Hydrobiologia (2023) 850:1715–1735
https://doi.org/10.1007/s10750-023-05181-y

REVIEW PAPER

A meta-analysis of drought effects on litter decomposition in streams

Verónica Ferreira · Manuel A. S. Graça · Arturo Elosegi

Received: 1 September 2022 / Revised: 1 February 2023 / Accepted: 16 February 2023 / Published online: 13 March 2023

Abstract Droughts, or severe reductions of water flow, are expected to become more frequent and intense in rivers in many regions under the ongoing climate change scenario. It is therefore important to understand stream ecosystem functioning under drought conditions. We performed a meta-analysis of studies addressing drought effects on litter decomposition in streams (50 studies contributing 261 effect sizes) to quantify overall drought effects on this key ecosystem process and to identify the main moderators controlling these effects. Drought reduced litter decomposition by 43% overall, which can impact energy and matter fluxes along heterotrophic food webs. The magnitude of drought effects on litter decomposition depended on the type of drought (natural drought > human-induced drought), type of decomposer community (microbes + macroinvertebrates > microbes) under natural drought, climate (warm and humid > temperate and Mediterranean) under human-induced drought, and on litter identity. The magnitude of drought effects on litter decomposition also increased with the severity of the drought. The effects of ongoing climate change will likely be strongest in streams with abundant shredders undergoing natural drought, especially if the streams become temporary. The composition of the riparian vegetation may modulate the magnitude of drought effects on litter decomposition, which may have management applications.

Keywords Ecosystem functioning · Heterotrophic pathway · Stream intermittency · Systematic review

Handling editor: Sally A. Entrekin

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10750-023-05181-y.

V. Ferreira (✉) · M. A. S. Graça
MARE – Marine and Environmental Sciences Centre, ARNET – Aquatic Research Network, Department of Life Sciences, University of Coimbra, Calçada Martim de Freitas, 3000-456 Coimbra, Portugal
e-mail: veronica@ci.uc.pt

A. Elosegi
Faculty of Science and Technology, University of the Basque Country (UPV/EHU), PO Box 644, 48080 Bilbao, Spain

Introduction

Litter decomposition is a key ecosystem process in forest streams, where it sustains aquatic food webs and is pivotal in the carbon and nutrient cycles (Wallace et al., 1997; Marks, 2019). Once in water, litter from the riparian vegetation is processed by microbial decomposers (mostly aquatic hyphomycetes, but also bacteria) and invertebrate shredders, which mediate the incorporation of litter carbon and nutrients into secondary production (Hieber & Gessner, 2002; González & Graça, 2003).

Aquatic decomposers (microbes and invertebrates) and litter decomposition are highly sensitive to environmental conditions and litter characteristics (Boyero et al., 2016; Yue et al., 2022). Drought, in particular, is a main factor structuring stream communities and processes (Rolls et al., 2012; Stubbington et al., 2017; Sabater et al., 2018). Drought periods result in severe reduction of surface flow and can even lead to the total drying in the so-called intermittent rivers. In fact, between 51 and 60% of global rivers length is intermittent (Messager et al., 2021) and the forecasted increases in air temperature, with the consequent increases in evapotranspiration and water abstraction, will exacerbate flow reduction in many areas, especially in arid regions (Asadieh & Krakauer, 2017). This reduction will likely be even stronger in regions subject to human-induced drought, e.g., where water is withdrawn from streams and rivers for irrigation agriculture (Meybeck, 2003; Milliman et al., 2008; Döll et al., 2009). Invertebrate shredders (mostly belonging to the orders Plecoptera and Trichoptera) are especially sensitive to the degradation of water quality (e.g., increases in temperature, dissolved nutrients and conductivity and decreases in dissolved oxygen) under drought conditions (Stubbington et al., 2017). Reduced flow velocity also decreases the activities of microbial decomposers due to less efficient diffusion of nutrients and oxygen at the water–biofilm interface (de Beer et al., 1996) and lack of physical stimulus for the release of spores by aquatic hyphomycetes (Ferreira & Graça, 2006; Bastias et al., 2020).

Reduced flow and deterioration of water quality under drought, and consequent impacts on microbial decomposers and shredders, often reduce litter decomposition (Sabater et al., 2018), especially in isolated pools and on dry streambeds, where it is extremely slow (Langhans & Tockner, 2006; Corti et al., 2011; Abril et al., 2016). Litter decomposition is thus slower in intermittent than in perennial streams, which has been attributed to legacy effects of past dry periods reducing shredder density when flow resumes (‘drying memory’; Datry et al., 2011). These legacy effects are likely less important for microbes, which can remain on litter even during emersed periods although becoming potentially less efficient when water returns after longer dry periods (Gonçalves et al., 2016, 2019; Arroita et al., 2018; Mora-Gómez et al., 2018). The effects of drought can, thus, depend on the severity of flow reduction, being especially pervasive when the streambed dries out (Langhans & Tockner, 2006; Foulquier et al., 2015; Abril et al., 2016).

As shredders are responsible for stimulating litter decomposition globally by 74% overall (Yue et al., 2022), litter decomposition mediated by the combined activities of microbial decomposers and shredders is likely to be more responsive to drought than microbial-mediated litter decomposition (Riedl et al., 2013). Also, as shredders play a larger role on the decomposition of litter that is soft, nutrient-rich and has low concentrations of recalcitrant and defensive compounds than on the decomposition of more recalcitrant litter (Hieber & Gessner, 2002; Yue et al., 2022), it is expected that litter type (e.g., leaves vs. wood) and identity (genus) will determine its sensitivity to drought (Hill et al., 1988).

Also, studies addressing drought effects on litter decomposition use a variety of methodological approaches and address varying drought magnitudes: studies with different drought severities, natural and cultural drought in real streams, mesocosm and experimental flume studies, litter bags incubated in and out of the water, seasonal comparisons in single streams versus comparisons between streams under contrasting drought regimes, before–after/control–impact studies of naturally occurring vs. experimentally induced drought, etc. All these can affect the magnitude of drought effects on litter decomposition and complicate between-study comparisons (Ferreira et al., 2015).

