002/2016JG003512.
- Catalán, N., Marcé, R., Kothawala, D.N., Tranvik, L.J., 2016. Organic carbon decomposition rates controlled by water retention time across inland waters. Nat. Geosci. 9, 501–504. https://doi.org/10.1038/ngeo2720.
- Cole, J.J., Prairie, Y.T., Caraco, N.F., McDowell, W.H., Tranvik, L.J., Striegl, R.G., Duarte, C.M., Kortelainen, P., Downing, J.A., Middelburg, J.J., Melack, J., 2007. Plumbing the global carbon cycle: integrating inland waters into the terrestrial carbon budget. Ecosystems 10, 172–185. https://doi.org/10.1007/s10021-006-9013-8.
- Cory, R.M., McKnight, D.M., 2005. Fluorescence spectroscopy reveals ubiquitous presence of oxidized and reduced quinones in dissolved organic matter. Environ. Sci. Technol. 39, 8142–8149. https://doi.org/10.1021/es0506962.
- Datry, T., Foulquier, A., Corti, R., Von Schiller, D., Tockner, K., Mendoza-Lera, C., Clément, J.C., Gessner, M.O., Moleón, M., Stubbington, R., Gücker, B., Albarinõ, R., Allen, D.C., Altermatt, F., Arce, M.I., Arnon, S., Banas, D., Banegas-Medina, A., Beller, E., Blanchette, M.L., Blanco-Libreros, J.F., Blessing, J.J., Boëchat, I.G., Boersma, K.S., Bogan, M.T., Bonada, N., Bond, N.R., Brintrup Barriá, K.C., Bruder, A., Burrows, R.M., Cancellario, T., Canhoto, C., Carlson, S.M., Cauvy-Fraunié, S., Cid, N., Danger, M., De Freitas Terra, B., De Girolamo, A.M., De La Barra, E., Del Campo, R., Diaz-Villanueva, V.D., Dyer, F., Elosegi, A., Faye, E., Febria, C., Four, B., Gafny, S., Ghate, S.D., Gómez, R., Gómez-Gener, L., Gracą, M.A.S., Guareschi, S., Hoppeler, F., Hwan, J.L., Jones, J.I., Kubheka, S., Laini, A., Langhans, S.D., Leigh, C., Little, C.J., Lorenz, S., Marshall, J.C., Martín, E., McIntosh, A.R., Meyer, E.I., Miliša, M., Mlambo, M.C., Morais, M., Moya, N., Negus, P.M., Niyogi, D.K., Papatheodoulou, A., Pardo, I., Pařil, P., Pauls, S.U., Pešić, V., Polášek, M., Robinson, C.T., Rodríguez-Lozano, P., Rolls, R.J., Sánchez-Montoya, M.M., Savić, A., Shumilova, O., Sridhar, K.R., Steward, A.L., Storey, R., Taleb, A., Uzan, A., Vander Vorste, R., Waltham, N.J., Woelfle-Erskine, C., Zak, D., Zarfl, C., Zoppini, A., 2018. A global analysis of terrestrial plant litter dynamics in non-perennial waterways. Nat. Geosci. 11, 497-503. https://doi.org/10.1038/s41561-018-0134-4.
- Datry, T., Larned, S.T., Tockner, K., 2014. Intermittent rivers: a challenge for freshwater ecology. Bioscience 64, 229–235. https://doi.org/10.1093/biosci/bit027.
- De Haan, H., De Boer, T., 1987. Applicability of light absorbance and fluorescence as measures of concentration and molecular size of dissolved organic carbon in humic Lake Tjeukemeer. Water Res. 21, 731–734. https://doi.org/10.1016/0043-1354(87) 90086-8.
- Dewey, J., Hatten, J., Choi, B., Mangum, C., Ouyang, Y., 2020. Climate Drivers and Sources of Sediment and Organic Matter Fluxes in Intermittent Rivers and Ephemeral Streams (IRES) of a Subtropical Watershed, USA. Clim. https://doi.org/10.3390/cli8100117.
