ECOSYSTEMS · CrossMark

When Water Vanishes: Magnitude and Regulation of Carbon Dioxide Emissions from Dry Temporary Streams

Lluís Gómez-Gener,[1]* Biel Obrador,[1] Rafael Marcé,[2] Vicenç Acuña,[2] Núria Catalán,[3] Joan Pere Casas-Ruiz,[2] Sergi Sabater,[2] Isabel Muñoz,[1] and Daniel von Schiller[4]

[1]Department of Ecology, University of Barcelona, Av. Diagonal 643, 08028 Barcelona, Barcelona, Spain; [2]Catalan Institute for Water Research, Scientific and Technological Park of the University of Girona, Carrer Emili Grahit 101, 17003 Girona, Spain; [3]Limnology, Department of Ecology and Genetics,Evolutionary Biology Centre, Uppsala University, Norbyvägen 18 D, 75236 Uppsala, Sweden; [4]Department of Plant Biology and Ecology, Faculty of Science and Technology, University of the Basque Country, Apdo. 644, 48080 Bilbao, Spain

ABSTRACT

Most fluvial networks worldwide include watercourses that recurrently cease to flow and run dry. The spatial and temporal extent of the dry phase of these temporary watercourses is increasing as a result of global change. Yet, current estimates of carbon emissions from fluvial networks do not consider temporary watercourses when they are dry. We characterized the magnitude and variability of carbon emissions from dry watercourses by measuring the carbon dioxide (CO_2) flux from 10 dry streambeds of a fluvial network during the dry period and comparing it to the CO_2 flux from the same streambeds during the flowing period and to the CO_2 flux from their adjacent upland soils. We also looked for potential drivers regulating the CO_2 emissions by examining the main physical and chemical properties of dry streambed sediments and adjacent upland soils. The CO_2 efflux from dry streambeds (mean ± SD = 781.4 ± 390.2 mmol m^{-2} day^{-1}) doubled the CO_2 efflux from flowing streambeds (305.6 ± 206.1 mmol m^{-2} day^{-1}) and was comparable to the CO_2 efflux from upland soils (896.1 ± 263.2 mmol m^{-2} day^{-1}). However, dry streambed sediments and upland soils were physicochemically distinct and differed in the variables regulating their CO_2 efflux. Overall, our results indicate that dry streambeds constitute a unique and biogeochemically active habitat that can emit significant amounts of CO_2 to the atmosphere. Thus, omitting CO_2 emissions from temporary streams when they are dry may overlook the role of a key component of the carbon balance of fluvial networks.

Key words: greenhouse gas emissions; fluxes; streams; intermittent; fluvial network; drought; dry streambeds.

INTRODUCTION

Fluvial networks emit significant amounts of carbon dioxide (CO_2) to the atmosphere (Raymond and others 2013; Lauerwald and others 2015). However, considerable uncertainties regarding the magnitude and controls of CO_2 emitted from fluvial networks still exist (Wehrli 2013). For instance, current global estimates do not accurately consider the CO_2 emitted from expanded areas of rivers and streams during floods, which can increase the areal extent of fluvial networks by several orders of magnitude (Richey and others 2002). Also, these estimates, based on continuous models, do not include the CO_2 emitted from local discontinuities along the fluvial network, such as weirs, rapids, waterfalls or turbine releases in hydropower plants (Wehrli 2013). Finally, current estimates do not consider the CO_2 emitted from the areas of temporary watercourses that recurrently desiccate (Raymond and others 2013; von Schiller and others 2014).

Temporary watercourses are found worldwide (Acuña and others 2014; Leigh and others 2015). In Australia, roughly 70% of the 3.5 million kilometres of watercourses are considered temporary (Sheldon and others 2010), and more than half of the total length of watercourses in the United States, Greece and South Africa are also temporary (Larned and others 2010). Temporary watercourses can also be found in humid areas such as Antarctica (McKnight and others 1999) and Amazonia (Chapman and Kramer 1991). Low-order streams deserve special attention, since they account for more than 70% of fluvial networks surface area and are particularly prone to flow intermittency (Lowe and others 2006). These are dynamic systems in time and space, and analysing their spatial coverage is particularly difficult to detect by traditional mapping techniques (Benstead and Leigh 2012). We can therefore suspect that the surface area of temporary watercourses in the global fluvial network can be higher than 50% (Datry and others 2014), whereas their importance is increasing as a result of the combined effects of climate and land-use changes (Palmer and others 2008; Larned and others 2010; Hoerling and others 2012).

The dry streambeds of temporary streams, also commonly referred to as dry riverbeds (Steward and others 2012), are dynamic habitats (Stanley and others 1997; Boulton 2003), representing transitional zones between dissimilar habitats, and transitional periods between persistent and dissimilar states (Naiman and Decamps 1997). These systems are constrained by the strength of interactions with their adjacent ecosystems. Thus, despite being traditionally neglected by aquatic and terrestrial ecologists and biogeochemists, dry streambeds are likely to be unique biogeochemical hotspots for materials transformations (McClain and others 2003). In fact, recent studies reported that carbon processing in dry streambed sediments can be maintained to some degree during stream desiccation by the activity of well-adapted biofilms (Zoppini and Marxsen 2011; Timoner and others 2012; Pohlon and others 2013). Likewise, first estimates also showed that dry streambeds are not inert but rather active sites for CO_2 release to the atmosphere (Gallo and others 2014; von Schiller and others 2014, Gómez-Gener and others 2015).

The carbon processed in dry streams has its own particular history, because it has either already left terrestrial ecosystems and entered the fluvial network or was produced within the fluvial network (Steward and others 2012). Therefore, emissions of CO_2 from dry streambeds should not be considered terrestrial, but mostly as a fundamental biogeochemical component of fluvial networks that experience large, often seasonal, hydrological expansions and contraction. Yet, there is an important lack of knowledge regarding the spatial variability and drivers of CO_2 emissions from dry streambeds and the differences and similarities with respect to CO_2 emissions from terrestrial soils.

The aim of this study was to quantify CO_2 emissions from dry streambeds of temporary streams within a fluvial network and to compare them to those during the period with flow and to those from adjacent upland soils. We also looked for potential drivers regulating the CO_2 emissions by examining the main physical and chemical properties of dry streambed sediments and adjacent upland soils. We predicted differences in both the magnitude and drivers controlling CO_2 emissions between dry streambeds and the other investigated habitats because of strong dissimilarities in physicochemical properties and biogeochemical dynamics.

METHODS

Study Site and Sampling Design

The Fluvià River (NE Iberian Peninsula) is 97 km long and drains a 990-km^2 catchment covered with mixed forests (78%), agricultural (19%) and urban (3%) areas (Land Cover Map of Catalonia 2009, Centre of Ecology and Forestry Research of Catalonia, http://www.creaf.uab.es/mcsc/). The

climate in the region is typically Mediterranean. Mean monthly air temperature ranges from 6°C in January to 26°C in July. Mean annual precipitation is 660 mm, with rainfall mainly occurring in autumn and spring (Data from 2004 to 2014, Catalan Water Agency, http://aca-web.gencat.cat). During the wet period (late autumn to early spring), hydrological connectivity is enhanced and most of the fluvial network area is covered with surface water. In contrast, during the dry period (late spring to early autumn) hydrological connectivity is reduced and the area of the fluvial network covered with surface water drastically decreases.

We conducted two samplings in 10 temporary tributaries of the Fluvià River spanning a wide range of physiographic and land-use conditions (Table 1; see Appendix 1 in Supplementary Materials for details). In the first sampling (dry period; August 2014), we measured CO_2 fluxes and took samples from the dry streambed sediments and adjacent upland soils. The upland was defined as the area occupied by terrestrial vegetation located close to the stream but beyond the strip of riparian vegetation. In the second sampling (flowing period, March 2015), we measured the CO_2 fluxes from the streambeds where flowing water was found, that is, 7 out of 10 streams (see Appendix 2 in Supplementary Materials for details). All the CO_2 flux measurements and associated sampling were carried out at each stream only once during the day.