We carried out a meta-analysis to assess the significance, magnitude, and direction of drought effects on litter decomposition in streams. We also aimed at determining the heterogeneity among studies and at assessing if drought effects on litter decomposition depended on type of drought, experimental approach, severity of drought, litter type, decomposer community, litter identity, and climate. The specific questions and hypotheses addressed are shown in Table 1. This meta-analysis includes 50 studies that contribute 261 comparisons of litter decomposition between drought-stressed and reference (non-stressed) conditions. We considered the effects of all types of drought (i.e., natural and human-induced) and addressed how methodological approaches (i.e., type of drought, type of human-induced drought, type of experimental drought), severity of drought and characteristics of

Table 1 Questions and hypotheses addressed, datasets used, and location of results

Questions	Hypotheses	Dataset used	Result
Q_1: Does drought affect litter decomposition in streams?	H_1: Drought reduces litter decomposition due to decreases in invertebrate shredder abundance and diversity and reduction of microbial decomposer activity	All	Table 2, Fig. 3
Q_2: Does the response of litter decomposition to drought depend on the type of drought (natural vs. human-induced drought)?	H_2: Human-induced drought has stronger effects on litter decomposition than natural drought where stream communities are adapted to low flow	All	Table 2, Fig. 3
Q_3: Does the response of litter decomposition to natural drought depend on the type of comparison (spatial vs. temporal)?	H_3: Natural drought has stronger effects when comparisons are made at spatial scales (i.e., comparison of perennial with intermittent reaches) than at temporal scales (comparison between before vs. after drought events) due to legacy effects ('drying memory') in the later comparison type (i.e., litter decomposition is already impaired in the before drought condition)	Natural drought	Table 2, Fig. 3
Q_4: Does the response of litter decomposition to drought depend on the type of human-induced drought (cultural vs. experimental drought)?	H_4: Experimental drought has stronger effects on litter decomposition than cultural drought due to better control of confounding variables in the former than latter conditions	Human-induced drought	Table 2, Fig. 3
Q_5: Does the response of litter decomposition to drought depend on the type of experimental drought (simulated water diversion vs. simulated desiccation vs. mesocosms)?	H_5: Simulated desiccation (i.e., comparison of immersed and emersed litter samples) has stronger effects on litter decomposition, followed by simulated water diversion (i.e., decreases on flow but generally still wet conditions) and mesocosms (i.e., generally decreases in flow) due to differences in drought severity among experimental approaches	Experimental drought	Table 2, Fig. 3
Q_6: Does the response of litter decomposition to drought depend on the severity of drought?	H_6: Drought effects on litter decomposition increase with drought severity since stronger reduction in flow or higher number of dry days have more severe impacts on aquatic communities (e.g., reduction in available habitat, desiccation) than milder reductions in flow of few dry days	Natural drought Experimental desiccation	Fig. 4A Fig. 4B
Q_7: Does the response of litter decomposition to drought depend on litter type (leaves vs. wood)?	H_7: Drought effects are stronger for the decomposition of leaves where invertebrates play a stronger role than of wood	Natural drought	Table 2, Fig. 5
Q_8: Does the response of litter decomposition to drought depend on the decomposer community (microbial vs. total)?	H_8: Drought effects are stronger for total litter decomposition (i.e., mediated by the activities of both microbes and invertebrates) than for microbial-mediated litter decomposition as invertebrates will be negatively affect by both the drought and the poor microbial conditioning of the litter	Natural drought Human-induced drought	Table 2, Fig. 5 Table 2, Fig. 6

Table 1 (continued)

Questions	Hypotheses	Dataset used	Result
Q_9: Does the response of litter decomposition to drought depend on litter identity?	H_9: Drought effects are stronger for the decomposition of palatable litter genera (e.g., soft, nutrient-rich, with low concentration of recalcitrant and secondary compounds) where invertebrate shredders play a relative larger role than for more recalcitrant litter	Natural drought, Total decomposer community	Table 2, Fig. 5
		Human-induced drought	Table 2, Fig. 6
Q_{10}: Does the response of litter decomposition to drought depend on climate?	H_{10}: Drought effects are stronger for humid climates where drought is less common and aquatic communities may not be adapted to drought stress, than for dry climates where streams naturally face severe seasonal reductions in flow	Natural drought, Total decomposer community	Table 2, Fig. 5
		Human-induced drought	Table 2, Fig. 6

the decomposing litter (i.e., type, identity and decomposer community involved) affected the response of litter decomposition to drought (Table 1). This meta-analysis is therefore complementary to a previous one assessing the effects of human-induced drought on streams (Sabater et al., 2018), including the effects on litter decomposition (7 studies, 41 comparisons), but addressing how drought effects are dependent on regional and stream characteristics (e.g., rainfall regime, season, stream order, nutrient status).

Methods

Literature search and study selection

Primary studies (i.e., empirical studies, including published papers and gray literature such as Master or PhD dissertations) addressing the effects of drought on litter decomposition were searched on May 2nd, 2022. Studies in English, published between January 1st, 1970, and April 30th, 2022 (including online first), were located using Web of Science (WoS) (database: Core Collection; indices: Science Citation Index Expanded, Conference Proceedings Citation Index – Science and Book Citation Index – Science). We used the following search strings (applied to the field 'Topic,' which includes title, abstract, keywords (defined in the study) and keywords plus (keyworks chosen for indexing purposes)): (i) '((stream OR river) AND (drought OR intermitten* OR temporary OR ephemeral) AND (decomposition OR processing OR breakdown OR decay) NOT (facies OR model* OR microcosm*))' to identify studies addressing effects of natural drought and (ii) '((stream OR river) AND (diversion OR abstraction OR scarc*) AND (decomposition OR processing OR breakdown OR decay) NOT (facies OR model* OR microcosm*))' to identify the studies addressing effects of human-induced drought (the 'NOT' component aimed at reducing the number of non-relevant studies). Search (i) identified 2855 records and search (ii) identified 2086 records; 4751 records remained after duplicates were removed (Fig. S1).