- Döll, P., Schmied, H.M., 2012. How is the impact of climate change on river flow regimes related to the impact on mean annual runoff?A global-scale analysis. Environ. Res. Lett. 7, 014037. https://doi.org/10.1088/1748-9326/7/1/014037.
- Ejarque, E., Freixa, A., Vazquez, E., Guarch, A., Amalfitano, S., Fazi, S., Romaní, A.M., Butturini, A., 2017. Quality and reactivity of dissolved organic matter in a Mediterranean river across hydrological and spatial gradients. Sci. Total Environ. 599–600, 1802–1812. https://doi.org/10.1016/j.scitotenv.2017.05.113.
- Fasching, C., Ulseth, A.J., Schelker, J., Steniczka, G., Battin, T.J., 2016. Hydrology controls dissolved organic matter export and composition in an Alpine stream and its hyporheic zone. Limnol. Oceanogr. 61, 558–571. https://doi.org/10.1002/lno.10232.
- Febria, C.M., Beddoes, P., Fulthorpe, R.R., Williams, D.D., 2012. Bacterial community dynamics in the hyporheic zone of an intermittent stream. ISME J. 6, 1078–1088. https://doi. org/10.1038/ismej.2011.173.
- Fellman, J.B., Dogramaci, S., Skrzypek, G., Dodson, W., Grierson, P.F., 2011. Hydrologic control of dissolved organic matter biogeochemistry in pools of a subtropical dryland river. Water Resour. Res. 47. https://doi.org/10.1029/2010WR010275.
- Gardecki, J.A., Maroncelli, M., 1998. Set of secondary emission standards for calibration of the spectral responsivity in emission spectroscopy. Appl. Spectrosc. 52, 1179–1189. https://doi.org/10.1366/0003702981945192.
- Gionchetta, G., Artigas, J., Arias-Real, R., Oliva, F., Romaní, A.M., 2020. Multi-model assessment of hydrological and environmental impacts on streambed microbes in Mediterranean catchments. Environ. Microbiol. 22, 2213–2229. https://doi.org/10.1111/1462-2920. 14990.
- Goletz, C., Wagner, M., Grübel, A., Schmidt, W., Korf, N., Werner, P., 2011. Standardization of fluorescence excitation–emission-matrices in aquatic milieu. Talanta 85, 650–656. https://doi.org/10.1016/j.talanta.2011.04.045.
- Gómez-Gener, L., Obrador, B., Marcé, R., Acuña, V., Catalán, N., Casas-Ruiz, J.P., Sabater, S., Muñoz, I., von Schiller, D., 2016. When water vanishes: magnitude and regulation of carbon dioxide emissions from dry temporary streams. Ecosystems 19, 710–723. https://doi.org/10.1007/s10021-016-9963-4.
- Gómez-Gener, L., Siebers, A.R., Arce, M.I., Arnon, S., Bernal, S., Bolpagni, R., Datry, T., Gionchetta, G., Grossart, H.-P., Mendoza-Lera, C., Pohl, V., Risse-Buhl, U., Shumilova, O., Tzoraki, O., von Schiller, D., Weigand, A., Weigelhofer, G., Zak, D., Zoppini, A., 2021. Towards an improved understanding of biogeochemical processes across surfacegroundwater interactions in intermittent rivers and ephemeral streams. Earth-Sci. Rev. 220, 103724. https://doi.org/10.1016/j.earscirev.2021.103724.
- Graça, D., Fernandes, I., Cássio, F., Pascoal, C., 2022. Eco-physiological responses of aquatic fungi to three global change stressors highlight the importance of intraspecific trait variability. Microb. Ecol. https://doi.org/10.1007/s00248-022-02007-7.

- Granados, V., Butturini, A., 2019. Dissolved organic matter variability along an impacted intermittent Mediterranean river. Limnetica 38, 555–573. https://doi.org/10.23818/ limn.38.32.
