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Contrary effects of flow intermittence and land uses on organic matter decomposition in a Mediterranean river basin

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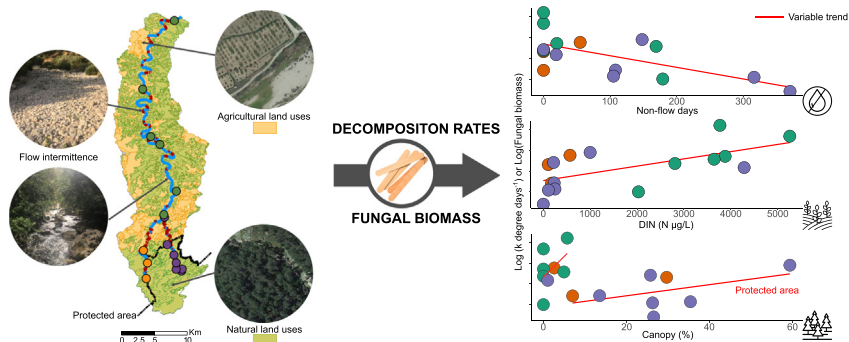
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HIGHLIGHTS

- Intermittent rivers are characterized by high variability in water connectivity.
- Organic matter processing was related to flow intermittence intensity and land uses.
- Negative effect of intermittence was counteracted by agriculture and canopy cover.
- These results complement our understanding of OM dynamics in intermittent rivers.

GRAPHICAL ABSTRACT



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ABSTRACT

Flow interruption in intermittent rivers (IRs) generates a mosaic of terrestrial and aquatic habitats across the river network affecting ecosystem processes, as organic matter (OM) decomposition. Water use for farming in arid and semi-arid climates intensifies the dry conditions and affects local river characteristics. In that way, flow intermittence and the distribution of land uses may affect the OM processing along the river. To understand the role of IRs in global OM dynamics and how global change affecting water flow regimes determines these dynamics, it is important to estimate OM-processing rates at a basin scale. The aim of this study was to evaluate the effect of the intensity of flow intermittence on OM processing, and how this effect was modulated by local environmental factors related to land uses across a Mediterranean river basin. To do this, wood decomposition (mass loss and fungal biomass) was selected as a functional indicator. Drying duration and frequency were measured to characterize flow intermittence in different reaches along the river, as well as local environmental factors. Linear models established the role of factors on decomposition. The results showed that differences in decomposition rates across the river network were negatively related to the duration of flow interruption. Dissolved inorganic nitrogen associated with agriculture counteracted the negative effect of intermittence on mass loss (increasing by up to three times); but with a higher duration of dry conditions, its effect was insignificant. An increase of 20% of canopy (higher in natural areas) resulted in increases of up to 5% of mass loss. Overall, our study is relevant to understanding the interaction between flow intermittence and land uses on OM processing, especially considering the intensification of flow intermittence and its increased distribution to other regions, which is expected to be a consequence of climate warming and human activities.

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1. Introduction

Intermittent rivers (IRs) are characterized by periods of flow cessation and are distributed across the world. Flow intermittence in IRs can be natural and/or induced by human impacts, such as water extraction, flow regulation, changes in land use, or climate change (Steward et al., 2012). Flow cessation implies the disruption of hydrological connectivity in one or more spatial dimensions (longitudinal, lateral and/or vertical) under the hierarchy of the time dimension that can reduce or extend the duration of flow cessation (Ward, 1989; Boulton et al., 2017). At the river basin scale, this variability results in a mosaic of terrestrial and aquatic habitats constantly shifting as a consequence of flow contraction and resumption (Datry et al., 2014) and contributes differentially to the processing of organic matter (OM). As the duration of the dry conditions and rewetting periods is a key factor in controlling microbial activity and OM decomposition (Foulquier et al., 2015), this spatial organization of habitats across the basin jointly with the intensity of temporality will determine the annual OM budget in IR networks, which represent more than half of global river networks (Messenger et al., 2021). To obtain insights into the role of IRs in global OM dynamics and how climate change and other factors affecting flow regimes determine these dynamics, it is important to estimate differences in OM-processing rates across the basin in IRs, including different habitats and conditions.

An increase in agricultural practice intensification in recent decades has generated large impacts on freshwater ecosystems, such as water nutrient enrichment, especially inorganic N and P concentrations (Paul et al., 2006). In addition, agriculture is the economic sector with the highest water demand, and 40.4% of the total water use in Europe in 2015 was for cultivation practices (EEA, 2018). In water-limited areas, such as in the Mediterranean region, the farming of crops has changed from rainfed to irrigated agriculture with higher water consumption. As a consequence, in Mediterranean regions, where IRs are the most common fluvial ecosystems due to their natural flow regimes, freshwater demand has increased mainly in summer when the water flow is the lowest (García-Ruiz et al., 2011), intensifying dry conditions and flow disconnection in the basin. Land for agricultural uses also modifies stream geomorphology, riparian canopy and hydrochemistry (e.g., higher nutrient concentration and presence of pollutants), and consequently, resulting effects are expected on community diversity and ecosystem functioning (Cooper et al., 2013). Knowledge about how these effects interact with flow intermittence is still limited mainly at basin scale where these pressures change spatially.

OM decomposition is a key process in stream ecosystems and represents an important source of carbon and energy for stream food webs (Tank et al., 2010); therefore, it has been suggested as an indicator of ecosystem functioning (Young et al., 2008). OM decomposition is a result of the interaction between several abiotic and biotic factors. The main biological drivers of stream OM decomposition are microbial decomposers (fungi and bacteria) and invertebrate shredders. In the first stages, aquatic hyphomycetes are the first colonizers producing detritus rich in nutrients and transforming leaf litter into a more palatable resource for shredders (Bärlocher, 1992; Gessner et al., 2010). The decomposition process is also affected by environmental factors, such as temperature (Gerald et al., 2012), dissolved nutrients (Menéndez et al., 2011), pH (Kok and Van der Velde, 1994) or flow regimes (Martínez et al., 2015). For instance, increased inorganic N and P concentrations stimulate the activity of aquatic hyphomycetes (Sridhar and Bärlocher, 2000; Menéndez et al., 2011), particularly for low-quality substrates (i.e., low nutrients and high lignin content) (Ferreira et al., 2006). In addition, the duration of flow interruption affects fungal activity as a result of the transition between aquatic and terrestrial habitats but fungal activity recovers when flow resumes (Mora-Gómez et al., 2018). Traditionally, OM decomposition was measured using the mass loss of leaf litter bags, which can be variable depending on litter quality because it has a high variability in chemical composition

(Lecerf and Chauvet, 2008). Nevertheless, several authors have proposed using alternative standardized substrates, which are less variable in their chemical composition (Tiegs et al., 2007; Young et al., 2008). One of these proposals is wooden sticks (Díez et al., 2002). Although wood decomposition is considered a slow process due to its recalcitrant nature, wooden sticks are small pieces with a high surface-to-volume ratio, which favours their decomposition (Arroita et al., 2012). In addition, wood decomposition responds in the same way to environmental factors as leaf decomposition (Gulis et al., 2004).

Studies at the basin scale have important implications for ecosystem services and functioning and, especially, for water resource management (Allan and Johnson, 1997; Elosegi and Sabater, 2013). Previous studies have shown that at this scale, the variability of OM decomposition depends especially on local factors, such as hydromorphological alterations (e.g., flow regulation) (Abril et al., 2015), land uses (Paul et al., 2006; Tonin et al., 2018) or dissolved nutrients (Molinero et al., 1996). For instance, Paul et al. (2006) analysed the effect of different catchment land uses on leaf decomposition and found that agricultural and urban land uses enhance leaf litter decomposition as a consequence of water nutrient enrichment, especially phosphorous. In the same way, Abril et al. (2015), identified a unimodal distribution of decay rates related to total agricultural land use. Aristi et al. (2012) also found a hump-shaped relationship between decomposition rates and phosphorous related to human activities in permanent reaches of four Mediterranean basins on the Iberian Peninsula. However, there is little knowledge about what happens at the basin scale in IRs considering spatial and temporal variations in flow, especially in understanding the interactions between natural flow intermittence and human stressors, such as nutrient addition (Von Schiller et al., 2017).