Determination of CO_2 Fluxes

In both dry streambeds and upland soils, we applied the enclosed dynamic chamber method (Livingston and Hutchinson 1995) to measure the CO_2 flux. Briefly, we monitored the gas concentration in an opaque chamber (SRC-1, PP-Systems, USA) every 4.8 s with an infrared gas analyser (EGM-4, PP-Systems, USA). According to the manufacturer's specifications, the measurement accuracy of the EGM-4 is estimated to be within 1% over the calibrated range. In all cases, flux measurements lasted until a change in CO_2 of at least 10 µatm was reached, with a maximum duration of 300 s and a minimum of 120 s. We calculated the CO_2 flux (F_{CO_2}, mmol m^{-2} day^{-1}) from the rate of change of CO_2 inside the chamber:

$$F_{CO_2} = \left(\frac{dp_{CO_2}}{dt}\right)\left(\frac{V}{RTS}\right), \qquad (1)$$

where dp_{CO_2}/dt is the slope of the gas accumulation in the chamber along time in µatm s^{-1}, V is the volume of the chamber (1.171 dm^3), S is the surface area of the chamber (0.78 dm^2), T is the air temperature in Kelvin and R is the ideal gas constant in l atm K^{-1} mol^{-1}. Positive F_{CO_2} values represent efflux of gas to the atmosphere, and negative F_{CO_2} values indicate influx of gas from the atmosphere. We performed 4 randomly distributed measurements within each site, that is, 4 in dry streambeds and 4 in upland soils.

In the flowing streambeds, we measured the CO_2 flux applying the Fick's First Law of gas diffusion:

$$F_{CO_2} = k_{CO_2} K_h \left(pCO_{2,w} - pCO_{2,a}\right), \qquad (2)$$

where F_{CO_2} is the estimated CO_2 flux between the surface stream water and the atmosphere in mmol m^{-2} day^{-1}, K_h is the Henry's constant in mmol µatm^{-1} m^{-3} adjusted for salinity and temperature (Weiss 1974; Millero 1995), $pCO_{2,w}$ and $pCO_{2,a}$ are the surface water and the atmosphere partial pressures of CO_2 in µatm, respectively, and k_{CO_2} is the specific gas transfer velocity for CO_2 in m day^{-1}.

We measured $pCO_{2,w}$ and $pCO_{2,a}$ with an infrared gas analyser (EGM-4, PP-Systems, USA). In the case of $pCO_{2,w}$ we coupled the gas analyser to a membrane contactor (MiniModule, Liqui-Cel, USA). The water was circulated via gravity through the contactor at 300 mL min^{-1}, and the equilibrated gas was continuously recirculated into the infrared gas analyser for instantaneous pCO_2 measurements (Teodoru and others 2010).

We followed the approach used by Gómez-Gener and others (2015) to estimate the k_{CO_2} from the night-time drop in dissolved oxygen concentration (Hornberger and Kelly 1972), a method that has been extensively applied in ecosystem metabolism studies in rivers and streams (for example, Aristegi and others 2009; Hunt and others 2012; Riley and Dodds 2013). Briefly, photosynthesis ceases from sunset to sunrise; thus night-time dynamics of oxygen depend on respiration and reaeration. During the night, respiration reduces the oxygen levels until atmospheric equilibrium is reached. In parallel, reaeration approaches the oxygen concentration to saturation. Thus, when we plot the night-time oxygen concentration per unit of time versus the oxygen saturation deficit, a linear trend is obtained. The intercept of the regression corresponds to the respiration rate in g O_2 m^{-2} h^{-1}, and the slope to the mean reaeration coefficient (K_{O_2}) in day^{-1}. We corrected the K_{O_2} for depth to obtain the mean gas transfer velocity of oxygen (k_{O_2}) in m day^{-1} (Raymond and others 2012) and we further transformed k_{O_2} to k_{CO_2} by applying equation (3).

Table 1. Physiographic and Land-Use Characteristics of the Study Sites and Their Corresponding Subcatchments

Stream name	Stream code	Site-specific parameters			Streambed grain sizes[b] (%)			Catchment-specific parameters					Lithology[c] (%)
		Coordinates		Stream order[a]	Small fractions	Cobbles	Boulders	Surface area[a] (ha)	Land uses[c] (%)				
		x	y						Scrubs	Pastures	Crops	Forest	
Riera de St. Miquel	1	473788	4663780	4	77.2	22.8	0.0	5191	1.2	2.6	10.7	84.6	L(66), C(17), G(16)
Riera de Mieres	2	470306	4663964	4	71.1	28.9	0.0	1825	1.1	5.1	18.4	72.9	L(65), G(22), C(12)
Torrent de Pujolars	3	464116	4665691	3	49.1	43.7	7.2	1219	0.2	0.1	7.9	91.7	C(87), G(13)
Torrent de Rocanegra	4	464289	4665909	2	58.8	41.2	0.0	1252	1.7	3.7	27.6	59.4	C(62), V(34), G(23)
Fluvià	5	454382	4662603	4	63.2	31.6	5.2	3078	0.9	10.7	16.9	70.2	C(64), G(18), S(7), SS(6), G(5)
Joanetes	6	453844	4663758	4	61.4	38.6	0.0	2954	1.3	4.1	11.4	81.9	C(66), G(18), L(11)
Torrent de St. Pere	7	453724	4673311	3	59.8	29.8	10.3	1480	0.2	2.1	10.5	86.2	C(85), L(9), G(5)
Riera d'Oix	8	462235	4680827	4	79.0	21.0	0.0	11085	4.4	1.4	1.9	92.2	L(49), C(33), G(16), LS(9)
Llierca	9	466415	4679576	5	67.6	32.4	0.0	16743	5.9	2.8	1.5	89.7	L(59), LS(23), SS(18)
Barranc de Junyell	10	476914	4671359	3	55.6	44.4	0.0	5238	0.5	0.3	1.9	97.3	C(76), G(21), SS(2)

[a] Stream order and subcatchment surface area were calculated with the Hydrological Extension in ESRI® ArcGISTM v. 10.0 software. Data obtained from a 2-meter digital elevation model (Centre of Ecology and Forestry Research of Catalonia)

[b] Surface grain-size characterization of studied streambeds was estimated following an image-processing-based procedure (Graham and others 2005). Results were obtained from an average of 3 high resolution photos along 50 m stream segments. Fraction classification was made according Wentworth (1922). Small fractions contain silt, clay, sand and gravel fractions.

[c] Subcatchments land uses and lithologies (S = silt, L = loams, C = conglomerates, G = gravels, V = volcanic deposits, LS = limestone) were calculated with ESRI® ArcGISTM v. 10.0 software from a Land cover map of Catalonia and a Lithological map of Catalonia, respectively (Centre of Ecology and Forestry Research of Catalonia)

$$k_{CO_2} = k_{O_2} \left(\frac{Sc_{CO_2}}{Sc_{O_2}} \right)^{-n}, \qquad (3)$$

where k_{CO_2} is the mean gas transfer velocity of CO_2 in m day^{-1}, Sc_{CO_2} and Sc_{O_2} are the Schmidt numbers of CO_2 and O_2, respectively, at a given water temperature (Wanninkhof 1992). Following Bade (2009), we set the exponent n to 1/2 for turbulent environments, that is, flowing waters. Our k_{CO_2} ranged from 0.075 to 15.21 m day^{-1}. We obtained the diel cycles of dissolved oxygen concentration and temperature at each site at a frequency of 5 min with an optical dissolved oxygen sensor (MiniDot, PME, USA). The oxygen probes were inter-calibrated before the sampling campaign.

Physical and Chemical Characterization of Dry Streambeds and Upland Soils

At each flux measurement location, we measured the substrate temperature by means of a portable soil probe (Decagon ECH_2O 10HS, Pullman, USA) and collected substrate samples, that is, dry streambed sediments and upland soils (0–10 cm depth), after the flux measurements had been carried out. In the laboratory, we measured the substrate pH from a 1:1 sample:deionized water mixture (McLean 1982) with a hand-held pH meter (pH 3110, WTW, Germany). We also determined, gravimetrically, the substrate water content by drying a fresh subsample at 105°C and the organic matter content by sample combustion following the loss on ignition method (Dean 1974). We sieved the air-dried samples (2-mm mesh) and determined their main textural fractions (% sand, % silt and % clay) and their mean particle size with a laser-light diffraction instrument (Coulter LS 230, Beckman-Coulter, USA). We determined the percentage of organic carbon (OC) and total nitrogen (TN) from a sieved and air-dried subsample on an Elemental Analyzer (Model 1108, Carlo-Erba, Italy) after grinding and eliminating the inorganic fraction by acidification (HCl 1.5 N).

Water Extractable Organic Matter (WEOM), the fraction of DOM extracted with deionized water and conceptually consisting of the mobile and available portion of the total DOM pool (Corvasce and others 2006; Vergnoux and others 2011), was obtained by shaking (100 rpm, 4°C) the air-dried, sieved and ground samples with deionized water in the dark for 48 h with a sample:water ratio of 1:10. After the extraction, we filtered the leachates through 0.70- and 0.45-µm pre-combusted glass microfiber filters (Whatman, USA). We determined their raw dissolved organic carbon (DOC) and total

dissolved nitrogen (TDN) concentration with a total organic carbon analyser (TOC-V CSH, Shimadzu, Japan). The detection limit of the analysis procedure was 0.05 mg C l^{-1} for DOC and 0.005 mg N l^{-1} for TDN. All samples were previously acidified with HCl 1.5 N and preserved at 4°C until analysis. The extraction efficiencies were calculated as the ratio between the mass of WEOM recovered and the mass of the dry sample used for the extraction.