- Granados, V., Gutiérrez-Cánovas, C., Arias-Real, R., Obrador, B., Harjung, A., Butturini, A., 2020. The interruption of longitudinal hydrological connectivity causes delayed responses in dissolved organic matter. Sci. Total Environ. 713, 136619. https://doi.org/ 10.1016/j.scitotenv.2020.136619.
- Grueber, C.E., Nakagawa, S., Laws, R.J., Jamieson, I.G., 2011. Multimodel inference in ecology and evolution: challenges and solutions. J. Evol. Biol. 24, 699–711. https://doi. org/10.1111/j.1420-9101.2010.02210.x.
- Guarch-Ribot, A., Butturini, A., 2016. Hydrological conditions regulate dissolved organic matter quality in an intermittent headwater stream. From drought to storm analysis. Sci. Total Environ. 571, 1358–1369. https://doi.org/10.1016/j.scitotenv.2016.07.060.
- Hansen, A.M., Kraus, T.E.C., Pellerin, B.A., Fleck, J.A., Downing, B.D., Bergamaschi, B.A., 2016. Optical properties of dissolved organic matter (DOM): effects of biological and photolytic degradation. Limnol. Oceanogr. 61, 1015–1032. https://doi.org/10.1002/lno.10270.
- Harjung, A., Perujo, N., Butturini, A., Romaní, A.M., Sabater, F., 2019. Responses of microbial activity in hyporheic pore water to biogeochemical changes in a drying headwater stream. Freshw. Biol. 64, 735–749. https://doi.org/10.1111/fwb.13258.
- Harjung, A., Sabater, F., Butturini, A., 2018. Hydrological connectivity drives dissolved organic matter processing in an intermittent stream. Limnologica 68, 71–81. https:// doi.org/10.1016/j.limno.2017.02.007.
- Helms, J.R., Stubbins, A., Ritchie, J.D., Minor, E.C., Kieber, D.J., Mopper, K., 2008. Absorption spectral slopes and slope ratios as indicators of molecular weight, source, and photobleaching of chromophoric dissolved organic matter. Limnol. Oceanogr. 53, 955–969. https://doi.org/10.4319/lo.2008.53.3.0955.
- Hoffman, G.E., Schadt, E.E., 2016. variancePartition: interpreting drivers of variation in complex gene expression studies. BMC Bioinformatics 17, 483. https://doi.org/10. 1186/s12859-016-1323-z.
- Huguet, A., Vacher, L., Relexans, S., Saubusse, S., Froidefond, J.M., Parlanti, E., 2009. Properties of fluorescent dissolved organic matter in the Gironde Estuary. Org. Geochem. 40, 706–719. https://doi.org/10.1016/j.orggeochem.2009.03.002.
- Inamdar, S., Singh, S., Dutta, S., Levia, D., Mitchell, M., Scott, D., Bais, H., McHale, P., 2011. Fluorescence characteristics and sources of dissolved organic matter for stream water during storm events in a forested mid-Atlantic watershed. J. Geophys. Res. Biogeosci. 116. https://doi.org/10.1029/2011JG001735.
- Koutroulis, A.G., Papadimitriou, L.V., Grillakis, M.G., Tsanis, I.K., Warren, R., Betts, R.A., 2019. Global water availability under high-end climate change: a vulnerability based assessment. Glob. Planet. Change 175, 52–63. https://doi.org/10.1016/j.gloplacha. 2019.01.013.
- Lakowicz, J.R., 2006. Principles of Fluorescence Spectroscopy. 3rd ed. SpringerNew York, NY, New York, NY https://doi.org/10.1007/978-0-387-46312-4.
- Lawaetz, A.J., Stedmon, C.A., 2009. Fluorescence intensity calibration using the raman scatter peak of water. Appl. Spectrosc. 63, 936–940. https://doi.org/10.1366/ 000370209788964548.
- Marxen, J., Zoppini, A., Wilczek, S., 2010. Microbial communities in streambed sediments recovering from desiccation. FEMS Microbiol. Ecol. 71, 374–386. https://doi.org/10. 1111/j.1574-6941.2009.00819.x.