Titles and abstracts were screened and studies were selected if they addressed the effects of drought (natural or human-induced) on benthic decomposition of litter derived from tree or macrophyte species (i.e., leaves or wood) and incubated in monocultures (i.e., not in litter mixture) on lotic systems (i.e., streams, rivers, outdoor artificial channels) by comparing at least one drought-stressed and one reference (non-stressed) condition. Studies addressing the effects of drought include those comparing perennial vs. intermittent (flowing, non-flowing or dry) streams (e.g., Datry et al., 2011; Abril et al., 2016), reaches with vs. without flow or dry in intermittent streams (e.g., Corti et al., 2011; Foulquier et al., 2015; Abril et al., 2016), reaches with flow in wet vs. dry years (Schlief & Mutz, 2011), upstream vs. downstream of dams that reduce discharge (Menéndez et al., 2012), water diversion (e.g., Dewson et al., 2007a, b; Death et al., 2009; Arroita et al., 2017), or simulated intermittency (e.g., Bruder et al., 2011; Foulquier et al., 2015). Therefore, drought conditions generally present discharge below normal baseflow. Studies that addressed the effects of hydrological changes (e.g., resulting from dams, seasonal flooding) but that did not provide evidence for drought stress (e.g., lower discharge in the affected location) were not considered. Also, studies comparing seasons, regions, or land uses that are expected to contrast in water availability but that did not address drought effects were not considered. After title and abstract screening, 47 records were kept (Fig. S1).

The full text was screened and studies were selected for inclusion in the database if they reported a decomposition estimate, and associated variability measure (not mandatory for all studies as this can be imputed if missing values are few) and sample size, for both drought-stressed and reference conditions; missing information was requested from authors before a decision to impute data or to exclude the study was made. After accounting for double publication (i.e., when the same data are published in multiple studies), 44 unique studies were included. Additionally, 6 studies known to the authors and that met the inclusion criteria but were not identified in the WoS search were added to the database. The final database thus included 50 studies (Fig. S1, Tables S1 and S2).

Data extraction

Studies included in the database satisfied the inclusion criteria, but for several studies not all information pertaining to litter decomposition did and, therefore, not all data were extracted from these studies (e.g., litter decomposition in the hyporheic zone, litter decomposition in litter mixtures, litter decomposition in the period before drought in before–after control–impact designs, litter decomposition affected by other treatments, decomposition of cotton strips; Table S2). Litter decomposition estimates that complied with inclusion criteria (Table S1 and S2), variability measures, and sample size reported in the text and in tables were extracted directly, information in graphs was extracted with WebPlotDigitizer (https://automeris.io/WebPlotDigitizer/), and missing information was requested from the authors. For studies that reported litter decomposition over time (e.g., Herbst & Reice, 1982; Boulton, 1991; Corti et al., 2011; Schlief & Mutz., 2011), only mass remaining or mass loss at the last sampling date was considered, and for those that reported both exponential and linear litter decomposition rates (e.g., Maamri et al., 1997), the former were considered.

Variation measures were extracted as provided in the primary studies or by the authors (i.e., standard deviation (SD), standard error (SE), or 95% confidence interval (CI)). SD values were used directly for estimating the variance associated with the effect size, while SE and 95% CI were first converted into SD. For studies that did not report variation associated with litter decomposition (e.g., Richardson, 1990; Boulton, 1991; Bernal, 2010; Riedl et al., 2013; Huang et al., 2018), SD values were imputed from studies with similar experimental designs and that reported litter decomposition in the same unit (Lajeunesse, 2013; Appendix 1).

Values extracted from graphs or imputed may deviate from the real values, but not considering them would have limited the analysis. However, the potential bias introduced into the database by extracting data from graphs and by data imputation was assessed in sensitivity analyses.

Effect size

The effects of drought on litter decomposition were estimated as the response ratio R, given by the ratio between the estimate in the drought-stressed condition ($\overline{X}_{drought}$) to the estimate in the reference condition ($\overline{X}_{reference}$); analyses were performed on lnR, i.e., $\ln(\overline{X}_{drought}/\overline{X}_{reference})$; for litter decomposition expressed as mass remaining (which varies in the opposite direction to mass loss or decomposition rate), the numerator and denominator were switched for the calculation of lnR (Hedges et al., 1999; Appendix 1). R = 1 (lnR = 0) indicates no effect of drought on litter decomposition, R < 1 (lnR < 0) indicates reduction and R > 1 (lnR > 0) indicates stimulation under drought. R values can be converted into percentage change for ease interpretation of the magnitude of the effect (Appendix 1).

The variance associated with lnR (V_{lnR}), needed to weigh each effect size in the analysis so that more precise effect sizes (i.e., with low variance) will be weighed more and contribute more to the overall estimate than less precise effect sizes, was calculated using the litter decomposition estimate, its SD and sample size (Borenstein et al., 2009; Appendix 1). The variance associated with R was also used to estimate the 95% CI associated with each effect size, so that R values with 95% CI that do not include 1 are significant (Appendix 1).

Individual litter decomposition studies contributed with multiple effect sizes to the database (2 – 36 per study) as a result from using coarse- and fine-mesh litter bags, several litter species, streams, or drought treatments. Therefore, the 50 studies included in the database contributed with a total of 261 effect sizes (Table S1 and S2). Although considering multiple effect sizes per study might affect results if non-independence of effect sizes is a problem, not considering them would have resulted in a low number of effect sizes, which would have precluded the analysis. We have, nevertheless, carried out sensitivity analyses to assess the effects of non-independence of effect sizes on the results.

Moderator variables

Methodological choices and environmental factors may affect the magnitude and direction of the response of litter decomposition to drought and are termed 'moderators' in meta-analysis. Therefore, information on several potential moderators, according to our hypotheses (Table 1), was recorded: type of drought (natural or human-induced), type of human-induced drought (cultural or experimental), type of experimental drought (simulated water diversion or desiccation or mesocosms), type of comparison being made for natural drought (spatial or temporal), percentage of dry days during the litter incubation period (continuous) and percentage of flow reduction (continuous), litter type (leaves or wood), litter identity (several genera), decomposer community involved (microbial or total: microbes + macroinvertebrates), and climate (several) (Table S3). Information on other variables (e.g., water temperature, dissolved nutrients, current velocity, wet width, and depth) was also extracted, but sample size was too small to be used in analyses.

Statistical analysis

Overall effect size

The studies differed in experimental conditions and, thus, the overall response of litter decomposition to drought, i.e., the grand mean effect size, was determined using the random-effects model of meta-analysis, which considers two sources of variance associated with effect sizes: within-study variance (V_{lnR}) and between-study variance (estimated by the restricted maximum likelihood (REML) method) (Borenstein et al., 2009). Individual effect sizes were weighed by the inverse of their variance, and the grand mean effect size (R) was considered significant if its 95% CI did not include 1. The percentage of total variability that was due to between-study variation (I^2) was also calculated (Borenstein et al., 2009).