UV/Vis absorbance and fluorescence spectra were obtained from diluted WEOM extracts (DOC $\approx$ 10 mg l^{-1}) (Anesio and others 2000). We measured the UV/Vis absorbance spectra (200–800 nm) using a 1-cm quartz cuvette on a spectrophotometer (Shimadzu UV-1700, Shimadzu, USA) with an analytical precision of 0.001 absorbance units. From the absorbance spectra, we calculated the specific UV absorbance at 254 nm ($SUVA_{254}$, L mg^{-1} m^{-1}) by dividing the absorbance at 254 nm by DOC concentration and cuvette path length (m). $SUVA_{254}$ is positively related with the aromaticity of DOM, with values generally ranging between 1 and 9 L mg^{-1} m^{-1} (Weishaar and others 2003).

We obtained the excitation–emission matrices (EEM) on a spectrofluorometer (Shimadzu RF-5301PC, Shimadzu, USA) using a 1-cm quartz cuvette. We ran the EEM scans over an emission range of 270–630 nm (1-nm increments) and an excitation range of 240–400 (10-nm increments). A water blank (Milli-Q Millipore) EEM, recorded under the same conditions, was subtracted from each sample to eliminate Raman scattering. The area underneath the water Raman scan was used to normalize all sample intensities. All the EEMs were corrected for instrument-specific biases, and inner-filter effects corrections were applied according to Kothawala and others (2013). From the EEMs, we calculated 3 indices: the fluorescence index (FI) as the ratio of the emission intensities at 470/520 nm for an excitation wavelength of 370 nm (Jaffé and others 2008). FI is an indicator of terrestrial (low FI) or microbial (high FI) origin of DOM. The humification index (HIX) was calculated as the peak area under the emission spectrum 435–480 nm divided by that of 300–345 nm, at an excitation of 254 (Zsolnay and others 1999). Higher values of HIX correspond to a higher degree of humification (Huguet and others 2009; Fellman and others 2010). Finally, we calculated the biological index (BIX) as the ratio of the emission intensities at 380/430 nm for an excitation of 310 nm (Huguet and others 2009). The BIX is an indicator of recent biological activity or recently

produced DOM. Higher values of BIX correspond to a predominantly autochthonous origin of DOM and to the presence of OM freshly released into the sample, whereas a lower DOM production will lead to a low value of BIX (Huguet and others 2009).

Data Analysis

We performed paired t tests to test the differences in terms of CO_2 flux among habitats, that is, dry streambed versus upland soil and dry streambed versus flowing streambed.

We applied a principal component analysis (PCA) on the correlation matrix to ordinate the dry streambeds ($n = 10$) and upland soil sites ($n = 10$) by their physical and chemical properties. All the variables included in the analysis are described in Table 2. We also examined differences in physical and chemical properties of dry streambed sediments and upland soils by means of paired t tests.

We built two PLS regression models (projections of latent structures by means of partial least squares, Wold and others 2001) to identify the potential physical and chemical drivers of CO_2 fluxes in dry streambeds ($n = 35$) and upland soils ($n = 34$). All the variables included in the models are described in Table 2. PLS is a regression extension of PCA and allows the exploration of relationships between multiple, collinear data matrices of X' and Y's. The model performance is expressed by R^2Y (explained variance) and by Q^2Y (predictive power estimated by cross validation). The PLS model was validated by comparing the goodness of fit with models built from randomized Y-variables. To summarize the influence of every X-variable on the Y-variable, across the extracted PLS components, we used the variable influence on projection (VIP). The VIP scores of every model term (X-variables) are cumulative across components and weighted according to the amount of Y-variance explained in each component (Eriksson and others 2006). X-variables with VIP > 1 are most influential on the Y-variable. A cutoff around 0.8 separates moderately important X-variables, whereas those below this threshold can be regarded as less influential.

All statistical analyses were conducted in the R statistical environment (R Core Team 2013) using the vegan package (Oksanen and others 2013), except for PLS analysis which was done with the software XLSAT (XLSTAT 2015.2.01, Addinsoft SRAL, Germany). Our data met the conditions of homogeneity of variance and normality. Statistical tests were considered significant at $p < 0.05$. Extreme outliers were excluded from the CO_2 flux dataset after careful data exploration using numerical and graphical tools, that is, Cook's influential outlier tests, boxplots, and Cleveland dotplots, following Zuur and others (2010).

RESULTS

CO_2 Emissions

Dry streambeds (mean $\pm$ SD = 781.4 $\pm$ 390.2 mmol m^{-2} day^{-1}), flowing streambeds (305.6 $\pm$ 206.1 mmol m^{-2} day^{-1}) and upland soils (896.1 $\pm$ 263.2 mmol m^{-2} day^{-1}) were net emitters of CO_2 to the atmosphere (Figure 1). The CO_2 efflux from dry streambeds experienced the highest intra-habitat variability and was significantly higher than the CO_2 efflux from flowing streambeds (Paired t

Table 2. Overview of X- and Y-Variables Included in the PCA and PLS Models

| Variable	Description	PCA model	PLS models
Fco$_2$	CO$_2$ flux (mmol m^{-2} day^{-1})	–	Y
WC	Water content (%)	X	X
Temp	Temperature (ºC)	X	X
Sand	Sand fraction (%)	X	X
Silt	Silt fraction (%)	X	X
Clay	Clay fraction (%)	X	X
P. Size	Mean particle size (µm)	X	X
OM	Organic matter content (%)	X	X
OC	Organic carbon content (%)	X	X
TN	Nitrogen content (%)	X	X
DOC	Dissolved organic carbon concentration of WEOM (mg g^{-1})	X	X
TDN	Total dissolved nitrogen concentration of WEOM (mg g^{-1})	X	X
SUVA	SUVA$_{254}$ index of WEOM (l mg^{-1})	X	X
FI	Fluorescence index of WEOM	X	X
HIX	Humification index of WEOM	X	X
BIX	Biological index of WEOM	X	X
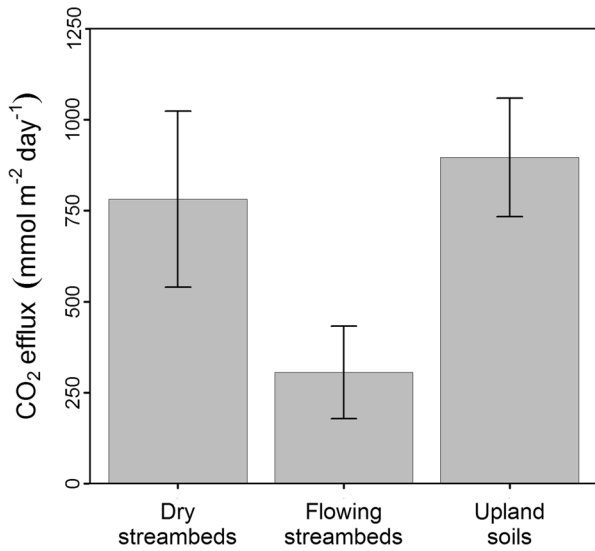
Figure 1. Mean CO_2 efflux from dry streambeds ($n = 10$), flowing streambeds ($n = 7$) and adjacent upland soils ($n = 10$) of the studied streams. The *error bars* represent standard deviations.

test: $p = 0.043$, $n = 7$), but not statistically different than the CO_2 efflux from upland soils (Paired t test: $p = 0.444$, $n = 10$).