- Mas-Martí, E., Romaní, A.M., Muñoz, I., 2015. Consequences of warming and resource quality on the stoichiometry and nutrient cycling of a stream shredder. PLoS One 10, 1–21. https://doi.org/10.1371/journal.pone.0118520.
- McClain, M.E., Boyer, E.W., Dent, C.L., Gergel, S.E., Grimm, N.B., Groffman, P.M., Hart, S.C., Harvey, J.W., Johnston, C.A., Mayorga, E., McDowell, W.H., Pinay, G., 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems 6, 301–312. https://doi.org/10.1007/s10021-003-0161-9.
- Messager, M.L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., Tockner, K., Trautmann, T., Watt, C., Datry, T., 2021. Global prevalence of non-perennial rivers and streams. Nature 594, 391–397. https://doi.org/10.1038/s41586-021-03565-5.
- Morin, A., Lamoureux, W., Busnarda, J., 1999. Empirical models predicting primary productivity from chlorophyll a and water temperature for stream periphyton and Lake and ocean phytoplankton. J. North Am. Benthol. Soc. 18, 299–307. https://doi.org/10. 2307/1468446.
- Ohno, T., 2002. Fluorescence inner-filtering correction for determining the humification index of dissolved organic matter. Environ. Sci. Technol. 36, 742–746. https://doi.org/ 10.1021/es0155276.

- Picazo, F., Vilmi, A., Aalto, J., Soininen, J., Casamayor, E.O., Liu, Y., Wu, Q., Ren, L., Zhou, J., Shen, J., Wang, J., 2020. Climate mediates continental scale patterns of stream microbial and the stream of stream microbial scale patterns of stream microbi
- functional diversity. Microbiome 8, 92. https://doi.org/10.1186/s40168-020-00873-2.
 R Development Core Team, 2011. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing https://doi.org/10.1007/978-3-540-74686-7.
- Reynolds, L.V., Shafroth, P.B., LeRoy Poff, N., 2015. Modeled intermittency risk for small streams in the Upper Colorado River Basin under climate change. J. Hydrol. 523, 768–780. https://doi.org/10.1016/j.jhydrol.2015.02.025.
- Shumilova, O., Zak, D., Datry, T., von Schiller, D., Corti, R., Foulquier, A., Obrador, B., Tockner, K., Allan, D.C., Altermatt, F., Arce, M.I., Arnon, S., Banas, D., Banegas-Medina, A., Beller, E., Blanchette, M.L., Blanco-Libreros, J.F., Blessing, J., Bočchat, I.G., Boersma, K., Bogan, M.T., Bonada, N., Bond, N.R., Brintrup, K., Bruder, A., Burrows, R., Cancellario, T., Carlson, S.M., Cauvy-Fraunié, S., Cid, N., Danger, M., de Freitas Terra, B., Girolamo, A.M.De, del Campo, R., Dyer, F., Elosegi, A., Faye, E., Febria, C., Figueroa, R., Four, B., Gessner, M.O., Gnohossou, P., Cerezo, R.G., Gomez-Gener, L., Graça, M.A.S., Guareschi, S., Gücker, B., Hwan, J.L., Kubheka, S., Langhans, S.D., Leigh, C., Little, C.J., Lorenz, S., Marshall, J., McIntosh, A., Mendoza-Lera, C., Meyer, E.I., Miliša, M., Mlambo, M.C., Moleón, M., Negus, P., Niyogi, D., Papatheodoulou, A., Pardo, I., Paril, P., Pešić, V., Rodriguez-Lozano, P., Rolls, R.J., Sanchez-Montoya, M.M., Savić, A., Steward, A., Stubbington, R., Taleb, A., Vorste, R.Vander, Waltham, N., Zoppini, A., Zarfl, C., 2019. Simulating rewetting events in intermittent rivers and ephemeral streams: a global analysis of leached nutrients and organic matter. Glob. Chang. Biol. 25, 1591–1611. https://doi.org/10.1111/gcb.14537.