Moderator analyses

The effects of categorical moderators on the magnitude and direction of the response of litter decomposition to drought were assessed for subsets of the database, considering available sample size (only moderator levels with at least three effect sizes were tested) and robustness to publication bias. Subgroup analysis was used to estimate mean effect sizes for moderator levels (subgroups), using the random-effects model (with the REML method for between-study variance) (Borenstein et al., 2009). Heterogeneity was compared between (Q_M) and within subgroups to assess the significance of each moderator and subgroup. Subgroups were significant if their 95% CI did not include 1, and two subgroups significantly differed if their 95% CI did not overlap. To avoid that other moderators confound the analysis of a given moderator, categorical moderators were tested hierarchically (Fig. 1).

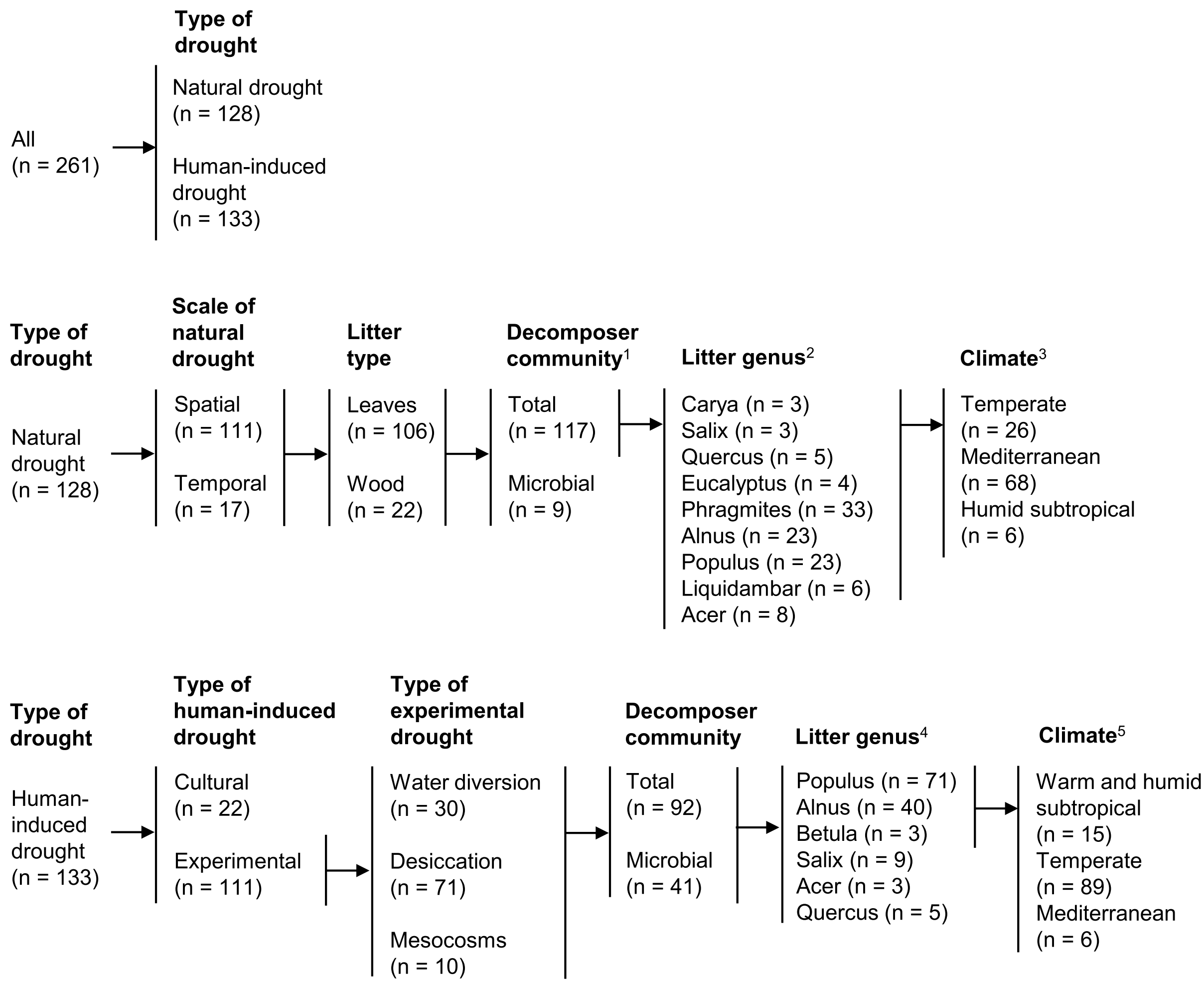

Fig. 1 Hierarchical approach used in the subgroup analyses showing moderator levels with n ≥ 3 (moderator levels with n < 3 were not considered in specific analyses of that moderator and are not shown); comparison of moderator levels in a subgroup analysis was done for specific levels of the previous moderator in the hierarchical approach, except if there were no significant differences among levels in which case the subsequent analysis was made considering all levels of the previous moderator together. [1]Data from Burrows et al. (2017) were not considered (total and microbial-mediated litter decomposition data are shown combined); [2]Data on *Castanea*, *Fraxinus*, *Nerium*, *Nothofagus* and *Ulmus* litters were not considered (n < 3); [3]Data on *Acer* litter was not considered (differs from most other litter genera in the previous analysis) and data on cold-dry climate was not considered (n < 3); [4]Data on *Fagus* and *Melicytus* litters were not considered (n < 3); [5]Data on *Acer*, *Quercus* and *Salix* litters were not considered (differ from most other litter genera in the previous analysis) and data on arid and boreal climates were not considered (n < 3)

The effects of continuous moderators on the response of litter decomposition to drought were assessed for subsets of the database by meta-regression, using the random-effects model (with the REML method for between-study variance) (Borenstein et al., 2009).

Sensitivity analyses

Effect sizes were coded as ‘provided’ when litter decomposition estimates and SD were provided in numerical format (i.e., shown directly in the text or in tables or provided by the authors) or as ‘estimated’ when values had to be extracted from graphs or imputed (Table S1 and S2). The potential bias introduced into the database by extracting data from graphs and by data imputation was assessed by subgroup analysis comparing the grand mean effect sizes for 'provided' and 'estimated' subgroups (as described above for subgroup analysis). Bias would be a concern if the grand mean effect size (R) would be significantly lower (i.e., stronger effect) for the 'estimated' than for the 'provided' subgroup. Also, the previous subgroup analyses based on the entire database were repeated using the 'provided' data only and bias would be a concern if results interpretation differs when considering the entire database and when considering 'provided' data only.