Physical and Chemical Properties of Dry Streambed Sediments and Upland Soils

The principal component analysis (PCA) based on physical and chemical properties of the dry streambed sediments and upland soils stressed differences between the two habitats (Figure 2). The two first axes of the PCA explained 71.6% of total variance. The first principal component (58.9% of total variance), clearly separated dry streambeds and upland soils, and was related to texture properties, water content and organic matter quantity. The second principal component (12.7% of total variance) was mainly related to temperature and quality of the WEOM, and exerted a minor effect on the scores distribution along the 2 planes.
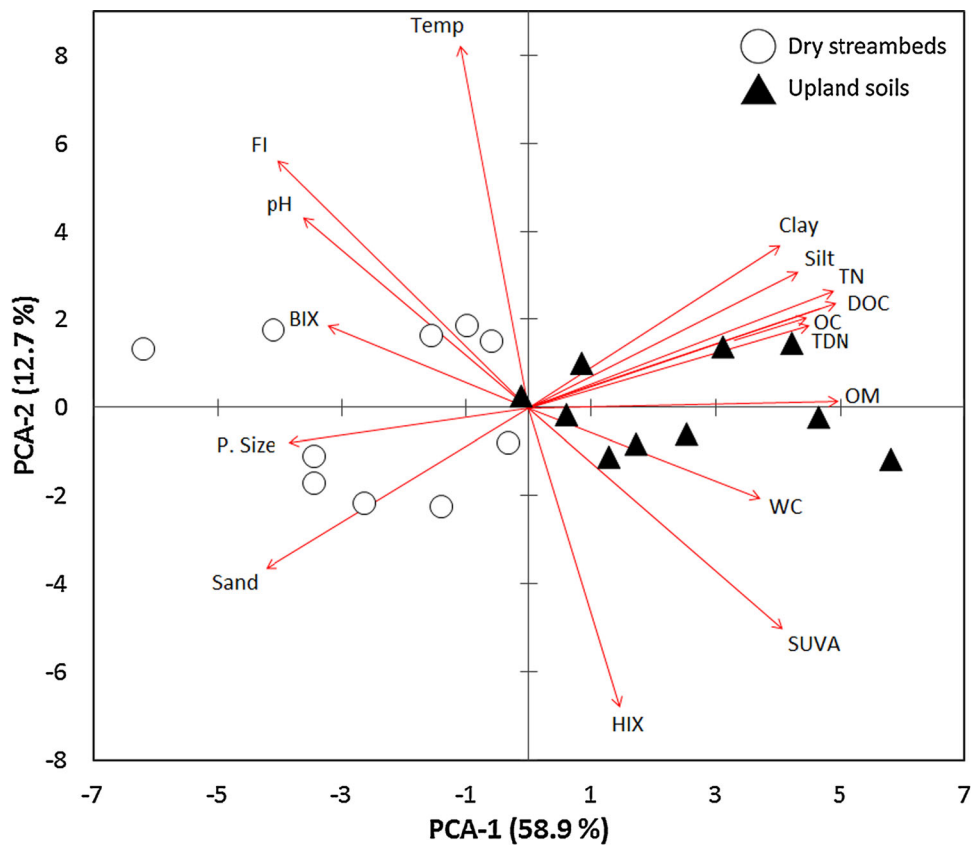

Figure 2. Multivariate ordination (PCA) of dry streambed sediments and upland soils based on physical and chemical descriptors (see Table 2 for the explanation of the abbreviations). The percentage of explained variation for each component is shown in *brackets*. The *symbols* represent the scores of the samples for the first two axes and the *arrows* represent the loadings of each descriptor for the first two axes.

The paired t tests further corroborated that dry streambed sediments and upland soils differed in several physical and chemical properties (Table 3). Water content was significantly lower in dry streambeds than in upland soils. The substrate texture differed significantly between habitats with dry streambeds having a higher sand fraction and mean particle size, whereas upland soils had higher silt and clay fractions. The pH was significantly higher in dry streambeds, whereas upland soils had higher organic matter, organic carbon and nitrogen contents, both in the solid and in the extracted phase (WEOM). The $SUVA_{254}$ and FI indices indicated that the WEOM from dry streambeds was less aromatic and had a more microbial-derived character than the WEOM from upland soils.

Drivers of CO_2 Emissions from Dry Streambed Sediments and Upland Soils

The PLS regression model for dry streambed sediments (Figure 3A) extracted two components from the data matrix that explained 40% of the variance ($R^2Y = 0.40$). The first (horizontal axis in Figure 3A) and the second PLS components (vertical axis in Figure 3A) explained, respectively, 20.1 and 19.7% of the variance. This analysis stressed the relevance (VIP > 1) of sediment temperature, mean particle size, DOC, TDN and TN explaining the variance in the CO_2 efflux from dry streambed sediments.

The PLS model for upland soils (Figure 3B) extracted two components that explained 42% of the variance ($R^2Y = 0.42$). The first and the second PLS components explained, respectively, 24.0 and 17.6% of the variance. The pH, mean particle size, sand, silt and clay fractions, $SUVA_{254}$, FI and HIX were the most influential descriptors explaining the variance in the CO_2 efflux from upland soils (VIP > 1).

DISCUSSION

Magnitude of CO_2 Emissions from Dry Streambeds

Dry streambeds from the studied fluvial network emitted substantial amounts of CO_2 to the atmosphere. Our measurements of CO_2 efflux from dry streambeds (mean = 781 mmol m^{-2} day^{-1}, range = 342–1533 mmol m^{-2} day^{-1}) are similar to those reported from a drying-rewetting experiment in dry desert streams in Arizona, USA (395 mmol m^{-2} day^{-1}, range = 20–1531 mmol m^{-2} day^{-1}; Gallo and others 2014) and higher than others observed in the same geographical area of our study but with lower spatial coverage (mean = 209 mmol m^{-2} day^{-1}, range = 189–220 mmol m^{-2} day^{-1}; von Schiller and others 2014; Gómez-Gener and others 2015). These are, to our knowledge, the only previous studies reporting CO_2 effluxes from dry streambeds.

In the present study, we further show that the CO_2 efflux from dry streams was higher than the CO_2 efflux from the same streams when they were flowing. This result indicates that energy flow, nutrient cycling and subsequent CO_2 production and efflux remain active after flow cessation (Boulton 1991; Jacobson and others 2000); Amalfitano and others 2008). This observation could be related to limitation of the CO_2 efflux due to reduced gas diffusivity and the likely higher uptake of CO_2 by primary producers in aquatic environments compared to dry streambeds. Interestingly, these results agree with recent studies highlighting the relevance of the dry hydrological phases on the CO_2 fluxes from temporary systems of different nature, including temporary ponds (Catalan and others 2014) or reservoir beds found along Mediterranean fluvial networks (Gómez-Gener and others 2015).

Contrary to our expectations, the CO_2 efflux from dry streambeds was similar to the CO_2 efflux from adjacent upland soils. Similarly, von Schiller and others (2014) observed a comparable CO_2 efflux between dry streambeds (median 212 mmol m^{-2} day^{-1}; range 36–455 mmol m^{-2} day^{-1}) and a compiled dataset of Mediterranean soils (median 188 mmol m^{-2} days^{-1}; range 44–371 mmol m^{-2} day^{-1}). However, as our results show, a similar magnitude of CO_2 efflux from dry streambeds and their adjacent upland soils does not necessarily imply that these habitats are equivalent in their physical and chemical structure and function, and therefore in the way they process and emit carbon.

Dry Streambeds as Unique Biogeochemical Hotspots

The studied streambeds and their upland soils were heterogeneous in terms of physical and chemical properties, but our results revealed a clear clustering of samples by habitat. In general, variables related to the textural composition and the organic matter content exerted the strongest influence on the differentiation between the two habitats. Specifically, dry streambed sediments showed a

Table 3. Physical and Chemical Properties of the Dry Streambed Sediments and Upland Soils at Each Study Site