The aim of this study is to evaluate the effect of the intensity of flow intermittence during a hydrological year on OM decomposition and how it is modulated by land uses at a river basin scale. To accomplish this objective, the decomposition rates and fungal biomass of wood sticks incubated in 16 sites along a small Mediterranean river are analysed in relation to flow intermittence descriptors and local environmental parameters. Part of the studied basin is located in a protected area conserving the natural vegetation; the other part is characterized by land used for agriculture, whereas urban uses were incidental. We hypothesize that a higher intensity (duration and frequency) of intermittence will negatively affect OM decomposition rates and fungal biomass. However, as agricultural activities can increase water nutrient availability to the microbial community, enhancing its activity and biomass accrual, the negative effects of flow intermittence will be reduced in those reaches where the effect of agriculture is present. This study examines at river basin scale, the spatial variation in the quantity of OM processed and relates it to differences in flow patterns (from permanent reaches to ephemeral) and land uses (agricultural and natural uses).

2. Methods

2.1. Study area

This study was conducted in the catchment of the Algars River, which flows into the Matarranya River, a tributary of the Ebro River, located in the northeastern part of the Iberian Peninsula (Fig. 1). The total area of the catchment is 405 km², and the mainstream is 70 km in length. Algars headwaters are divided into two streams, Estrets and Algars, located in the natural park of Els Ports. The climate is typically Mediterranean characterized by scarce precipitation concentrated in spring and autumn with drier and warmer summers. The main land uses were extensive agriculture (44.6% of the total basin, mainly olive groves, fruit trees and vineyards), and natural vegetation (55.3%, mainly coniferous forests, bare rocks, sclerophyllous vegetation and transitional woodland-shrub) while urban land uses were incidental (<0.45%) (© European Union, Copernicus Land Monitoring Service 2018, European Environment Agency (EEA)). We selected 16 sites

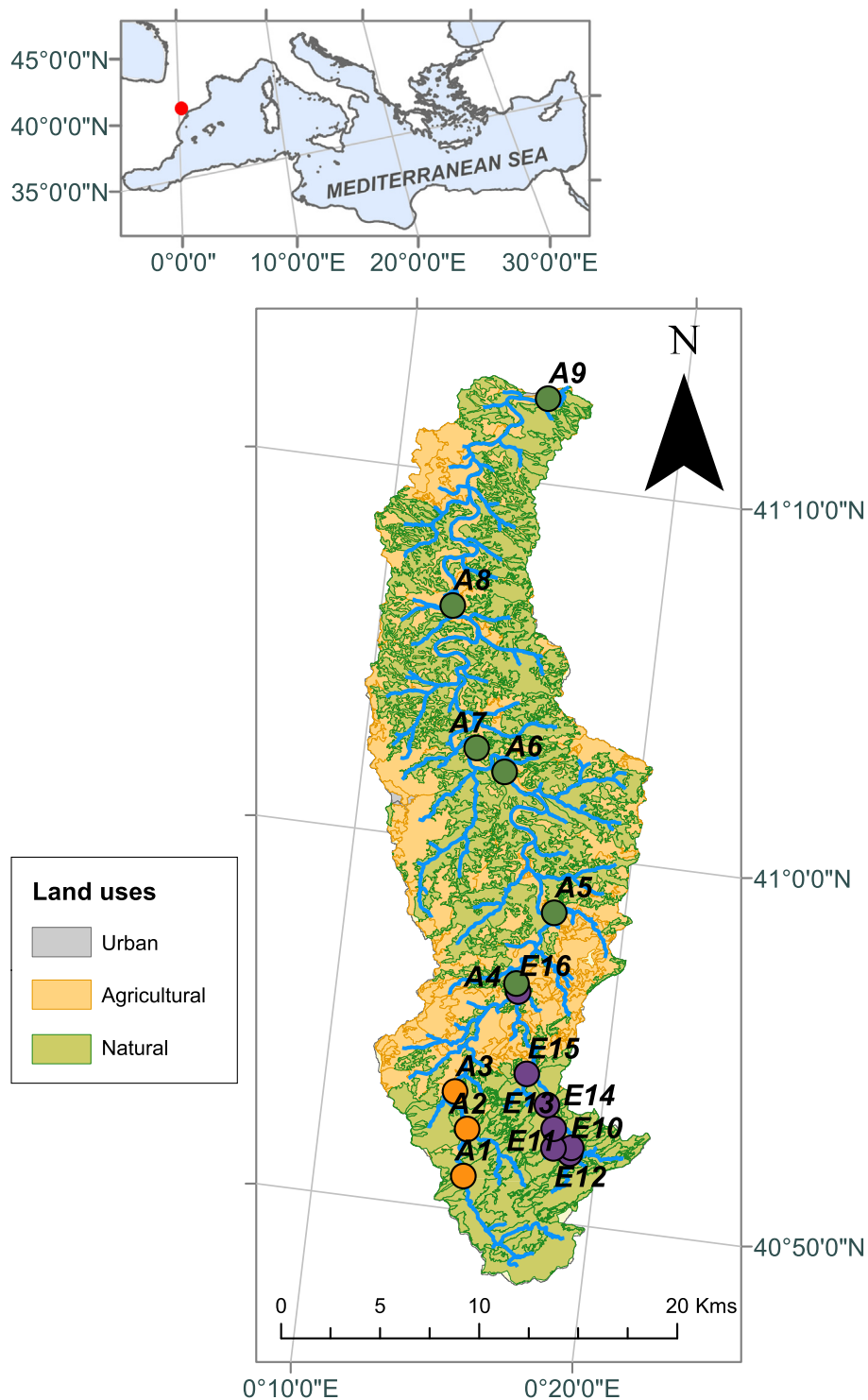


Fig. 1. Location of Algars basin (NE Iberian Peninsula) in the Mediterranean region and land uses distribution in the river basin. Natural land-uses are in green, agricultural land-uses are in orange and urban land-uses in grey. Dots indicate the location of study sites. Purple dots correspond to Estrets stream sites, orange dots correspond to Algars stream sites before the confluence, and green dots correspond to sites on the Algars stream after the confluence. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

across the catchment, 7 sites on the Estrets stream, 3 sites on the Algars headwater stream before the confluence with the Estrets and 6 sites on the Algars mainstream after the confluence (Fig. 1). The study was conducted during a hydrological year (November 2018 to November 2019). During this period, the accumulated precipitation in the basin was 368.9 mm, and the mean temperature was 15.1 °C, with a maximum temperature of 40.6 °C at the end of June and a minimum temperature of −4 °C in January (Meteorological Service of Catalonia, METEOCAT).

2.2. Stream flow intermittence

To characterize flow intermittence, two variables were calculated. The total non-flow days, as a measure of the duration of intermittence, and the total times that flow was interrupted, as a measure of the frequency of intermittence. Both were calculated at each site using the water level and daily streambed temperature variation as an indicator of water presence, recorded every hour during the year with levelloggers

(Solinst Levellogger Edge, full-scale reading accuracy of 0.05%) placed on the streambed (Constantz et al., 2001). To correct the recorded data, atmospheric pressure variations from barologgers (Solinst Barologger, full-scale reading accuracy of 0.05%) installed at the riparian zone at each site were used.

2.3. Environmental parameters

During the study period, water physical and chemical parameters were seasonally (November 2018, February 2019, May 2019 and August 2019) measured at each site (Tables 1 & S1). A portable probe (YSI Professional Plus Multiparameter Instrument, USA) was used in situ for electric conductivity, water temperature, water dissolved oxygen and pH ($\pm 1 \mu\text{S cm}^{-1}$, $\pm 0.1 \text{ }^\circ\text{C}$, $\pm 0.1 \text{ mg L}^{-1}$ and $\pm 0.005 \text{ pH}$, respectively). To characterize water nutrient concentrations, three water samples were filtered through glass fibre filters (0.7- μm pore size; Whatman GF/F, Germany) into prewashed polyethylene containers, transported to the laboratory and stored at $4 \text{ }^\circ\text{C}$ in the dark until analysis. Water samples were analysed by ionic chromatography ($\pm 2.8\%$ at 1 ppm; IC5000, DIONEX, USA) to obtain concentrations of magnesium (Mg^{+2}), calcium (Ca^{+2}) and dissolved nitrogen (N) in nitrite form (NO_2^-), nitrate form (NO_3^-) and ammonium form (NH_4^+). The sum of dissolved N forms was expressed as DIN. Dissolved organic carbon (DOC) was measured by a TOC analyser (TOC-V CSH, Shimadzu Corporation, Japan). The concentration of soluble reactive phosphorus (SRP) was determined by a colorimetrically discrete analyser (Alliance Instruments Smartchem 140, AMS, France).

To characterize land uses, a sub-basin at each site was delineated from a digital elevation model at a 25-m resolution by computing the flow direction and using a watershed tool with geospatial-processing software (ArcMap 10, ArcGIS, USA). The percentages of simplified land-use cover (urban, natural and agricultural land uses) adapted from Corine Land Cover 2018 were calculated at each site.