The potential effects of the non-independence of effect sizes, which results from each study contributing with multiple effect sizes to the database, on the results were assessed by repeating the analyses (to the extent possible) considering a single effect size per study (estimated in a subgroup analysis with 'study code' as the moderator and each study as a subgroup). Non-independence of effect sizes would be a problem if results interpretation based on independent effect sizes (i.e., one effect size per study) differ from those obtained using the full database (i.e., with multiple effects sizes per study).

Publication bias

Evidence of publication bias was assessed for the entire database by the funnel plot. This is a scatter plot that contrasts the effect sizes (lnR) with their precision (SE), with symmetrical distribution of effect sizes around the grand mean effect size indicating no publication bias. The impact of publication bias on the grand mean effect size was assessed by the Duval and Tweedie's trim and fill method (Duval & Tweedie, 2000). This method estimates a new grand mean effect size considering the 'missing' effect sizes, which are imputed assuming that the funnel plot should be symmetric. Overlap between the 95% CIs of the original and of the new grand mean effect size indicates that the original grand mean effect size is not strongly affected by publication bias.

Evidence of publication bias in subsets of the database was assessed by the Rosenberg's fail-safe number (N_{fs}). This value gives the number of missing effect sizes showing an insignificant effect that would be needed to nullify the mean effect size, with $N_{fs} > 5 \times n + 10$ (n = number of effect sizes) indicating that the dataset can be considered robust to publication bias.

Standard analytic methods were used (grand mean effect size, subgroup analyses, meta-regressions, and publication bias analyses; Borenstein et al., 2009). Analyses were performed using OpenMEE (Wallace et al., 2017), except for publication bias analyses that were performed using the metafor package (Viechtbauer, 2010) in RStudio (RStudio, 2012).

Results

Database

The earliest study included in the database dates from 1982 (Herbst & Reice, 1982), and since then, the number of studies addressing drought effects on litter decomposition in streams has been accumulating exponentially reaching 50 in April 2022 (Fig. S2). There was an average of 0.3 studies/year before 2000, which increased to 0.8 in 2000 – 2009, 2.6 in 2010 – 2019, and 3.3 studies/year between 2020 and April 2022. Most studies were carried out in Europe (30), North America (8) and Oceania (7) (Fig. 2). Out of 261 comparisons of litter decomposition between drought-stressed and non-stressed conditions contributed by the selected studies, 49% originated from studies addressing natural drought, 43% from studies addressing experimental drought, and 8% from studies addressing cultural drought (i.e., human-induced drought, not caused on purpose for the study) (Fig. 1, Tables S1 and S3). Studies addressing effects of natural drought on litter decomposition more often performed spatial (e.g., perennial vs. intermittent stream; 87%) than temporal comparisons (before vs. after drought; 13%) (Fig. 1, Tables S1 and S3). Studies addressing effects of experimental drought on litter decomposition most often used desiccation (immersed vs. emersed litter bags; 64%), followed by experimental water diversion (27%) and mesocosm (9%) approaches (Fig. 1, Tables S1 and S3). Most comparisons (91%) derived from leaf litter and addressed litter decomposition by both microbes and invertebrates (80%) (Tables S1 and S3). Litter from 17 tree and macrophyte genera were used, with *Populus* (36%), *Alnus* (26%), and *Phragmites* (13%) leaf litter contributing most comparisons (Tables S1).

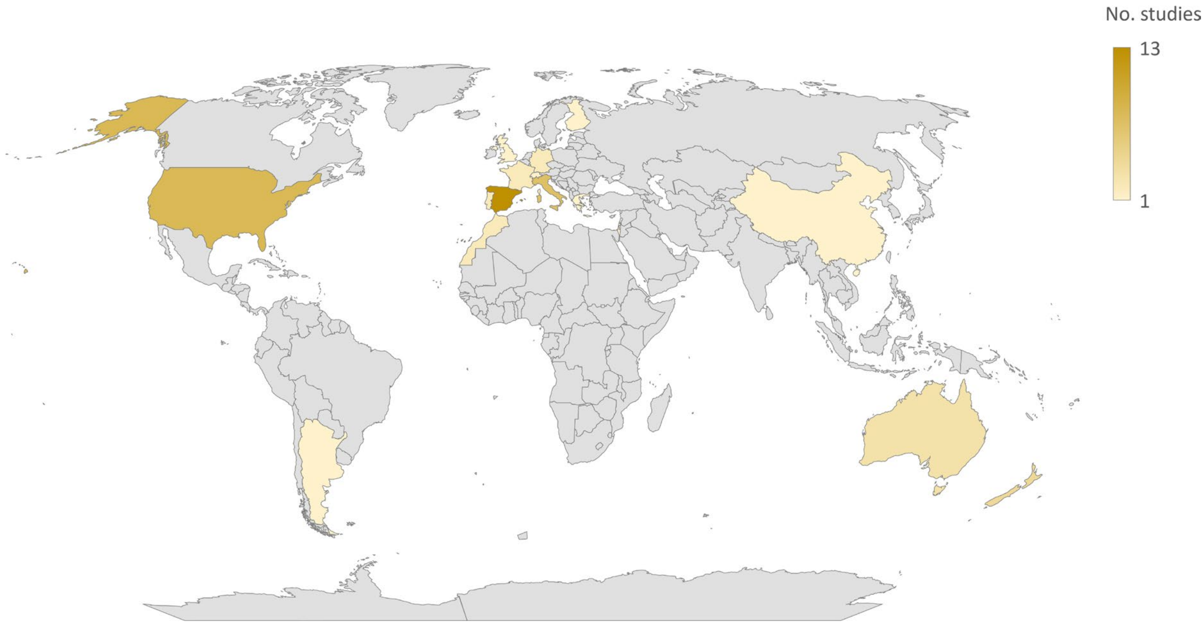

Fig. 2 Global distribution of the studies included in the database (n = 50)