Stream code	Habitat	Physical characteristics						Chemical characteristics									
								Solid phase				Extracted phase					
		Temperature	Water content	Sand	Silt	Clay	Mean particle size	pH	Organic matter	OC	TN	DOC	TDN	SUVA$_{254}$	FI	HIX	BIX
		°C	%	%	%	%	μm		%	%	%	mg g DW^{-1}	mg g DW^{-1}	L mg^{-1} m^{-1}			
1	Dry streambed	18.5 ± 0.3	5.5 ± 0.5	81.4 ± 1.4	11.2 ± 1.1	7.5 ± 0.4	1483.6 ± 168.5	8.49 ± 0.04	1.01 ± 0.18	0.94 ± 0.76	0.03 ± 0.01	0.06 ± 0.01	0.00 ± 0.00	3.12 ± 0.29	2.20 ± 0.17	7.62 ± 1.36	0.52 ± 0.06
	Upland soil	19.0 ± 0.0	16.4 ± 1.4	45.2 ± 9.4	34.8 ± 6.4	20.0 ± 3.2	407.7 ± 306.5	8.43 ± 0.05	6.68 ± 2.36	3.15 ± 2.05	0.20 ± 0.13	0.39 ± 0.12	0.03 ± 0.01	5.93 ± 1.05	2.08 ± 0.01	6.27 ± 0.70	0.54 ± 0.01
2	Dry streambed	19.8 ± 0.4	13.0 ± 6.2	38.9 ± 33.5	34.3 ± 16.5	26.8 ± 17.2	1326.4 ± 235.9	7.96 ± 0.17	2.50 ± 1.92	1.00 ± 0.44	0.09 ± 0.04	0.18 ± 0.08	0.01 ± 0.01	3.58 ± 1.00	2.29 ± 0.08	3.77 ± 0.78	0.57 ± 0.03
	Upland soil	19.9 ± 0.3	21.9 ± 3.8	59.8 ± 3.5	29.7 ± 2.6	10.5 ± 2.7	1239.3 ± 296.0	8.08 ± 0.07	10.10 ± 2.41	5.96 ± 1.32	0.36 ± 0.08	0.47 ± 0.02	0.05 ± 0.01	6.19 ± 0.79	2.09 ± 0.13	5.18 ± 1.61	0.50 ± 0.06
3	Dry streambed	17.7 ± 0.3	20.3 ± 5.6	72.5 ± 34.8	19.9 ± 26.2	7.6 ± 8.6	1039.1 ± 373.8	8.40 ± 0.13	3.79 ± 2.00	1.02 ± 1.07	0.08 ± 0.06	0.11 ± 0.07	0.01 ± 0.00	4.40 ± 0.50	2.14 ± 0.06	6.24 ± 0.65	0.54 ± 0.04
	Upland soil	18.3 ± 0.2	27.0 ± 6.2	48.6 ± 5.2	33.9 ± 4.6	17.5 ± 2.5	147.1 ± 12.7	8.27 ± 0.22	15.83 ± 8.53	6.05 ± 2.73	0.36 ± 0.14	0.55 ± 0.11	0.11 ± 0.01	5.86 ± 0.66	2.14 ± 0.11	5.40 ± 0.28	0.50 ± 0.03
4	Dry streambed	20.9 ± 1.1	10.0 ± 1.7	88.3 ± 7.9	6.7 ± 4.7	4.9 ± 3.3	1411.5 ± 217.6	7.94 ± 0.33	1.65 ± 0.57	0.37 ± 0.03	0.03 ± 0.00	0.07 ± 0.02	0.02 ± 0.00	5.48 ± 0.57	2.14 ± 0.05	7.00 ± 0.98	0.50 ± 0.01
	Upland soil	20.1 ± 0.5	15.3 ± 1.0	24.6 ± 2.4	48.2 ± 1.2	27.3 ± 1.8	855.7 ± 282.1	8.80 ± 0.29	11.07 ± 2.07	5.59 ± 1.50	0.39 ± 0.14	0.56 ± 0.13	0.12 ± 0.04	7.91 ± 0.55	2.04 ± 0.04	9.14 ± 1.37	0.47 ± 0.01
5	Dry streambed	21.2 ± 0.6	9.3 ± 1.9	89.1 ± 6.6	6.9 ± 3.9	4.0 ± 2.7	1305.0 ± 155.1	9.25 ± 0.06	1.11 ± 0.25	0.33 ± 0.14	0.03 ± 0.02	0.06 ± 0.02	0.01 ± 0.00	4.32 ± 0.55	2.18 ± 0.03	6.12 ± 1.00	0.53 ± 0.01
	Upland soil	21.0 ± 0.7	17.0 ± 1.4	55.7 ± 8.0	32.7 ± 6.2	11.5 ± 1.9	101.2 ± 18.7	8.14 ± 0.36	5.97 ± 0.70	1.85 ± 0.53	0.11 ± 0.07	0.30 ± 0.02	0.06 ± 0.01	4.88 ± 0.25	2.09 ± 0.02	5.65 ± 0.59	0.53 ± 0.02
6	Dry streambed	23.4 ± 1.1	15.4 ± 8.7	60.1 ± 30.7	28.0 ± 20.7	11.9 ± 10.0	686.1 ± 557.6	7.98 ± 0.05	4.25 ± 5.01	2.17 ± 2.22	0.15 ± 0.14	0.23 ± 0.16	0.05 ± 0.03	4.09 ± 0.66	2.27 ± 0.17	4.25 ± 0.59	0.53 ± 0.08
	Upland soil	21.1 ± 0.6	14.8 ± 1.1	60.4 ± 3.7	27.2 ± 2.5	12.4 ± 1.3	221.6 ± 49.6	7.78 ± 0.17	6.39 ± 1.39	1.50 ± 0.12	0.14 ± 0.02	0.28 ± 0.04	0.06 ± 0.02	5.60 ± 0.48	2.21 ± 0.03	5.73 ± 0.74	0.60 ± 0.04
7	Dry streambed	21.8 ± 0.7	9.2 ± 3.5	47.4 ± 11.1	36.3 ± 7.9	16.3 ± 3.2	440.2 ± 608.1	7.82 ± 0.26	2.05 ± 0.77	1.18 ± 0.52	0.10 ± 0.05	0.12 ± 0.02	0.02 ± 0.00	5.23 ± 0.47	2.15 ± 0.06	8.74 ± 1.20	0.51 ± 0.02
	Upland soil	22.1 ± 0.7	18.0 ± 2.5	25.0 ± 4.6	55.5 ± 3.7	19.5 ± 1.1	67.9 ± 26.9	7.13 ± 0.24	10.03 ± 3.12	5.17 ± 2.58	0.39 ± 0.18	0.52 ± 0.19	0.09 ± 0.01	5.14 ± 0.78	2.14 ± 0.02	6.14 ± 1.94	0.50 ± 0.03
8	Dry streambed	22.9 ± 1.4	7.2 ± 6.2	79.2 ± 7.9	14.8 ± 5.6	6.0 ± 2.3	1538.1 ± 238.8	8.14 ± 0.10	1.54 ± 1.03	2.13 ± 0.83	0.05 ± 0.04	0.10 ± 0.05	0.02 ± 0.01	2.83 ± 0.27	2.35 ± 0.10	4.64 ± 0.51	0.56 ± 0.01
	Upland soil	20.3 ± 0.4	24.2 ± 3.8	63.9 ± 2.0	24.5 ± 1.3	11.6 ± 0.8	242.4 ± 32.2	8.20 ± 0.14	8.56 ± 2.68	2.66 ± 0.83	0.13 ± 0.05	0.32 ± 0.05	0.03 ± 0.01	5.67 ± 0.68	2.07 ± 0.14	5.56 ± 1.07	0.43 ± 0.05
9	Dry streambed	22.1 ± 0.3	3.4 ± 1.2	96.5 ± 1.5	2.3 ± 0.9	1.3 ± 0.6	1886.6 ± 213.8	7.53 ± 0.52	0.52 ± 0.17	0.16 ± 0.04	0.01 ± 0.00	0.06 ± 0.00	0.00 ± 0.00	2.22 ± 0.16	2.36 ± 0.07	4.58 ± 0.82	0.60 ± 0.04
	Upland soil	22.0 ± 0.3	13.3 ± 1.0	23.4 ± 13.0	46.3 ± 6.9	30.3 ± 6.9	685.8 ± 286.5	8.40 ± 0.08	7.00 ± 1.95	5.02 ± 1.26	0.31 ± 0.09	0.57 ± 0.21	0.03 ± 0.01	4.53 ± 0.53	2.11 ± 0.16	7.54 ± 1.56	0.42 ± 0.05
10	Dry streambed	22.8 ± 0.2	16.1 ± 8.5	56.6 ± 27.7	29.3 ± 18.8	14.1 ± 8.9	800.9 ± 1093.9	8.41 ± 0.10	4.42 ± 2.87	2.87 ± 0.46	0.17 ± 0.05	0.32 ± 0.04	0.02 ± 0.00	3.90 ± 0.86	2.28 ± 0.13	4.93 ± 0.82	0.51 ± 0.03
	Upland soil	22.7 ± 0.3	11.6 ± 1.6	55.7 ± 4.9	29.7 ± 3.7	14.6 ± 1.7	683.5 ± 610.3	8.45 ± 0.16	7.24 ± 2.76	3.34 ± 1.46	0.20 ± 0.09	0.50 ± 0.18	0.04 ± 0.01	5.33 ± 0.57	2.14 ± 0.01	5.34 ± 0.53	0.47 ± 0.01
Mean ± sd	Dry streambed	21.1 ± 1.9	11.0 ± 5.2	71.0 ± 19.3	19.0 ± 12.4	10.0 ± 4.5	1191.7 ± 442.7	8.19 ± 0.48	2.28 ± 1.41	1.22 0.90	0.07 ± 0.05	0.13 ± 0.09	0.02 ± 0.01	3.92 ± 1.02	2.24 ± 0.08	5.79 ± 1.63	0.54 ± 0.03
Mean ± sd	Upland soil	20.6 ± 1.4	18.0 ± 4.9	46.2 ± 16.1	36.3 ± 10.2	17.5 ± 6.9	465.2 ± 387.6	8.17 ± 0.45	8.89 ± 3.01	4.03 1.73	0.26 ± 0.11	0.45 ± 0.11	0.06 ± 0.03	5.70 ± 0.93	2.11 ± 0.05	6.19 ± 1.24	0.50 ± 0.05
p value	dsb vs. us	0.220	**<0.001**	**0.020**	**0.009**	**0.040**	**<0.001**	**0.009**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.019**	**<0.001**	**<0.001**	0.472	0.105

Values reported means and standard deviations (mean ± sd; n =4). Results of the paired T-tests for differences between dry streambeds and upland soils are shown in the lower part of the table. Significant differences (p<0.05) are marked in bold.

higher mean particle size and a higher proportion of sand, whereas upland soils were associated with lower mean particle size and higher proportions of clay and silt fractions. Because they act as hydrological flow paths, streambeds are more exposed to higher and recurrent surface stress in comparison to soils (Hickin 1995), making it more likely for water flow to initiate sediment erosion and transport. Thus, finer particles can be more easily mobilized in streams, but tend to be more retained in soils (Jacobson and others 2000). Dry streambed sediments also contained less organic matter, that is, OM, OC, TN, DOC, TDN, in comparison to upland soils. Dry streambeds and upland soils are subject to different temporal and spatial dynamics of transport, retention and processing of organic matter (Wagener and others 1998). Accordingly, we expect that recurrent periods of flow recession and subsequent reflowing in temporary streams may favour the oxidation and subsequent washing of OM from dry streambeds, thus lowering its concentration of OM (Acuña and others 2007; Larned and others 2010).