The average of canopy cover percentage at each site was calculated using a spherical densitometer (Lemmon, 1956), taking four measures (upstream, downstream, right side and left side of the site) at three points of each site.

2.4. Decomposition rates and fungal biomass

To calculate decomposition rates, 10 tongue depressor sticks of Canadian poplar wood (*Populus x canadensis*) ($15 \times 2 \times 0.2 \text{ cm}$) (Arroita et al., 2012) were placed in the riverbed at each site in November 2018. All wood sticks were previously marked, oven-dried ($70 \text{ }^\circ\text{C}$, 72 h) and weighed. Five wood sticks were collected after 90 days, and the other five were collected after one year of incubation. Sticks were placed in zip-lock bags and transported to the laboratory in refrigerated containers. To avoid ergosterol degradation and changes in weight, wood sticks were processed immediately in the laboratory. First, wood sticks were brushed to remove adhered material and washed with distilled water. Later, an aliquot of 1 cm of each stick was cut and frozen at $-80 \text{ }^\circ\text{C}$ for later determination of ergosterol concentration as a proxy of fungal biomass (Gessner, 2005). The remaining part of each wood stick was dried ($70 \text{ }^\circ\text{C}$, 72 h), weighed and summed to the fraction of the frozen aliquot to measure ergosterol (see below). Then, another 1-cm-long aliquot of each wood stick was cut and incinerated ($500 \text{ }^\circ\text{C}$, 5 h) to remove inorganic components and to determine the AFDM⁶. The initial AFDM was determined from an extra set of 20 sticks. This set was also transported into the field but not placed in the river and returned to the laboratory, which was processed as described above to calculate a conversion factor between the initial air-dry mass and the initial AFDM, considering manipulation losses.

To determine ergosterol concentration, frozen aliquots of each wood stick were lyophilized and weighed. Lipid extraction and

saponification were performed using 0.14 M KOH methanol (8 g L^{-1}) in a shaking bath at $80 \text{ }^\circ\text{C}$ for 30 min. To purify lipid extractions, solid-phase extraction cartridges were used (Waters Sep-Pak® Vac RC, 500 mg tC18 cartridges, Waters Corp, Milford, MA, USA), and ergosterol was eluted using isopropanol. High-pressure liquid chromatography (HPLC; Jasco HPLC system, USA) was used at 282 nm to detect and quantify ergosterol using a Gemini-NX 5 μm C18 250 \times 4.6 mm column (Phenomenex, UK). The ergosterol measurement was converted into fungal biomass using a conversion factor of 5.5 mg of ergosterol per gram of fungal mycelium (Gessner and Chauvet, 1993). The results were expressed as mg of fungal biomass per gram of dry mass.

Decomposition rates were calculated following the negative exponential equation $M_t = M_0 \cdot e^{-kt}$, where M_0 is the initial percentage of AFDM, M_t is the remaining AFDM at time t , k is the decay rate, and time t was replaced by the mean daily temperatures accumulated to express decay rates in degree days (dd^{-1}), i.e., in terms of accumulated heat (Stout, 1989). The mean daily temperatures were obtained from levelloggers.

2.5. Data analysis

To explore the environmental variables jointly and their relationships with sites, Principal Components Analysis (PCA) was performed. All environmental variables, including flow intermittence descriptors, were used. This analysis will also allow us to assess the relationship between variables.

To analyse how flow intermittence and environmental characteristics affected the decomposition rates, automated model selection for the linear regression model was performed using the R package MuMIn (Barton, 2009) to select the best combination of all predictor variables based on AICc (Akaike Information Criterion corrected version for small samples). To assess collinearity between explanatory variables, pairwise Pearson correlations and the variance inflator factor (vifstep of usdm R Package) (Feld et al., 2016) were previously estimated. Therefore, agricultural land uses (highly correlated with DIN³ concentration), conductivity (correlated with Ca and DOC) and Mg (correlated with Ca) were discarded (Table S2). Then, the final set of explanatory variables tested in the automated model included the annual means of seasonal variables (DIN, Ca and DOC), flow intermittence variables (non-flow periods and non-flow days) and basin descriptors (canopy).

To analyse the effects of flow intermittence and environmental characteristics on fungal biomass, automated model selection for the mixed linear model was performed using the R package MuMIn (Barton, 2009) to select the best combination of predictors. Fungal biomass values at two sampling times (90 and 365 days) were used considering time as a fixed effect factor, while site was considered a random effect factor. For these analyses, the averages of seasonal variables (DIN, Ca, Mg, DOC, water temperature and conductivity) and flow intermittence variables (non-flow periods and non-flow days) were calculated at 90 and 365 days (Table S2). To assess predictor collinearity, the same previous methodology explained above was conducted. Here, DIN, non-flow days, Ca, water temperature, conductivity and canopy were included in the analysis.

To relate fungal biomass to decomposition rates, linear regression was performed.

The linear model assumptions were assessed and verified for all models performed (Poole and O'Farrell, 1971). The distribution of all variables was explored before the statistical analysis. All explanatory variables, except non-flow periods, were squared-root-transformed. Decomposition rates (k_{dd}) and fungal biomass were log-transformed. All variables were finally Z-standardized (mean = 0, SD = 1) to facilitate model coefficient comparison and avoid the influence of the measurement units in PCA. All statistical analyses were performed using R software (R Core Team, 2020).

3. Results

3.1. Environmental characteristics

The Algars river presented permanent, intermittent and dry sites across the basin (Table 1). Intermittent sites presented great variability in intermittence intensity in the studied period. Specifically, for intermittent sites, non-flow days varied between 19 and 315 days, with a mean of 124 days, and non-flow periods varied between 1 and 4, with a mean of 1.8. Water characteristics were variable across sites (Tables 1 & S1). Magnesium ($4.5\text{--}13.4\text{ mg L}^{-1}$), calcium ($30.0\text{--}68.7\text{ mg L}^{-1}$), DOC ($2.9\text{--}101.0\text{ mg L}^{-1}$), and conductivity ($297.2\text{--}1086.9\text{ }\mu\text{S cm}^{-1}$) showed a similar trend, increasing downstream except in the Estrets stream. The percentage of dissolved oxygen presented values between 66.1 and 107.0, where E12 had the lowest value and E13 the highest (Table 1). The pH varied between 7.9 and 9.0. Dissolved inorganic nitrogen (DIN) was used as representative of all nitrogen forms and varied between 105.3 and 5261.5 $\mu\text{g/L}$. The main dissolved nitrogen form was nitrate and was related to agricultural practices in each sub-basin. For instance, the concentration of DIN at site A4 was the highest, which was also the site with the highest percentage of agricultural land use (73.3%). Canopy cover varied between 0 and 59%, which was related to headwater sites and smaller width of the streambed.

The first two components of PCA with the environmental variables explained almost 70% of the total variance. (Table S3). Specifically, PC1 explained 43.31%, while PC2 explained 26.08% (Fig. 2). PC1 indicated environmental characteristics and separated headwater sites (Estrets and Algars headwater streams) characterized by lower conductivity and a higher percentage of canopy than downstream sites (Algars after the confluence). PC2 separated sites according to flow intermittence measures and agricultural land uses (Table S4). However, intermittent sites with low non-flow days (E16, A3 and A6) were situated next to permanent sites because these sites were characterized by low canopy cover and high DIN concentrations. On the other hand, permanent sites A4, A5 and A7 were characterized by high DIN concentrations and a great proportion of agricultural land uses, while sites E12, A1 and A2 were permanent but with a high percentage of natural land uses and low DIN concentrations.

3.2. Decomposition rates

Decomposition rates (k_{dd}) varied between $9.2 \cdot 10^{-6}$ and $4.1 \cdot 10^{-4}\text{ dd}^{-1}$ (Fig. 3A; Table S5). The highest values corresponded to A4 and A5 ($2.4 \cdot 10^{-4}$ and $4.1 \cdot 10^{-4}$, respectively), sites located downstream, permanent sites and sites with the highest DIN concentration. The lowest values corresponded to E11, E15 and A8 ($9.2 \cdot 10^{-6}$, $1.8 \cdot 10^{-5}$ and $1.7 \cdot 10^{-5}$, respectively), sites with the highest duration of intermittence (370, 316 and 179 days, respectively). The results of model selection showed that k_{dd} was associated with DIN, canopy and non-flow days (adjusted $R^2 = 0.58$; $F_{3,11} = 7.35$; $p\text{-value} = 0.006$). All variables were significant (Table S6). DIN and canopy had a positive coefficient, which implies an increase in k_{dd} with higher values of DIN and canopy. However, non-flow days had a negative coefficient, which indicates a decrease in k_{dd} with higher values of non-flow days.