Overall effects of drought on litter decomposition

The majority (85%) of individual effect sizes lnR were negative, with a large number being strongly negative (Table S1), which contributed to a grand mean effect size lnR of – 0.57 (95% CI: – 0.66 to – 0.48) (Fig. S3). This translated into a grand mean effect size R of 0.57 (95% CI: 0.52 – 0.62), indicating a significant reduction of litter decomposition by 43% under drought conditions ($p < 0.001$) (Fig. 3). The funnel plot was, however, asymmetric, with 39 effect sizes 'missing' to the left of the grand mean effect size (Fig. S4A), which suggests publication bias. The new grand mean effect size R estimated by the trim and fill method (after imputing the 'missing' effect sizes) was 0.49 (95% CI: 0.45 – 0.54), which suggests a reduction of litter decomposition under drought by 51%. The original and the new grand mean effects sizes were, however, not significantly different (their 95% CIs overlapped), indicating that the grand mean effect size based on the database was not strongly affected by publications bias. In fact, the Rosenberg's fail-safe number was well above the threshold for considering the database robust to publication bias (Table 2). The percentage of total variability that is due to between-study variation was high ($I^2 > 99\%$), suggesting that the response of litter decomposition to drought is affected by methodological choices and environmental factors.

Effects of moderators on the response of litter decomposition to drought

The effect of drought on litter decomposition significantly depended on the type of drought with stronger reduction under natural than under human-induced drought (51% vs. 35% reduction), although significant in both cases (Table 2, Fig. 3). However, drought effects on litter decomposition did not depend on the type of comparison for natural drought (spatial or temporal), type of human-induced drought (cultural or experimental), or type of experimental drought (water diversion, desiccation, or mesocosm studies) (Table 2, Fig. 3). Drought effects on litter decomposition depended on the severity of the drought, with effects becoming stronger as the percentage flow reduction increased in studies addressing natural drought (Fig. 4A) and as the percentage number of dry days during the litter incubation period increased in studies addressing experimental desiccation (Fig. 4B). In the case of human-induced drought, no significant relationship was found between the

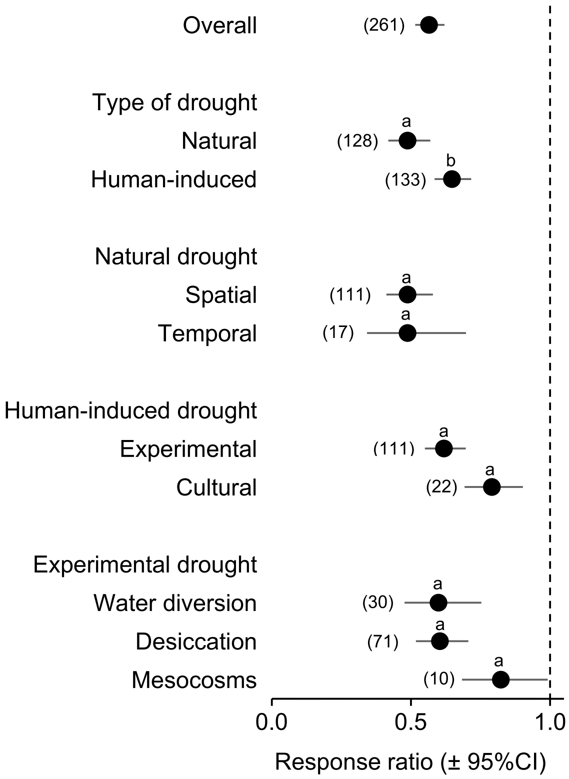

Fig. 3 Effect of drought on litter decomposition, overall and as a function of the type of drought, scale of natural drought, type of human-induced drought and type of experimental drought; values are response ratios (R; ± 95% CI). R = 1 (dashed line) indicates no effect of drought on litter decomposition, R > 1 indicates stimulation and R < 1 indicates reduction of litter decomposition under drought conditions (reduction in litter decomposition under drought conditions can be converted into % by considering the difference between R and 1 multiplied by 100: (1 – R) × 100). The effect is significant when the 95% CI does not include 1 (black circles). For the moderators, levels with overlapping 95% CI do not significantly differ (same letter). Values in brackets are sample sizes (moderator levels with < 3 effects sizes were not considered)

severity of drought (i.e., percentage flow reduction) and its effects on litter decomposition ($p = 0.115$).

Reduction of litter decomposition by natural drought did not significantly depend on litter type or climate (Table 2, Fig. 5). Effects of natural drought significantly depended on decomposer community with stronger reduction for total than for microbial-mediated litter decomposition (54% vs. 22%) (Table 2, Fig. 5). Effects of natural drought on litter decomposition were similar across litter identities, except that they were non-significant for *Carya* and *Acer* litters while decomposition was reduced for other litter genera (Table 2, Fig. 5).

Reduction of litter decomposition by human-induced drought did not significantly depend on the decomposer community (Table 2, Fig. 6). However, the effects of human-induced drought on litter decomposition depended on litter identity, with stronger reduction of *Populus* (46%) and *Alnus* (29%) litter decomposition than of most other litter genera, and on climate, with stronger reduction in warm and humid (66%) than in temperate and Mediterranean climates (33 – 36%) (Table 2, Fig. 6).

Sensitivity analysis

The grand mean effect size was not significantly affected by the type of data ('provided' vs. 'estimated'; $Q_M = 0.640$, df = 1, $p = 0.424$; Table S4), suggesting that estimated data did not strongly affect the results. The grand mean effect size R considering provided data only was 0.53 (95% CI: 0.45 – 0.63), indicating a significant reduction of litter decomposition by 47% under drought conditions ($p < 0.001$) (Table S4). Although there were 11 effect sizes 'missing' to the left of the grand mean effect size in the funnel plot (Fig. S4B), the new grand mean effect size estimated by the trim and fill method (R: 0.47, 95% CI: 0.40 – 0.56) overlapped the original grand mean effect size (Table S4), which indicates that the grand mean effect size based on provided data was not strongly affected by publications bias. The results interpretation in subgroup analyses also did not change in most cases; in some cases, however, the effects became non-significant (i.e., litter decomposition under cultural drought or in mesocosms, microbial litter decomposition under natural drought) due to the reduction in sample size by not considering estimated data (Table S4).