Our results also show that dry streambed sediments and upland soils were different in terms of the quality of organic matter. Significant differences in $SUVA_{254}$ and FI values between habitats indicate lower aromaticity and a higher signal of in situ produced OM from dry streambed sediments. Mediterranean streams can receive a higher leaf input from the riparian forest (direct and lateral fluxes) in comparison to their upland soils during drought periods (Acuña and others 2007). However, the recurrent periods of hydrological connections and disconnections may prevent the stabilization and further humification of stored OM, thereby decreasing the signal of plant structural compounds such as lignin in the WEOM fraction. The dry streambeds also showed higher BIX values than upland soils, pointing again towards a higher proportion of fresh DOM compounds likely derived from fluvial microbial sources (Birdwell and Engel 2010). The stronger microbial character of the WEOM from dry streambed sediments compared to upland soils was likely due to the extracellular release and leachate from decaying bacteria and algae as a result of stream drying (Fierer and Schimel 2003; Borken and Matzner 2009; Kaiser and others 2015).

Regulation of CO_2 Effluxes from Dry Streambeds and Upland Soils

The physical and chemical variables that controlled the CO_2 efflux differed between dry streambeds and upland soils, despite some variables, that is, temperature and textural composition, being involved in the regulation of the efflux in both habitats. The positive relationship between temperature and many biogeochemical processes by stimulation of the microbial activity, for example, autotrophic and heterotrophic respiration, has been widely reported (Raich and Schlesinger 1992; Mielnick and Dugas 2000; Raich and others 2002). Soil texture also influenced the CO_2 efflux from dry streambeds and from upland soils but in opposite directions in each habitat. The CO_2 efflux from dry streambeds increased with decreasing mean particle size. Burke and others (1989) and Buschiazzo and others (2004) also reported that higher proportions of small particles, that is, silt and clay fractions, correlated positively with DOC, TDN and TN concentrations and with water holding capacity, while Austin and others (2004) showed that this promoted microbial heterotrophic respiration in soils of arid and semiarid ecosystems. On the contrary, our upland soils responded inversely to the textural properties and showed higher CO_2 efflux with increasing proportion of coarse-textured soils. This observation can be attributed to a higher diffusion of air and higher infiltration of water to the rooting zone of vegetated soils, resulting in a significant contribution of autotrophic respiration to the total CO_2 efflux in the investigated soils (Noy-Meir 1973; Cable and others 2008; Catalán and others 2014).

Apart from these common drivers of the CO_2 efflux, some variables specifically regulated the efflux from dry streambeds and upland soils. The concentration of the particulate and water extracted fractions of organic carbon and nitrogen were involved in the regulation of the CO_2 efflux only in dry streambeds. The availability of OM can be enhanced during drying periods by release of high amounts of fresh and labile materials to sediment interfaces through microbial cell lysis and physical processes (Fierer and Schimel 2003; Borken and Matzner 2009). However, the microbial activity in dry streambeds could be partially limited by the low concentration of DOC, TDN and TN in the substrate (Table 3), thus explaining the positive effect of OM concentration variables (TDN, DOC, TN) on the CO_2 efflux (Figure 3A). In contrast, the CO_2 efflux from upland soils was related to OM quality rather than to OM quantity (Figure 3B). Efflux from upland soils, which had a lower proportion of fresh and labile fractions in comparison to the dry streambed sediments (Table 3), was limited by the high aromaticity of the OM. Thus, low aromaticity and molecular complexity and high microbial signal
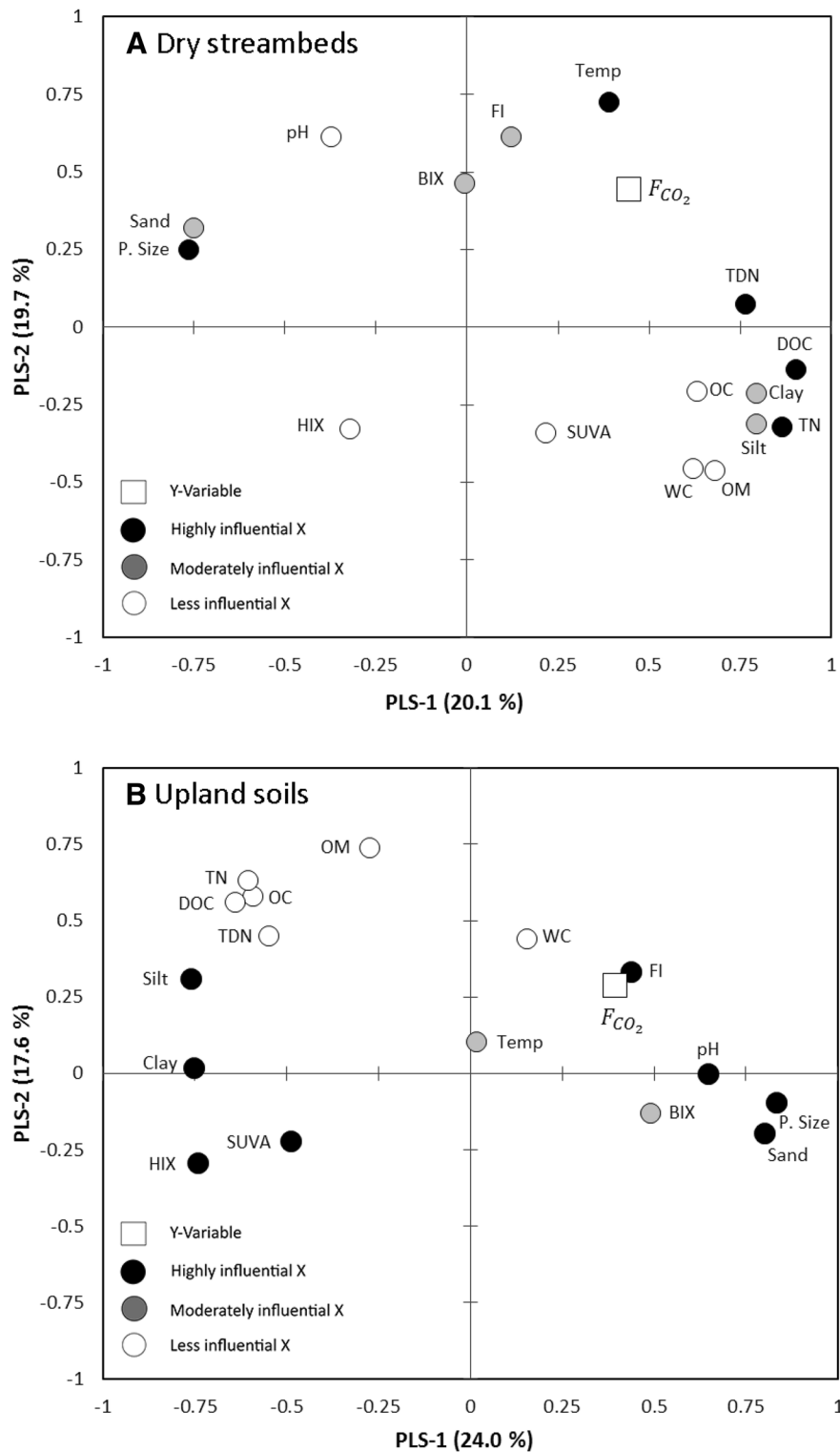
Figure 3. Loadings plot of the PLS regression analysis of the CO_2 emissions from dry streambeds (**A**) and adjacent upland soils (**B**). The graph shows how the *Y*-variable (*square*) correlates with *X*-variables (*circles*) and the correlation structure of the *X*'s. The *X*-variables are classified according to their variable influence on projection value (VIP): highly influential (*black circles*), moderately influential (*grey circles*) and less influential (*white circles*). The *X*-variables situated near *Y*-variables are positively correlated to them and those situated on the opposite side are negatively correlated. See Table 2 for the explanation of the abbreviations.

were associated with high CO_2 efflux in the upland soils. The amount and composition of soil organic matter have been previously identified as important factors affecting CO_2 efflux from soils (Casals and others 2009, Grogan and Jonasson 2005; Paré and Bedard-Haughn 2013).