The percentage of AFDM lost increased between 15 and 55% due to the DIN effect (Fig. 4) depending on the hydrological regime. For instance, permanent sites with low DIN concentrations (A1, A2 and E12) had AFDM losses of 12.2%, 18.0% and 20.1%, respectively, while A4 and A5, permanent sites but with 30 times more DIN, had the highest AFDM losses (56.8% and 66.8%, respectively). In intermittent reaches, sites with a high DIN (E10, A6 and A9) had a higher AFDM loss (39.7%, 27.6% and 24.9%, respectively) than sites with a low DIN (E13, E14 and E15 with 13.0%, 11.1% and 6.9%, respectively). Then, the effect of non-flow days was clear on E12, E13 and E14 with low DIN concentration values, and AFDM loss decreased almost 20% with an increase in non-flow days. However, E11, E15 and A8, with different DIN concentrations, had a similar AFDM loss because the severity of intermittence was the highest at these sites. In addition, an increase of 20% of canopy meant increases next to 5% of AFDM lost. For example, A1 and A2 were permanent sites with similar DIN concentrations and 7.0% and 29.7% of the canopy, respectively. A2 presented 6% more AFDM loss than A1. Another example was intermittent reaches E10 and E16: E16 had 76.7% higher DIN concentrations, 129 non-flow days less and 58.3% less canopy cover than E10, but E10 had 19.1% more AFDM loss than E16.

3.3. Fungal biomass

Fungal biomass associated with wood litter varied between 2.8 and 294.8 $\mu\text{g/g}$ AFDM (Fig. 3B; Table S7). In general, the one-year fungal biomass presented greater variability and values than that observed after

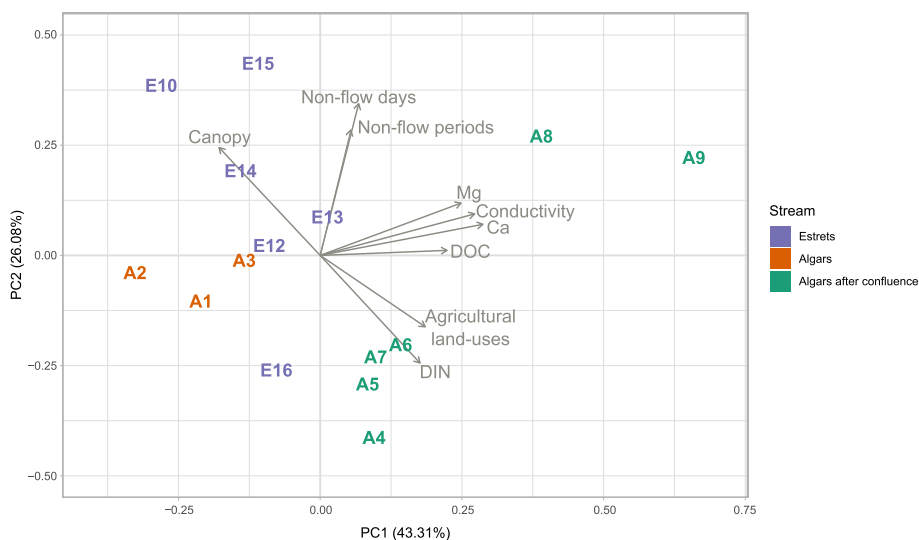


Fig. 2. PCA biplot representation using PC1 (43.3% variability) and PC2 (26.1% variability). Sites are represented by their names and with colours of their respective streams (purple for the Estrets stream, orange for the Algars stream before the confluence, and green for the Algars sites after the confluence). The grey arrows represent the component weights and allow us to understand the relationship between variables and principal components. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

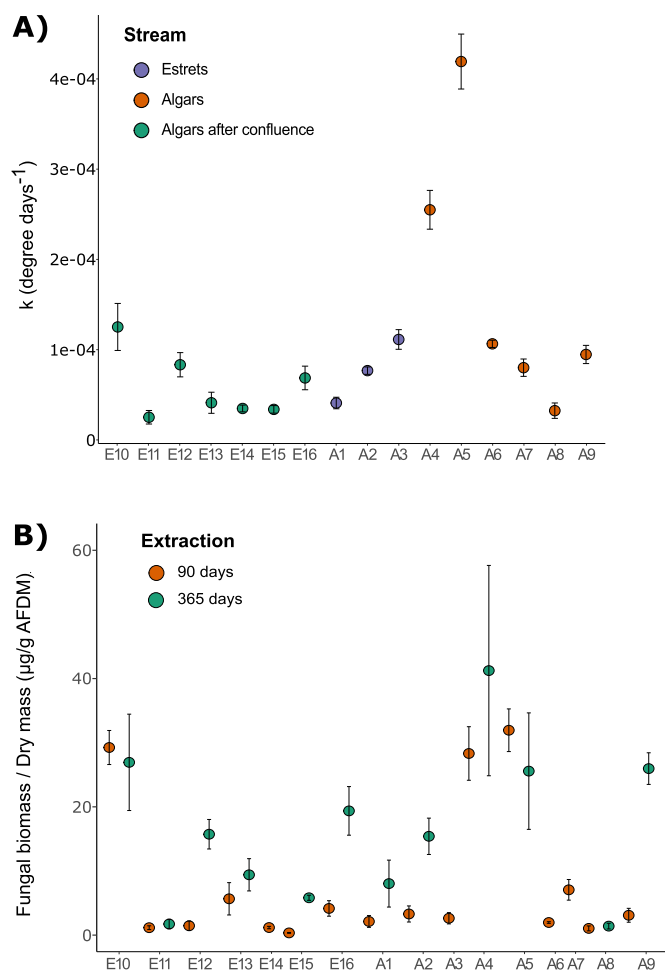


Fig. 3. A) Mean plot of decomposition rates at all study sites of the Algars river basin. Decomposition rates are in degree days⁻¹. Colours correspond to the respective streams of each site (purple for the Estrets stream, orange for the Algars stream before the confluence, and green for the Algars sites after the confluence). B) Mean plot of fungal biomass at each site and at each extraction. Orange colour corresponds to the 90-day extraction, and green colour corresponds to the 365-day extraction. All dots represent the means, while the bars represent standard error. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

three months of incubation. A linear and positive relationship was found between the logarithm of decomposition rate and fungal biomass (adjusted $R^2 = 0.55$; $F_{2,25} = 17.64$; p -value < 0.0001 ; Table S8; Fig. S1).

The model obtained with model selection showed that the fungal biomass was related to DIN, canopy, non-flow days and extraction days (conditional $R^2 = 0.70$). DIN, estimated parameters of canopy cover and extraction days were significant and showed a positive coefficient (Table S9), which implies an increase in fungal biomass related to incubation time at higher DIN concentrations and canopy cover. The estimated parameter of non-flow days was marginally significant (p -value = 0.069) and had a negative coefficient, indicating a decrease in fungal biomass with an increase in non-flow days.

4. Discussion

The distribution of land uses in the basin reveals interactive effects with flow intermittence on OM decomposition. We hypothesized that an increase in intermittence intensity negatively affected the decomposition rates in the study basin. Our results confirmed this prediction, and the sites with more than 170 days of flow cessation showed the lowest decomposition rates. Non-flow days were one of the predictors of the decomposition dynamics selected by the linear model with a negative effect. This effect was counteracted by the presence of nutrients (DIN)

coming mainly from agricultural activity and, with a lower intensity, from canopy cover, which was not expected in our initial hypothesis.

In natural reaches (without anthropogenic activities), intermittence reduced the processing of OM (measured as AFDM) by a mean of 14.9% in comparison with permanent sites, and this reduction was higher with an increase in intermittence duration, as previous studies found (Corti et al., 2011; Datry et al., 2011). As flow fragmentation is variable along the river, spatial and temporal habitat heterogeneity creates different ecological conditions that result in a diverse decomposition process in accordance with the prevailing environmental conditions (Abril et al., 2016). For instance, in dry streambeds, such as site E11, the decomposition process is terrestrial with lower mass losses because terrestrial detritivores are scarce and microbial activity declines (Maamri et al., 1997; Corti et al., 2011). Thus, OM decomposition is faster in aquatic systems than in terrestrial systems due to enhanced leaching, microbial metabolism, and aquatic invertebrate activity (Mora-Gómez et al., 2020).