When considering a single effect size per study (i.e., database with independent effect sizes, $n = 50$), the grand mean effect size R was 0.62 (95% CI: 0.53 – 0.73) (Table S5), which is fairly similar to the grand mean effect size based on the entire database ($R = 0.57$, 95% CI: 0.52 – 0.62; $n = 261$), suggesting that the non-independency of effect sizes in the entire database is not strongly affecting the grand mean effect of drought on litter decomposition. The funnel plot was slightly asymmetric with 3 studies missing to the left of the grand mean effect size (Fig. S4C),

Table 2 Datasets, moderators, and levels within moderators tested in the analyses (moderator levels with < 3 effect sizes were not considered), sample size (n), Rosenberg's fail-safe number (N_{fs}; a dataset is robust to publication bias if $N_{fs} > 5 \times n + 10$, n = number of effect sizes), test for heterogeneity between levels within moderators (Q_M), degrees of freedom (df), and p values (significant differences among levels within moderators exist if p < 0.050)

Dataset	Moderator	Levels	Total n	Rosenberg N_{fs}	Q_M	df	p
All	Type of drought	2: Natural × Human-induced	261	19,855,273	8.498	1	0.004
Natural drought	Scale of natural drought	2: Spatial × Temporal	128	21,439,665	< 0.001	1	0.998
Human-induced drought	Type of human-induced drought	2: Experimental × Cultural	133	20,645	3.252	1	0.071
Experimental drought	Type of experimental drought	3: Water diversion × Desiccation × Mesocosms	111	16,569	1.749	2	0.417
Natural drought	Litter type	2: Leaves × Wood	128	21,439,665	1.741	1	0.187
Natural drought[1]	Decomposer community	2: Total × Microbial	126	21,185,907	3.048	1	0.008
Natural drought, total decomposer community[2]	Litter identity	9: Carya × Salix × Quercus × Eucalyptus × Phragmites × Alnus × Populus × Liquidambar × Acer	108	21,185,907	11.594	8	0.170
Natural drought, total decomposer community[3]	Climate	3: Temperate × Mediterranean × Humid subtropical	100	17,679,258	2.462	2	0.292
Human-induced drought	Decomposer community	2: Total × Microbial	133	20,645	2.164	1	0.141
Human-induced drought[4]	Litter identity	6: Populus × Alnus × Betula × Salix × Acer × Quercus	131	20,334	15.352	5	0.009
Human-induced drought[5]	Climate	3: Warm and humid subtropical × Temperate × Mediterranean	110	29,138	10.555	2	0.005

[1]withouth Burrows et al. (2017). [2]*Castanea*, *Fraxinus*, *Nerium*, *Nothofagus,* and *Ulmus* litters not considered (n < 3). [3]several climate types not considered as a result from exclusion of certain litter genera (see Fig. 1). [4]*Fagus* and *Melicytus* litters not considered (n < 3). [5]several climate types not considered as a result from exclusion of certain litter genera (see Fig. 1); arid and boreal climates also not considered (n < 3)

but the new grand mean effect size estimated by the trim and fill method (R: 0.59, 95% CI: 0.50 – 0.69) did not significantly differ from the original grand mean effect size (Table S5). However, due to strong decreases in sample size, type of drought and type of human-induced drought became non-significant in moderating drought effects on litter decomposition (Table S5).

Discussion

Drought is expected to become an increasing stressor for freshwaters, potentially altering ecosystem processes and consequently ecosystem services (Sabater et al., 2018). In this compilation of 261 effect sizes derived from 50 studies, drought reduced litter decomposition in streams on average by 43%. The magnitude of the effects, however, depended on the type and severity of drought, as well as on the decomposer community involved and on litter identity. The moderators of drought effects on litter decomposition identified in this meta-analysis, together with those identified in an earlier meta-analysis that focused on human-induced drought (climate, rainfall regime, season, river size and river nutrient status; Sabater et al., 2018), contribute to better anticipate the effects of drought on stream ecosystem functioning.

Drought conditions reduce litter decomposition

Litter decomposition was overall strongly reduced under drought conditions (by 43%), as hypothesized, which likely resulted from impaired decomposer activity (Langhans & Tockner, 2006; Corti et al., 2011; Datry et al., 2011; Mora-Gómez et al.,

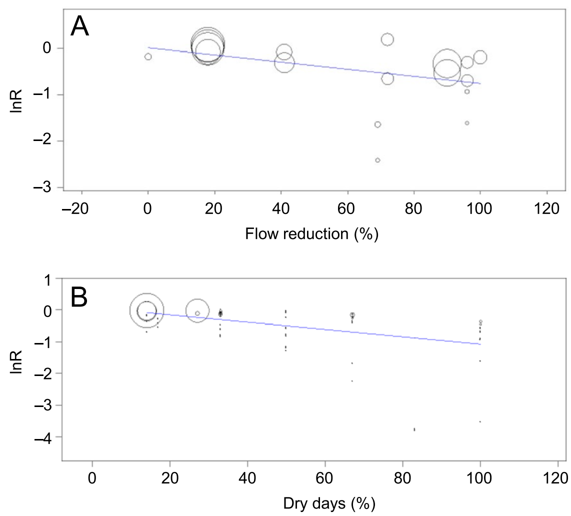

Fig. 4 Relationship between drought effects on litter decomposition (lnR) and percentage flow reduction under natural drought (n = 18; A) and percentage number of dry days during the litter incubation period in studies addressing experimental desiccation (n = 71; B). Circle size indicates the contribution (based on precision) of individual effect sizes to the meta-regression (on panel B, the precision of effect sizes below the regression line is very small). A: lnR = –0.008 × flow reduction (%) + 0.020 ($p = 0.039$, $R^2 = 0.21$); B: lnR = – 0.012 × dry days (%) + 0.073 ($p < 0.001$, $R^2 = 0.20$)