The PLS models only accounted for 50% of the total variance in CO_2 emissions, indicating that other factors involved in the production of CO_2 potentially contributed to the final CO_2 efflux. Such factors could include differences in microbial community structure, biomass and activity (Amalfitano and others 2008), or non-biotic CO_2-generating processes, such as groundwater CO_2 import (Rey 2015), reactions with the carbonate system (Angert and others 2014), photochemical degradation (Austin and Vivanco 2006) or the effect of wind and air-pressure on the exchange of CO_2 (Suleau and others 2009; Redeker and others 2015). Our results represent an initial attempt at identifying and quantifying the main drivers regulating CO_2 emissions from dry streambeds.

CONCLUSIONS

Temporary watercourses can be found worldwide, and the spatial and temporal extent of the dry phase of these systems is increasing as a result of global change. Despite the prevalence of temporary watercourses, most knowledge in stream ecosystem ecology has been exclusively derived from studies in perennial streams. Thus, fundamental concepts, including the role of fluvial networks in global biogeochemical cycles, may be challenged when temporary watercourses are considered. Our study shows that streams do not turn into inert ecosystems when they become dry. On the contrary, they remain as unique biogeochemical hotspots processing and degassing significant amounts of carbon to the atmosphere comparable to those from upland soils. Our results strongly suggest that not considering streams when they are dry will lead to inaccurate estimates of CO_2 emissions from fluvial networks.

REFERENCES

Acuña V, Giorgi A, Muñoz I, Sabater F, Sabater S. 2007. Meteorological and riparian influences on organic matter dynamics in a forested Mediterranean stream. J N Am Benthol Soc 26:54–69.

Acuña V, Datry T, Marshall J, Barceló D, Dahm CN, Ginebreda A, McGregor G, Sabater S, Tockner K, Palmer M. 2014. Why should we care about temporary waterways? Science 343:1080–2.

Amalfitano S, Fazi S, Zoppini A, Caracciolo AB, Grenni P, Puddu A. 2008. Responses of benthic bacteria to experimental drying in sediments from mediterranean temporary rivers. Microb Ecol 55:270–9.

Anesio AM, Theil-Nielsen J, Graneli W. 2000. Bacterial growth on photochemically transformed leachates from aquatic and terrestrial primary producers. Microb Ecol 40:200–8.

Angert A, Yakir D, Rodeghiero M, Preisler Y, Davidson EA, Weiner T. 2014. Using O_2 to study the relationships between soil CO_2 efflux and soil respiration. Biogeosci Discuss 11:12039–68.

Aristegi L, Izagirre O, Elosegi A. 2009. Comparison of several methods to calculate reaeration in streams, and their effects on estimation of metabolism. Hydrobiologia 635:113–24.

Austin AT, Yahdjian L, Stark JM, Belnap J, Porporato A, Norton U, Ravetta DA, Schaeffer SM. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. Oecologia 141:221–35.

Austin AT, Vivanco L. 2006. Plant litter decomposition in a semi-arid ecosystem controlled by photodegradation. Nature 442:555–8.

Bade DL. 2009. Gas exchange across the air-water interface. In: Gene EL, Ed. Encyclopedia of Inland waters. Oxford: Academic Press. p 70–78.

Belnap J, Welter JR, Grimm NB, Barger N, Ludwig JA. 2005. Linkages between microbial and hydrologic processes in arid and semiarid watersheds. Ecology 86:298–307.

Benstead JP, Leigh DS. 2012. An expanded role for river networks. Nat Geosci 5:678–9.

Birdwell JE, Engel AS. 2010. Characterization of dissolved organic matter in cave and spring waters using UV-Vis absorbance and fluorescence spectroscopy. Org Geochem 41:270–80.

Borken W, Matzner E. 2009. Reappraisal of drying and wetting effects on C and N mineralization and fluxes in soils. Glob Change Biol 15:808–24.

Boulton AJ. 1991. Eucalypt leaf decomposition in an intermittent stream in South-Eastern Australia. Hydrobiologia 211:123–36

Boulton AJ. 2003. Parallels and contrasts in the effects of drought on stream macroinvertebrate assemblages. Freshw Biol 48:1173–85.

Burke IC, Yonker CM, Parton WJ, Cole CV, Flach K, Schimel DS. 1989. Texture, climate, and cultivation effects on soil organic matter content in U.S. grassland soils. Soil Sci Soc Am J 53:800–5.

Buschiazzo DE, Estelrich HD, Aimar SB, Viglizzo E, Babinec FJ. 2004. Soil texture and tree coverage influence on organic matter. Rangel Ecol Manag 57:511–16.

Cable JM, Ogle K, Williams DG, Weltzin JF, Huxman TE. 2008. Soil texture drives responses of soil respiration to precipitation pulses in the Sonoran desert: implications for climate change. Ecosystems 11:961–79.

Casals P, Gimeno C, Carrara A, Lopez-Sangil L, Sanz M. 2009. Soil CO_2 efflux and extractable organic carbon fractions under simulated precipitation events in a Mediterranean Dehesa. Soil Biol Biochem 41:1915–22.

Catalán N, von Schiller D, Marcé R, Koschorreck M, Gómez-Gener L, Obrador B. 2014. Carbon dioxide efflux during the flooding phase of temporary ponds. Limnetica 33:349–60.

Chapman LJ, Kramer DL. 1991. The consequences of flooding for the dispersal and fate of poeciliid fish in an intermittent tropical stream. Oecologia 87:299–306.

Corvasce M, Zsolnay A, D'Orazio V, Lopez R, Miano TM. 2006. Characterization of water extractable organic matter in a deep soil profile. Chemosphere 62:1583–90.

Datry T, Larned ST, Tockner K. 2014. Intermittent rivers: a challenge for freshwater ecology. Bioscience 64:229–35.

Dean WE. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: comparison with other method. J Sediment Petrol 44:242–8.

Eriksson L, Johansson E, Kettaneh-Wold N, Wold S. 2001. Multi- and megavariate data analysis: principles and applications. Umea, Sweden: Umetrics AB.

Fellman JB, Hood E, Spencer RGM. 2010. Fluorescence spectroscopy opens new windows into dissolved organic matter dynamics in freshwater ecosystems: a review. Limnol Oceanogr 55:2452–62.

Fierer N, Schimel JP. 2003. A proposed mechanism for the pulse in carbon dioxide production commonly observed following the rapid rewetting of a dry soil. Soil Sci Soc Am J 67:798–805.

Gallo EL, Lohse KA, Ferlin CM, Meixner T, Brooks PD. 2014. Physical and biological controls on trace gas fluxes in semi-arid urban ephemeral waterways. Biogeochemistry 121:189–207.

Gómez-Gener L, Obrador B, von Schiller D, Marcé R, Casas Ruiz JP, Proia L, Acuña V, Catalán N, Muñoz I, Koschorreck M. 2015. Hot spots for carbon emissions from Mediterranean fluvial networks during summer drought. Biogeochemistry 19:1–18.

Grogan P, Jonasson S. 2005. Temperature and substrate controls on intra-annual variation in ecosystem respiration in two subarctic vegetation types. Glob Change Biol 11:465–75.

Hickin EJ. 1995. River geomorphology. Chichester: Wiley.

Hoerling M, Eischeid J, Perlwitz J, Quan X, Zhang T, Pegion P. 2012. On the increased frequency of Mediterranean drought. J Clim 25:2146–61.

Hornberger GM, Kelly MG. 1972. The determination of primary production in a stream using an exact solution to the oxygen balance equation. Water Resour Bull 8:795–801.

Huguet A, Vacher L, Relexans S, Saubusse S, Froidefond JM, Parlanti E. 2009. Properties of fluorescent dissolved organic matter in the Gironde Estuary. Org Geochem 40:706–19.

Hunt RJ, Jardine TD, Hamilton SK, Bunn SE. 2012. Temporal and spatial variation in ecosystem metabolism and food web carbon transfer in a wet-dry tropical river. Freshw Biol 57:435–50.

Jacobson PJ, Jacobson KM, Angermeier PL, Cherry DS. 2000. Hydrologic influences on soil properties along ephemeral rivers in the Namib desert. J Arid Environ 45:21–34.