Intermittence intensity was measured by non-flow days and the number of dry periods, but only non-flow days were a selected predictor for decomposition rates and fungal biomass. The first variable could be considered a measure of the duration of the flow interruption, while the second could be considered a measure of its frequency (Langhans and Tockner, 2006). Coinciding with our results, previous studies found that the duration of dry periods had more influence on OM decomposition than their frequency because the activity of aquatic decomposers decreased with a reduction in flow, but they quickly recovered their activity after rewetting (Pohlon et al., 2013; Foulquier et al., 2015; Niyogi et al., 2020), especially microbial decomposers, considering that aquatic invertebrates take slightly longer to recolonize the reach (Corti et al., 2011).

In Mediterranean rivers, the drying phase is a scaled and prolonged process during the summer period, while the resumption of flow is usually faster across the network during autumn (Vazquez et al., 2013; Boulton et al., 2017). Our results showed an increase in fungal biomass with time, which suggested a fast recovery of fungi after autumnal rewetting. However, during the drying phase, aquatic decomposer communities were affected by changes in environmental conditions in different ways. For instance, isolated pools characterized by a decrease in water flow and low oxygen and detritus accumulation were harsh habitats for fungi (Canhoto et al., 2016), while these conditions did not affect bacteria. Abril et al. (2016) found a decrease in fungal biomass in isolated pools during the drying phase compared with running waters, while bacterial biomass did not show differences between these habitats. In any case, the presence of water determines the continuity of the processing of OM by microbial assemblages, and when water disappears, this process practically stops. Even so, previous studies showed that fungi could be less sensitive to severe drought than bacteria (Maamri et al., 2001; Duarte et al., 2017). In our study, the close relationship between decomposition rates and fungal biomass would suggest that fungi were the main driver of wood decomposition and that their responses to flow variability (although marginally significant in the model) could explain differences in OM processing in the studied basin.

On the other hand, and as we hypothesized, agricultural land uses increased water nutrient enrichment in streams, which positively affected OM decomposition rates. A positive effect of water nutrient enrichment was also observed in relation to fungal biomass. For instance, Abril et al. (2015) identified a unimodal distribution of decay rates related to total agricultural land use in summer in a Mediterranean basin, when temperature and nutrient concentrations increased. In addition, they found that high order reaches presented lower decay rates and less variability between winter and summer than low order reaches, where agricultural practises had a greater presence. These results are consistent with previous studies (Stelzer et al., 2003; Gulis et al., 2004). Fungi have the capability to use inorganic nutrients from water, especially when they colonize a poor-quality substrate, such as

Table 1

Land uses, flow intermittence, canopy cover and chemical water characteristics in the studied reaches. Percentages of land use cover refer to the total sub-basin area associated with each site. Urb. = urban, Agr. = agricultural, and Nat. = natural land uses. DOC = dissolved organic carbon. DIN = dissolved inorganic nitrogen. Values (Mean ± SE) are the mean of the four field campaigns. NA: only one value was available to calculate the mean. Site E11 was always dry when we went to the field.

Site	Catchment land-uses (%)			Flow intermittence				Canopy cover (%)		Chemical water characteristics					
	Urb.	Agr.	Nat.	Non-flow periods	Flow periods	Non-flow days	Flow days	Mg (mg Mg/L)	Ca (mg Ca/L)	DOC (mg C/L)	DIN (µg N/L)	Conductivity (µS/cm)	DO (%)	pH	
E10	0	33.41	66.59	4	3	148	222	59.4 ± 6.4	4.6 ± 4.3	30.5 ± 9.0	22.1 ± 7.2	999.8 ± 422.6	311.3 ± 20.2	81.4 ± 6.2	8.5 ± 0.1
E11	0	0	100	0	0	370	0	26.6 ± 3.9	-	-	-	-	-	-	-
E12	0	0	100	0	0	0	370	25.8 ± 5.3	7.0 ± 6.5	43.4 ± 11.1	54.0 ± 18.2	218.8 ± 14.8	522.5 ± 36	65.2 ± 1.3	7.9 ± 0.2
E13	0	33.41	66.59	1	1	108	262	13.5 ± 1.1	7.9 ± 7.4	40.8 ± 8.7	56.2 ± 27.3	231.7 ± 46.9	489.3 ± 34.9	107.0 ± 4.4	8.8 ± 0.3
E14	0	33.41	66.59	2	2	105	265	35.4 ± 2.6	6.2 ± 5.7	34.5 ± 8.2	41.7 ± 20.1	247.7 ± 74.1	414.2 ± 47.3	87.3 ± 3.7	8.7 ± 0.2
E15	0	0.21	99.79	1	1	316	54	26.3 ± 4.6	12.2 ± NA	43.9 ± NA	2.9 ± NA	109.0 ± NA	297.2 ± 43.9	85.2 ± 12.0	8.6 ± 0.2
E16	0	33.41	66.59	1	1	19	351	1.0 ± 0.4	5.0 ± 4.3	30.0 ± 2.4	32.6 ± 11.4	4287.0 ± 1941.9	420.6 ± 18.6	91.8 ± 4.4	8.8 ± 0.1
A1	0	3.10	96.90	0	0	0	370	7.0 ± 2.9	5.8 ± 5.4	35.9 ± 9.1	30.0 ± 9.9	177.5 ± 52.9	360.4 ± 18.5	95.3 ± 3.0	9 ± 0.1
A2	0	3.10	96.90	0	0	0	370	29.7 ± 2.5	4.8 ± 4.4	31.1 ± 9.6	25.6 ± 8.8	105.3 ± 28.1	325 ± 27.3	86.4 ± 3.9	8.9 ± 0.1
A3	0	3.10	96.90	1	1	55	315	2.6 ± 2.3	6.6 ± 6.0	37.3 ± 10.0	34.4 ± 11.0	569.8 ± 359.8	395.3 ± 32.1	87.8 ± 4.2	8.3 ± 0.6
A4	0	73.33	26.67	0	0	0	370	0.0 ± 0.0	7.2 ± 6.2	38.9 ± 9.7	34.9 ± 11.2	5261.5 ± 1291.5	434.8 ± 27.6	90.9 ± 5.9	8.9 ± 0.1
A5	0.01	57.57	42.42	0	0	0	370	5.7 ± 2.5	7.5 ± 6.0	45.3 ± 10.9	40.8 ± 13.2	3770.3 ± 1461.9	442.5 ± 35.6	100.8 ± 4.5	9.1 ± 0.1
A6	0.01	57.57	42.41	1	1	20	350	0.0 ± 0.0	9.9 ± 8.2	46.5 ± 12.4	33.9 ± 15.9	3881.0 ± 1377.5	427.4 ± 58.7	100.0 ± 6.2	9 ± 0.1
A7	0.45	47.79	51.76	0	0	0	370	0.0 ± 0.0	10.4 ± 8.7	48.6 ± 12.3	32.2 ± 14.9	2810.0 ± 1413.3	470.1 ± 31.9	83.0 ± 10.9	8.8 ± 0.1
A8	0.45	47.79	51.76	3	2	179	191	0.0 ± 0.0	11.8 ± 9.9	55.7 ± 10.8	44.7 ± 21.1	2031.3 ± 1206.0	986.1 ± 473.3	87.0 ± 7.8	8.8 ± 0.3
A9	0.24	46.73	53.02	2	2	169	201	4.9 ± 2.0	13.5 ± 10.0	68.7 ± 8.0	101.0 ± 56.6	3645.3 ± 955.4	1086.9 ± 346.2	81.8 ± 12.8	8.5 ± 0.4