- Siebers, A.R., Pettit, N.E., Skrzypek, G., Fellman, J.B., Dogramaci, S., Grierson, P.F., 2016. Alluvial ground water influences dissolved organic matter biogeochemistry of pools within intermittent dryland streams. Freshw. Biol. 61, 1228–1241. https://doi.org/10. 1111/fwb.12656.
- Vazquez, E., Amalfitano, S., Fazi, S., Butturini, A., 2011. Dissolved organic matter composition in a fragmented Mediterranean fluvial system under severe drought conditions. Biogeochemistry 102, 59–72. https://doi.org/10.1007/s10533-010-9421-x.
- Vázquez, E., Ejarque, E., Ylla, I., Romaní, A.M., Butturini, A., 2015. Impact of drying/ rewetting cycles on the bioavailability of dissolved organic matter molecular-weight fractions in a Mediterranean stream. Freshw. Sci. 34, 263–275. https://doi.org/10. 1086/679616.
- von Schiller, D., Datry, T., Corti, R., Foulquier, A., Tockner, K., Marcé, R., García-Baquero, G., Odriozola, I., Obrador, B., Elosegi, A., Mendoza-Lera, C., Gessner, M.O., Stubbington, R., Albariño, R., Allen, D.C., Altermatt, F., Arce, M.I., Arnon, S., Banas, D., Banegas-Medina, A., Beller, E., Blanchette, M.L., Blanco-Libreros, J.F., Blessing, J., Boëchat, I.G., Boersma, K.S., Bogan, M.T., Bonada, N., Bond, N.R., Brintrup, K., Bruder, A., Burrows, R.M., Cancellario, T., Carlson, S.M., Cauvy-Fraunié, S., Cid, N., Danger, M., de Freitas Terra, B., Dehedin, A., De Girolamo, A.M., del Campo, R., Díaz-Villanueva, V., Duerdoth, C.P., Dyer, F., Faye, E., Febria, C., Figueroa, R., Four, B., Gafny, S., Gómez, R., Gómez-Gener, L., Graça, M.A.S., Guareschi, S., Gücker, B., Hoppeler, F., Hwan, J.L., Kubheka, S., Laini, A., Langhans, S.D., Leigh, C., Little, C.J., Lorenz, S., Marshall, J., Martín, E.J., McIntosh, A., Meyer, E.I., Miliša, M., Mlambo, M.C., Moleón, M., Morais, M., Negus, P., Niyogi, D., Papatheodoulou, A., Pardo, I., Pařil, P., Pešić, V., Piscart, C., Polášek, M., Rodríguez-Lozano, P., Rolls, R.J., Sánchez-Montoya, M.M., Savić, A., Shumilova, O., Steward, A., Taleb, A., Uzan, A., Vander Vorste, R., Waltham, N., Woelfle-Erskine, C., Zak, D., Zarfl, C., Zoppini, A., 2019. Sediment respiration pulses in intermittent Rivers and ephemeral streams. Glob. Biogeochem. Cycles 33, 1251-1263. https://doi.org/10. 1029/2019GB006276.
- von Schiller, D., Graeber, D., Ribot, M., Timoner, X., Acuña, V., Martí, E., Sabater, S., Tockner, K., 2015. Hydrological transitions drive dissolved organic matter quantity and composition in a temporary Mediterranean stream. Biogeochemistry 123, 429–446. https://doi. org/10.1007/s10533-015-0077-4.
- Weishaar, J.L., Aiken, G.R., Bergamaschi, B.A., Fram, M.S., Fujii, R., Mopper, K., 2003. Evaluation of specific ultraviolet absorbance as an indicator of the chemical composition and reactivity of dissolved organic carbon. Environ. Sci. Technol. 37, 4702–4708. https://doi. org/10.1021/es030360x.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2009. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210x. 2009.00001.x.