Jaffé R, McKnight D, Maie N, Cory R, McDowell WH, Campbell JL. 2008. Spatial and temporal variations in DOM composition in ecosystems: the importance of long-term monitoring of optical properties. J Geophys Res: Biogeosci 113:1–15.

Kaiser M, Kleber M, Berhe AA. 2015. How air-drying and rewetting modify soil organic matter characteristics: an assessment to improve data interpretation and inference. Soil Biol Biochem 80:324–40.

Kothawala DN, Murphy KR, Stedmon CA, Weyhenmeyer GA, Tranvik LJ. 2013. Inner filter correction of dissolved organic matter fluorescence. Limnol Oceanogr: Methods 11:616–30.

Larned ST, Datry T, Arscott DB, Tockner K. 2010. Emerging concepts in temporary-river ecology. Freshw Biol 55:717–38.

Lauerwald R, Laruelle GG, Hartmann J, Ciais P, Regnier G. 2015. Spatial patterns in CO_2 evasion from the global river network. Global Biogeochem Cycl 29:534–54.

Leigh C, Boulton AJ, Courtwright JL, Fritz K, May CL, Walker RH, Datry T. 2015. Ecological research and management of intermittent rivers: an historical review and future directions. Freshwater Biology. doi:10.1111/fwb.12646.

Livingston GP, Hutchinson GL. 1995. Enclosure-based measurement of trace gas exchange: applications and sources of error. In: Matson PA, Harriss RC, Eds. Biogenic trace gases: measuring emissions from soil and water. Oxford: Blackwell Scientific Publications. p 14–51.

Lowe WH, Likens GE, Power ME. 2006. Linking scales in stream ecology. Bioscience 56:591–7.

McClain ME, Boyer EW, Dent CL, Gergel SE, Grimm NB, Groffman PM, Hart SC, Harvey JW, Johnston CA, Mayorga E, McDowell WH, Pinay G. 2003. Biogeochemical hot spots and hot moments at the interface of terrestrial and aquatic ecosystems. Ecosystems 6:301–12.

Mcknight DM, Niyogi DK, Alger AS, Bomblies A, Peter A, Tate CM, Conovitz A, Mcknight DM, Niyogi DEVK, Bomblies A, Tate M. 2008. Valley streams Antarctica: ecosystems waiting for water. Bioscience 49:985–95.

McKnight DM, Boyer EW, Westerhoff PK, Doran PT, Kulbe T, Andersen DT. 2001. Spectrofluorometric characterization of dissolved organic matter for indication of precursor organic material and aromaticity. Limnol Oceanogr 46:38–48.

McLean EO. 1982. Soil pH and lime requirement. In: Page AL, Ed. Methods of soil analysis, part 2: chemical and microbiological properties. Madison: American Society of Agronomy Inc. p 199–224.

Mielnick PC, Dugas WA. 2000. Soil CO_2 flux in a tallgrass prairie. Soil Biol Biochem 32:221–8.

Millero F. 1995. Thermodynamics of the carbon dioxide system in the oceans. Geochim Cosmochim Acta 59:661–77.

Naiman RJ, Decamps H. 1997. The ecology of interfaces: riparian zones. Annu Rev Ecol Syst 28:621–58.

Noy-Meir I. 1973. Desert ecosystems: environment and producers. Annu Rev Ecol Syst 4:25–51.

Oksanen, J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, et al. 2013. Vegan: community ecology package. R package version 2.0–10. http://CRAN.R-project.org/package=vegan.

Palmer MA, Reidy Liermann CA, Nilsson C, Flörke M, Alcamo J, Lake PS, Bond N. 2008. Climate change and the world's river basins: anticipating management options. Front Ecol Environ 6:81–9.

Paré MC, Bedard-Haughn A. 2013. Soil organic matter quality influences mineralization and GHG emissions in cryosols: a

field-based study of sub- to high Arctic. Glob Change Biol 19:1126–40.

Pohlon E, Ochoa Fandino A, Marxsen J. 2013. Bacterial community composition and extracellular enzyme activity in temperate streambed sediment during drying and rewetting. PLoS One 8:e83365.

Raich J, Potter C, Bhagawati D. 2002. Interannual variability in global soil respiration, 1980–94. Glob Chang Biol 8:800–12.

Raich J, Schlesinger W. 1992. The global carbon dioxide flux in soil respiration and its relationship to vegetation and climate. Tellus B 44:81–99.

Raymond PA, Zappa CJ, Butman D, Bott TL, Potter J, Mulholland P, Laursen AE, McDowell WH, Newbold D. 2012. Scaling the gas transfer velocity and hydraulic geometry in streams and small rivers. Limnol Oceanogr: Fluids Environ 2:41–53.

Raymond PA, Hartmann J, Lauerwald R, Sobek S, McDonald C, Hoover M, Butman D, Striegl R, Mayorga E, Humborg C, Kortelainen P, Dürr H, Meybeck M, Ciais P, Guth P. 2013. Global carbon dioxide emissions from inland water. Nature 503:355–9.

Redeker KR, Baird AJ, Teh YA. 2015. Quantifying wind and pressure effects on trace gas fluxes across the soil–atmosphere interface. Biogeosci Discuss 12:4801–32.

Rey A. 2015. Mind the gap: non-biological processes contributing to soil CO_2 efflux. Glob Change Biol 21:1752–61.

Richey JE, Melack JM, Aufdenkampe AK, Ballester VM, Hess LL. 2002. Outgassing from Amazonian rivers and wetlands as a large tropical source of atmospheric CO_2. Nature 416:617–20.

Riley AJ, Dodds WK. 2013. Whole-stream metabolism: strategies for measuring and modeling diel trends of dissolved oxygen. Freshw Sci 32:56–69.

Sheldon F, Bunn SE, Hughes JM, Arthington AH, Balcombe SR, Fellows CS. 2010. Ecological roles and threats to aquatic refugia in arid landscapes: dryland river waterholes. Mar Freshw Res 61:885–95.

Stanley E, Fisher S, Grimm N. 1997. Ecosystem expansion and contraction in streams. Bioscience 47:427–35.

Steward AL, von Schiller D, Tockner K, Marshall JC, Bunn SE. 2012. When the river runs dry: human and ecological values of dry riverbeds. Front Ecol Environ 10:202–9.

Suleau M, Debacq A, Dehaes V, Aubinet M. 2009. Wind velocity perturbation of soil respiration measurements using closed dynamic chambers. Eur J Soil Sci 60:515–24.

Teodoru CR, Prairie YT, Del Giorgio PA. 2010. Spatial heterogeneity of surface CO_2 fluxes in a newly created eastmain-1 reservoir in Northern Quebec, Canada. Ecosystems 14:28–46.

Timoner X, Acuña V, von Schiller D, Sabater S. 2012. Functional responses of stream biofilms to flow cessation, desiccation and rewetting. Freshw Biol 57:1565–78.

von Schiller D, Marcé R, Obrador B, Gómez-Gener L, Casas-Ruiz JP, Acuña V, Koschorreck M. 2014. Carbon dioxide emissions from dry watercourses. Inland Water 4:377–82.

Vergnoux A, Di Rocco R, Domeizel M, Guiliano M, Doumenq P, Théraulaz F. 2011. Effects of forest fires on water extractable organic matter and humic substances from Mediterranean soils: UV-vis and fluorescence spectroscopy approaches. Geoderma 160:434–43.

Wagener SM, Oswood MW, Schimel JP. 1998. Rivers and soils: parallels in carbon and nutrient processing. Bioscience 48:104–8.

Wanninkhof R. 1992. Relationship between wind speed and gas exchange over the ocean. J Geophys Res: Oceans 97:7373–82.

Wehrli B. 2013. Conduits of the carbon cycle. Nature 503:9–10.

Weishaar JL, Aiken GR, Bergamaschi BA, Fram MS, Fujii R, Mopper K. 2003. Evaluation of specific ultra-violet absorbance as an indicator of the chemical content of dissolved organic carbon. Environ Chem 41:843–5.

Weiss R. 1974. Carbon dioxide in water and seawater: the solubility of a non-ideal gas. Mar Chem 2:203–15.

Wold S, Sjöström M, Eriksson L. 2001. PLS-regression: a basic tool of chemometrics. Chemometr Intell Lab Syst 58:109–30.

Zoppini A, Marxsen J. 2011. Importance of extracellular enzymes for biogeochemical processes in temporary river sediments during fluctuating dry-wet Conditions. In: Shukla G, Varma A, Eds. Soil enzymology. Berlin: Springer. p 103–17.

Zsolnay A, Baigar E, Jimenez M, Steinweg B, Saccomandi F. 1999. Differentiating with fluorescence spectroscopy the sources of dissolved organic matter in soils subjected to drying. Chemosphere 38:45–50.

Zuur AF, Ieno EN, Elphick CS. 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol Evol 1:3–14.