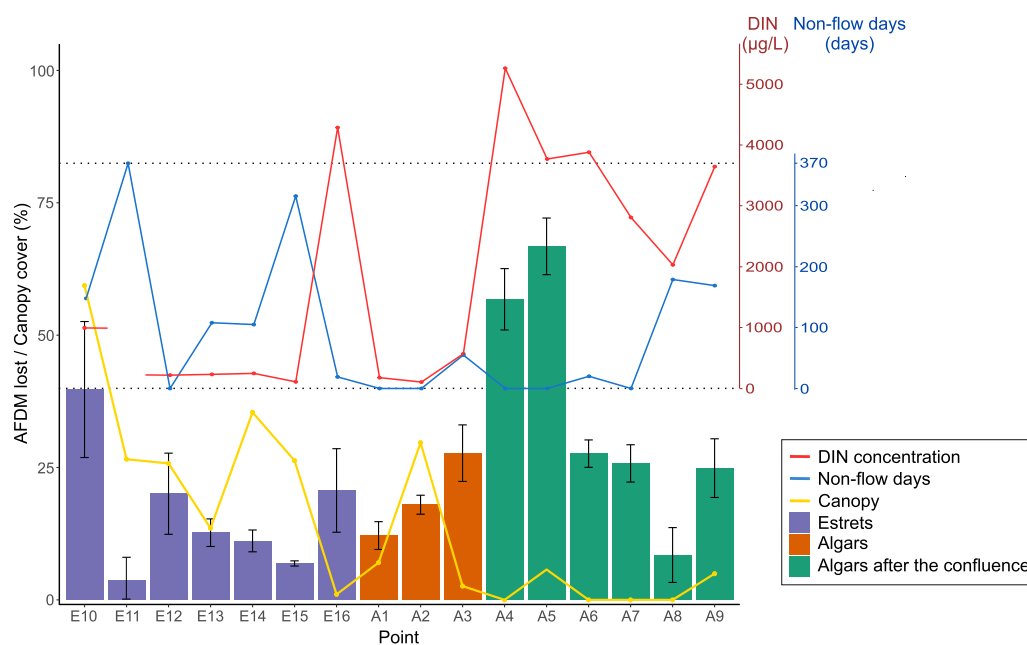


Fig. 4. Barplot of percentage of mean of ash free dry mass (AFDM) lost, filled with colours that correspond to their respective streams (purple for the Estrets stream, orange for the Algars stream before the confluence, and green for the Algars sites after the confluence). The yellow line is the percentage of canopy cover at each site. The blue line corresponds to the total number of non-flow days at each site. The red line is the mean DIN concentration at each site (µg N/L). Vertical bars represent the standard errors. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

wood, which is rich in lignin with a high ratio of C:N (Suberkropp, 1998; Sridhar and Bärlocher, 2000; Stelzer et al., 2003; Ferreira et al., 2006). The predominant form of DIN in the study basin was nitrate (Table S1), which is associated with anthropogenic activities, especially with agricultural practices (Lassaletta et al., 2009), and it could cause a significant change in decomposition rates and fungal biomass with small increases (Ferreira et al., 2006).

Our results suggested that DIN concentration modulated the negative effects of the duration of flow intermittence: the presence of DIN favoured OM processing. For instance, at sites with a similar number of non-flow days, the processing of OM was up to three times lower with low DIN concentrations, while the processing of OM when comparing permanent and intermittent reaches was reduced almost two times at sites with high DIN concentrations. However, if the severity of the intermittence increased, the effect of DIN seemed to be insignificant. This interaction between factors existed across the basin, especially at downstream sites, where agricultural practices were more important.

Additionally, our results showed that the percentage of canopy cover also affected decomposition rates and fungal biomass. Canopy cover is related to forestry land uses extending to headwater sites, where fungi are considered the main decomposers of leaf litter and bacteria play a secondary role (Hieber and Gessner, 2002). This could justify the differences found in decomposition rates and fungal biomass at headwater sites with similar durations of intermittency and low DIN concentrations. High canopy cover implies an entry of allochthonous leaf litter, which could stimulate fungal biomass and their activity (Gessner et al., 1999). Canopy cover reduces sunlight incidence, especially ultraviolet radiation (UV), which has direct effects on fungal development (Newsham et al., 1997). The decrease in light availability limits the growth of algal biofilms, reducing competition with fungi for inorganic nutrients (Daufresne and Loreau, 2001). Algal biofilms are also an indirect competitor for fungal decomposers because algae are a more nutritive resource than leaf litter for invertebrates (Tonin et al., 2018). In summary, light affects microbial assemblages in streams, limiting fungal development, favouring algae and having low or no effect on bacteria (Albariño et al., 2008), but other authors have also considered that algae stimulate the presence of bacterial decomposers (Danger et al., 2013), maintaining the processing of OM, especially in downstream sites. All this will have an effect on the processing of OM in streams. For instance, site E16 presented a high light incidence, which explained the presence of a high density of filamentous algae (personal observation), which could be related to the low decomposition rate and fungal biomass observed, even with a high DIN concentration. However, the effect of canopy cover was clear only in headwater reaches, where this factor showed variability, but not downstream, where all sites were open and unshaded.

Fungal biomass explained more than 50% of the decomposition rates in the study basin. Nevertheless, the site with the highest decomposition rates (A5) did not have the highest fungal biomass, and other biotic components affected decomposition processes in the Algars basin. Previously, we mentioned the competition between microbial communities (algae, fungi and bacteria) related to nutrients and light availability, but in addition to this permanent site, we observed a high density of American crabs (*Procambarus clarkii* Girard, 1852), which fragmented the wood sticks, causing mass loss. *Procambarus clarkii* is an invasive species on the Iberian Peninsula with high plasticity to environmental variability (Geiger et al., 2005) but is usually found in downstream reaches with low riparian quality and eutrophication (Maceda-Veiga et al., 2013).

Flow intermittence affects OM decomposition and fungal biomass in the entire basin, but the drying phase is variable across the river network and time, resulting in differences in flow disruption and its duration. The mosaic between terrestrial and aquatic habitats and the duration of flow interruption imply great variability in the quantity of processed OM and the potential for its transport among the habitats, which was not studied here. In addition, land uses and human activities,

such as water nutrient enrichment, also affect the decomposition process in the entire basin, but this effect is related to local impacts and their position in the river network. However, as a generalization, agricultural land uses were located on downstream and forested streams on headwater. Even so, local characteristics are important in explaining the differences across the basin in the processing of OM and in the global budget of carbon in receiving downstream waters (Del Campo et al., 2021).

5. Conclusions

This study demonstrated the negative effect of the duration of flow intermittence on OM decomposition, and how interacted with other local environmental factors across the river basin. An increase in the intensity of flow intermittence reduced OM decomposition, but water nutrient enrichment – favoured by agricultural activities – and canopy cover – related to forested headwaters – counteracted this effect. Nutrients artificially accelerate natural OM processing in the study basin and canopy cover also have a positive effect on OM processing. However, if the severity of the intermittence increased, the effect of counteracted factors seemed to be insignificant. Flow intermittence is a natural perturbation in Mediterranean rivers, but its intensification and increase to other regions is expected to be a consequence of climate warming and an increase in freshwater demand. In the current context of global change, it is especially relevant to further investigate the interactions between flow intermittence and other factors on OM processing at the basin scale to incorporate these data into the global carbon dynamics in IRs. Locally, our results will help to preserve natural resources in the study basin, as well as to improve river management, maintain natural uses in headwaters to guarantee the role of riparian forests as a source of OM inputs, limit light and stimulate microbial decomposition, and control nutrient inputs from agricultural downstream areas.

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CRedit authorship contribution statement

A. Viza: Conceptualization, Methodology, Software, Formal analysis, Writing - original draft. **F. Oliva:** Formal analysis, Writing - review & editing. **I. Muñoz:** Conceptualization, Methodology, Writing - review & editing, Supervision, Funding acquisition. **M. Menéndez:** Conceptualization, Methodology, Writing - review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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References

- Abril, M., Muñoz, I., Casas-Ruiz, J.P., Gómez-Gener, L., Barceló, M., Oliva, F., Menéndez, M., 2015. Effects of water flow regulation on ecosystem functioning in a Mediterranean river network assessed by wood decomposition. *Sci. Total Environ.* 517, 57–65. <https://doi.org/10.1016/j.scitotenv.2015.02.015>.

- 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>.
- Albariño, R., Villanueva, V.D., Canhoto, C., 2008. The effect of sunlight on leaf litter quality reduces growth of the shredder *klapopteryx kuscheli*. *Freshw. Biol.* 53 (9), 1881–1889. <https://doi.org/10.1111/j.1365-2427.2008.02016.x>.
- Allan, J.D., Johnson, L.B., 1997. Catchment-scale analysis of aquatic ecosystems. *Freshw. Biol.* 37 (1), 107–111. <https://doi.org/10.1046/j.1365-2427.1997.00155.x>.
- Aristi, I., Díez, J.R., Larrañaga, A., Navarro-Ortega, A., Barceló, D., Elosegi, A., 2012. Assessing the effects of multiple stressors on the functioning of Mediterranean rivers using poplar wood breakdown. *Sci. Total Environ.* 440, 272–279. <https://doi.org/10.1016/j.scitotenv.2012.06.040>.
- Arroita, M., Aristi, I., Flores, L., Larrañaga, A., Díez, J., Mora, J., Romani, A.M., Elosegi, A., 2012. The use of wooden sticks to assess stream ecosystem functioning: comparison with leaf breakdown rates. *Sci. Total Environ.* 440, 115–122. <https://doi.org/10.1016/j.scitotenv.2012.07.090>.
- Bärlocher, F., 1992. Research on Aquatic Hyphomycetes: Historical Background and Overview. *The Ecology of Aquatic Hyphomycetes*. Springer, Berlin, Heidelberg, pp. 1–15 https://doi.org/10.1007/978-3-642-76855-2_1.
- Barton, K., 2009. Mu-Min: Multi-model inference. R Package Version 0.12.2/r18. <http://R-Forge.R-project.org/projects/mumin/>.
- Boulton, A.J., Rolls, R.J., Jaeger, K.L., Detry, T., 2017. Hydrological connectivity in intermittent rivers and ephemeral streams. *Intermittent Rivers and Ephemeral Streams: Ecology and Management*. Elsevier Inc. <https://doi.org/10.1016/B978-0-12-803835-2.00004-8>.
- Canhoto, C., Gonçalves, A.L., Bärlocher, F., 2016. Biology and ecological functions of aquatic hyphomycetes in a warming climate. *Fungal Ecol.* 19, 201–218. <https://doi.org/10.1016/j.funeco.2015.09.011>.
- Constantz, J., Stonestrom, D., Stewart, A.E., Niswonger, R., Smith, T.R., 2001. Analysis of streambed temperatures in ephemeral channels to determine streamflow frequency and duration. *Water Resour. Res.* 37 (2), 317–328. <https://doi.org/10.1029/2000WR900271>.
- Cooper, S.D., Lake, P.S., Sabater, S., Melack, J.M., Sabo, J.L., 2013. The effects of land use changes on streams and rivers in Mediterranean climates. *Hydrobiologia* 719 (1), 383–425. <https://doi.org/10.1007/s10750-012-1333-4>.
- Corti, R., Detry, T., Drummond, L., Larned, S.T., 2011. Natural variation in immersion and emersion affects breakdown and invertebrate colonization of leaf litter in a temporary river. *Aquat. Sci.* 73 (4), 537–550. <https://doi.org/10.1007/s00027-011-0216-5>.
- Danger, M., Cornut, J., Chauvet, E., Chavez, P., Elger, A., Lecerf, A., 2013. Benthic algae stimulate leaf litter decomposition in detritus-based headwater streams: a case of aquatic priming effect? *Ecology* 94 (7), 1604–1613. <https://doi.org/10.1890/12-0606.1>.
- Detry, T., Arscott, D.B., Sabater, S., 2011. Recent perspectives on temporary river ecology. *Aquat. Sci.* 73 (4), 453–457. <https://doi.org/10.1007/s00027-011-0236-1>.
- Detry, T., Larned, S.T., Tockner, K., 2014. Intermittent rivers: a challenge for freshwater ecology. *Bioscience* 64 (3), 229–235. <https://doi.org/10.1093/biosci/bit027>.
- Daufresne, T., Loreau, M., 2001. Ecological stoichiometry, primary producer-decomposer interactions, and ecosystem persistence. *Ecology* 82 (11), 3069–3082. [https://doi.org/10.1890/0012-9658\(2001\)082\[3069:ESPDDI\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2001)082[3069:ESPDDI]2.0.CO;2).
- Del Campo, R., Foulquier, A., Singer, G., Detry, T., 2021. Plant litter decomposition in intermittent rivers and ephemeral streams. *The Ecology of Plant Litter Decomposition in Stream Ecosystems*. Springer, Cham, pp. 73–100 https://doi.org/10.1007/978-3-030-72854-0_5.
- Díez, J., Elosegi, A., Chauvet, E., Pozo, J., 2002. Breakdown of wood in the Agüera stream. *Freshw. Biol.* 47 (11), 2205–2215. <https://doi.org/10.1046/j.1365-2427.2002.00965.x>.
- Duarte, S., Mora-Gómez, J., Romani, A.M., Cássio, F., Pascoal, C., 2017. Responses of microbial decomposers to drought in streams may depend on the environmental context. *Environ. Microbiol. Rep.* 9 (6), 756–765. <https://doi.org/10.1111/1758-2229.12592>.
- Elosegi, A., Sabater, S., 2013. Effects of hydromorphological impacts on river ecosystem functioning: a review and suggestions for assessing ecological impacts. *Hydrobiologia* 712 (1), 129–143. <https://doi.org/10.1007/s10750-012-1226-6>.
- European Environment Agency, 2018. Climate change and water – warmer oceans, flooding and droughts. *EEA Signals* (Issue 1) <https://doi.org/10.2800/52469>.
- Feld, C.K., Segurado, P., Gutiérrez-Cánovas, C., 2016. Analysing the impact of multiple stressors in aquatic biomonitoring data: a 'cookbook' with applications in R. *Sci. Total Environ.* 573, 1320–1339. <https://doi.org/10.1016/j.scitotenv.2016.06.243>.
- Ferreira, V., Gulis, V., Graça, M.A.S., 2006. Whole-stream nitrate addition affects litter decomposition and associated fungi but not invertebrates. *Oecologia* 149 (4), 718–729. <https://doi.org/10.1007/s00442-006-0478-0>.
- Foulquier, A., Artigas, J., Pesce, S., Detry, T., 2015. Drying responses of microbial litter decomposition and associated fungal and bacterial communities are not affected by emersion frequency. *34* (4), 1233–1244. <https://doi.org/10.1086/682060>.
- García-Ruiz, J.M., López-Moreno, I.I., Vicente-Serrano, S.M., Lasanta-Martínez, T., Beguería, S., 2011. Mediterranean water resources in a global change scenario. *Earth Sci. Rev.* 105 (3–4), 121–139. <https://doi.org/10.1016/j.earscirev.2011.01.006>.
- Geiger, W., Alcorlo, P., Baltanás, A., Montes, C., 2005. Impact of an introduced crustacean on the trophic webs of Mediterranean wetlands. *Biol. Invasions* 7 (1), 49–73. <https://doi.org/10.1007/s10530-004-9635-8>.
- Geraldes, P., Pascoal, C., Cássio, F., 2012. Effects of increased temperature and aquatic fungal diversity on litter decomposition. *Fungal Ecol.* 5 (6), 734–740. <https://doi.org/10.1016/j.funeco.2012.05.007>.
- Gessner, M.O., 2005. In: Graça, M.A.S., Bärlocher, F., Gessner, M.O. (Eds.), *Ergosterol as a Measure of Fungal Biomass BT – Methods to Study Litter Decomposition: A Practical Guide*. Springer, Netherlands, pp. 189–195 https://doi.org/10.1007/1-4020-3466-0_25.
- Gessner, M.O., Chauvet, E., 1993. Ergosterol-to-biomass conversion factors for aquatic hyphomycetes. *Appl. Environ. Microbiol.* 59 (2), 502–507. <https://doi.org/10.1128/aem.59.2.502-507.1993>.
- Gessner, M.O., Chauvet, E., Dobson, M., 1999. A perspective on leaf litter breakdown in streams. *Oikos*, 377–384. <http://www.jstor.org/stable/3546505>.
- Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H., Hättenschwiler, S., 2010. Diversity meets decomposition. *25* (6), 372–380. <https://doi.org/10.1016/j.tree.2010.01.010>.
- Gulis, V., Rosemond, A.D., Suberkropp, K., Weyers, H.S., Benstead, J.P., 2004. Effects of nutrient enrichment on the decomposition of wood and associated microbial activity in streams. *Freshw. Biol.* 49 (11), 1437–1447. <https://doi.org/10.1111/j.1365-2427.2004.01281.x>.
- Hieber, M., Gessner, M.O., 2002. Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. *Ecology* 83 (4), 1026–1038. [https://doi.org/10.1890/0012-9658\(2002\)083\[1026:CODSFA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2002)083[1026:CODSFA]2.0.CO;2).
- Kok, C.J., Van Der Velde, G., 1994. Decomposition and macroinvertebrate colonization of aquatic and terrestrial leaf material in alkaline and acid still water. *Freshw. Biol.* 31, 65–75.
- Langhans, S.D., Tockner, K., 2006. The role of timing, duration, and frequency of inundation in controlling leaf litter decomposition in a river-floodplain ecosystem (Tagliamento, northeastern Italy). *Oecologia* 147 (3), 501–509. <https://doi.org/10.1007/s00442-005-0282-2>.
- Lassaletta, L., García-Gómez, H., Gimeno, B.S., Rovira, J.V., 2009. Agriculture-induced increase in nitrate concentrations in stream waters of a large Mediterranean catchment over 25 years (1981–2005). *Sci. Total Environ.* 407 (23), 6034–6043. <https://doi.org/10.1016/j.scitotenv.2009.08.002>.
- Lecerf, A., Chauvet, E., 2008. Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. *9* (5), 598–605. <https://doi.org/10.1016/j.baae.2007.11.003>.
- Leemans, P.E., 1956. *For. Sci.* 2 (4), 314–320. <https://doi.org/10.1093/forestscience/2.4.314>.
- Maamri, A., Chergui, H., Pattee, E., 1997. Leaf litter processing in a temporary northeastern Moroccan river. *140* (4), 513–531. <https://doi.org/10.1127/archiv-hydrobiol/140/1997/513>.
- Maamri, A., Bärlocher, F., Pattee, E., Chergui, H., 2001. *Int. Rev. Hydrobiol.* 86 (3), 337–348. [https://doi.org/10.1002/1522-2632\(200106\)86:3<337::AID-IROH337>3.0.CO;2-N](https://doi.org/10.1002/1522-2632(200106)86:3<337::AID-IROH337>3.0.CO;2-N).
- Maceda-veiga, A., De Sostoa, A., Sánchez-Espada, S., 2013. Factors affecting the establishment of the invasive crayfish *Procambarus clarkii* (Crustacea, Decapoda) in the Mediterranean rivers of the northeastern Iberian Peninsula. *Hydrobiologia* 703 (1), 33–45. <https://doi.org/10.1007/s10750-012-1335-2>.
- Martínez, A., Pérez, J., Molinero, J., Sagarduy, M., Pozo, J., 2015. Effects of flow scarcity on leaf-litter processing under oceanic climate conditions in calcareous streams. *Sci. Total Environ.* 503–504, 251–257. <https://doi.org/10.1016/j.scitotenv.2014.06.018>.
- Menéndez, M., Descals, E., Riera, T., Moya, O., 2011. Leaf litter breakdown in Mediterranean streams: effect of dissolved inorganic nutrients. *Hydrobiologia* 669 (1), 143–155. <https://doi.org/10.1007/s10750-011-0657-9>.
- Messenger, M.L., Lehner, B., Cockburn, C., Lamouroux, N., Pella, H., Snelder, T., Detry, T., 2021. Global prevalence of non-perennial rivers and streams. *Nature* 594 (7863), 391–397. <https://doi.org/10.1038/s41586-021-03565-5>.
- Molinero, J., Pozo, J., Gonzalez, E., 1996. Litter breakdown in streams of the Agüera catchment: influence of dissolved nutrients and land use. *Freshw. Biol.* 36 (3), 745–756. <https://doi.org/10.1046/j.1365-2427.1996.00125.x>.
- Mora-Gómez, J., Duarte, S., Cássio, F., Pascoal, C., Romani, A.M., 2018. Microbial decomposition is highly sensitive to leaf litter emersion in a permanent temperate stream. *Sci. Total Environ.* 621, 486–496. <https://doi.org/10.1016/j.scitotenv.2017.11.055>.
- Mora-Gómez, J., Boix, D., Duarte, S., Cássio, F., Pascoal, C., Elosegi, A., Romani, A.M., 2020. Legacy of summer drought on autumnal leaf litter processing in a temporary Mediterranean stream. *Ecosystems* 23 (5), 989–1003. <https://doi.org/10.1007/s10021-019-00451-0>.
- Newsham, K.K., Low, M.N.R., McLeod, A.R., Greenslade, P.D., Emmett, B.A., 1997. Ultraviolet-B radiation influences the abundance and distribution of phylloplane fungi on pedunculate oak (*Quercus robur*). *New Phytol.* 136 (2), 287–297. <https://doi.org/10.1046/j.1469-8137.1997.00740.x>.
- Niyogi, D.K., Hu, C.Y., Vessell, B.P., 2020. Response of stream fungi on decomposing leaves to experimental drying. *Int. Rev. Hydrobiol.* 105 (1–2), 52–58. <https://doi.org/10.1002/iroh.201902015>.
- Paul, M.J., Meyer, J.L., Couch, C.A., 2006. Leaf breakdown in streams differing in catchment land use. *Freshw. Biol.* 51 (9), 1684–1695. <https://doi.org/10.1111/j.1365-2427.2006.01612.x>.
- Pohlner, E., Fandino, A.O., Marxsen, J., 2013. Bacterial community composition and extracellular enzyme activity in temperate streambed sediment during drying and rewetting. *PLoS ONE* 8 (12). <https://doi.org/10.1371/journal.pone.0083365>.
- Poole, M.A., O'Farrell, P.N., 1971. The assumptions of the linear regression model. *Trans. Inst. Br. Geogr.* 52 (52), 145. <https://doi.org/10.2307/621706>.
- R Core Team, 2020. *R: A Language and Environment for Statistical Computing*. <https://www.r-project.org/>.
- Sridhar, K.R., Bärlocher, F., 2000. Initial colonization, nutrient supply, and fungal activity on leaves decaying in streams. *Appl. Environ. Microbiol.* 66 (3), 1114–1119. <https://doi.org/10.1128/AEM.66.3.1114-1119.2000>.
- Stelzer, R.S., Heffernan, J., Likens, G.E., 2003. The influence of dissolved nutrients and particulate organic matter quality on microbial respiration and biomass in a forest stream. *Freshw. Biol.* 48 (11), 1925–1937. <https://doi.org/10.1046/j.1365-2427.2003.01141.x>.
- Steward, A.L., Von Schiller, D., Tockner, K., Marshall, J.C., Bunn, S.E., 2012. When the river runs dry: human and ecological values of dry riverbeds. *Front. Ecol. Environ.* 10 (4), 202–209. <https://doi.org/10.1890/110136>.

- Stout, R.J., 1989. Effects of condensed tannins on leaf processing in mid-latitude and tropical streams: a theoretical approach. *Can. J. Fish. Aquat. Sci.* 46 (7), 1097–1106. <https://doi.org/10.1139/f89-142>.
- Suberkropp, K., 1998. Effect of dissolved nutrients on two aquatic hyphomycetes growing on leaf litter. *Mycol. Res.* 102 (8), 998–1002. <https://doi.org/10.1017/S0953756297005807>.
- Tank, J.L., Rosi-Marshall, E.J., Griffiths, N.A., Entekin, S.A., Stephen, M.L., 2010. A review of allochthonous organic matter dynamics and metabolism in streams. *J. N. Am. Benthol. Soc.* 29 (1), 118–146. <https://doi.org/10.1899/08-170.1>.
- Tiegs, S.D., Langhans, S.D., Tockner, K., Gessner, M.O., 2007. Cotton strips as a leaf surrogate to measure decomposition in river floodplain habitats. *J. N. Am. Benthol. Soc.* 26 (1), 70–77. [https://doi.org/10.1899/0887-3593\(2007\)26\[70:CSAALS\]2.0.CO;2](https://doi.org/10.1899/0887-3593(2007)26[70:CSAALS]2.0.CO;2).
- Tonin, A.M., Hepp, L.U., Gonçalves, J.F., 2018. Spatial variability of plant litter decomposition in stream networks: from litter bags to watersheds. *Ecosystems* 21 (3), 567–581. <https://doi.org/10.1007/s10021-017-0169-1>.
- Vazquez, E., Acuña, V., Artigas, J., Bernal, S., Ejarque, E., Gaudes, A., Ylla, I., Martí, E., Mas-Martí, E., Guarch, A., Muñoz, I., Romani, A., Sabater, S., Sabater, E., Von Schiller, D., Butturini, A., 2013. Fourteen years of hydro-biogeochemical monitoring in a Mediterranean catchment. *Bodenkultur* 64 (3–4), 13–20.
- Von Schiller, D., Bernal, S., Dahm, C.N., Martí, E., 2017. Nutrient and organic matter dynamics in intermittent rivers and ephemeral streams. *Intermittent Rivers and Ephemeral Streams: Ecology and Management*. Elsevier Inc. <https://doi.org/10.1016/B978-0-12-803835-2.00006-1>.
- Ward, J.V., 1989. The four-dimensional nature of lotic ecosystems. *J. N. Am. Benthol. Soc.* 8 (1), 2–8. <https://doi.org/10.2307/1467397>.
- Young, R.G., Matthaei, C.D., Townsend, C.R., 2008. Organic matter breakdown and ecosystem metabolism: functional indicators for assessing river ecosystem health. *J. N. Am. Benthol. Soc.* 27 (3), 605–625. <https://doi.org/10.1899/07-121.1>.