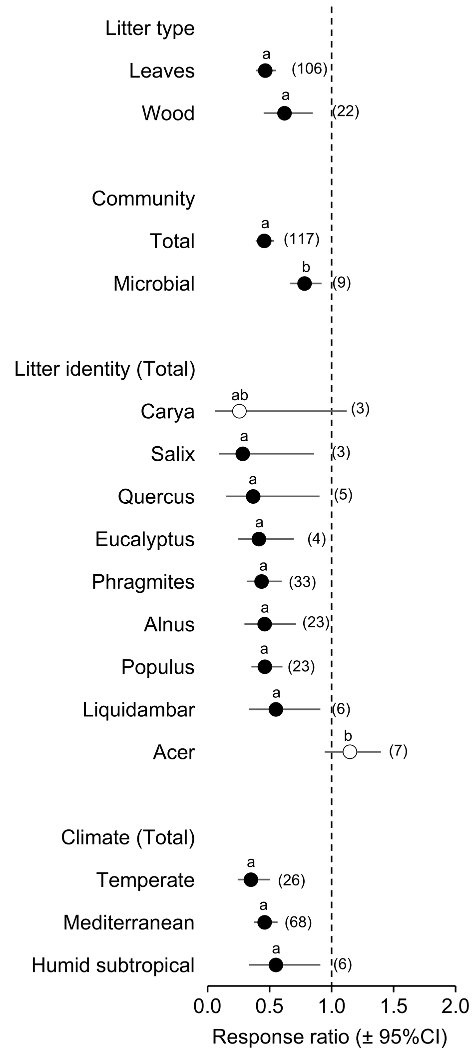

Fig. 5 Effect of natural drought on litter decomposition as a function of litter type, decomposer community, litter identity (for the data subset considering total litter decomposition; without *Castanea*, *Fraxinus*, *Nerium*, *Nothofagus,* and *Ulmus* litters that had n < 3), and climate (for the data subset considering total litter decomposition without *Castanea*, *Fraxinus*, *Nerium*, *Nothofagus,* and *Ulmus* litters that had n < 3, and without *Acer* litter that differs from most other litter genera); values are response ratios (R; ± 95% CI). R = 1 (dashed line) indicates no effect of drought on litter decomposition, R > 1 indicates stimulation, and R < 1 indicates reduction of litter decomposition under drought conditions (reduction in litter decomposition under drought conditions can be converted into % by considering the difference between R and 1 multiplied by 100: (1 – R) × 100). The effect is significant when the 95% CI does not include 1 (black circles). For the moderators, levels with overlapping 95% CI do not significantly differ (same letter). Values in brackets are sample sizes (moderator levels with < 3 effect sizes were not considered)

2018). Impaired decomposer activity may result from altered community composition with more efficient decomposer species being replaced by less efficient ones. In fact, drying is a strong environmental factor controlling the composition of aquatic hyphomycete communities in intermittent streams, which selects for drying specialists over drying-sensitive species (Arias-Real et al., 2022). Adaptation costs, however, result in a weak association between drying specialists and litter decomposition (Arias-Real et al., 2022), which can contribute to lower litter decomposition rates under aquatic conditions in natural intermittent streams or in streams affected by water abstraction than in perennial streams (Mora-Gómez et al., 2015; Mariluan et al., 2015; Monroy et al., 2016; Solagaistua et al., 2016). Similarly, drought affects invertebrate communities by selecting drought-resistant species over drought sensitive ones in intermittent streams (Stubbington et al., 2017). Because invertebrate shredder species mostly belong to orders Plecoptera (stoneflies) and Trichoptera (caddisflies), which

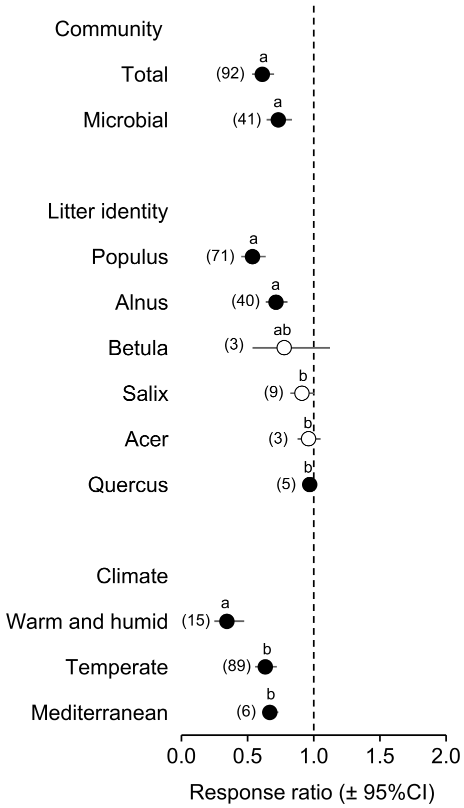

Fig. 6 Effect of human-induced drought on litter decomposition as a function of decomposer community, litter identity (without *Fagus* and *Melicytus* litters that had n < 3), and climate (for the data subset used to address litter identity without *Acer*, *Quercus* and *Salix* litters that differ from other litter genera and without arid and boreal climates that had n < 3); values are response ratios (R; ± 95% CI). R = 1 (dashed line) indicates no effect of drought on litter decomposition, R > 1 indicates stimulation and R < 1 indicates reduction of litter decomposition under drought conditions (reduction in litter decomposition under drought conditions can be converted into % by considering the difference between R and 1 multiplied by 100: (1 − R) × 100). The effect is significant when the 95% CI does not include 1 (black circles). For the moderators, levels with overlapping 95% CI do not significantly differ (same letter). Values in brackets are sample sizes (moderator levels with < 3 effect sizes were not considered)

are generally sensitive to drought, litter decomposition is generally slower in intermittent streams and streams affected by water abstraction than in perennial streams, even during flowing conditions (Datry et al., 2011; Schlief & Mutz., 2011; Menéndez et al., 2012; Vanlandingham et al., 2021). Additionally, under dry conditions, aquatic invertebrates are not replaced with terrestrial invertebrates to the same extent, and therefore, litter decomposition proceeds at a slower rate under terrestrial than aquatic conditions (Corti et al., 2011; Abril et al., 2016).

Decomposer activity can also be impaired by changing environmental conditions under drought. Reduced flow limits gas and nutrient exchange between biofilms and the water column (de Beer et al., 1996), which impairs microbial activity (Ferreira & Graça, 2006; Bastias et al., 2020). Microbial activity is also reduced under low dissolved oxygen concentrations and elevated salinization (Medeiros et al., 2009; Canhoto et al., 2021), which generally accompany flow reductions during the warm season. Abundances of sensitive stonefly and caddisfly shredders also decrease with deterioration of water quality (e.g., decrease in dissolved oxygen concentration, increases in conductivity and temperature; Pascoal et al., 2003; Gulis et al., 2006), which generally accompany flow reduction (Rolls et al., 2012).

Microbial activity is also highly sensitive to dehydration, even if leaf litter is emersed only for short periods (Bruder et al., 2011; Mora-Gómez et al., 2018). After 7 days emersion, fungal and bacterial biomass accumulation, fungal reproduction, and microbial enzymatic activity associated with black poplar (*Populus nigra* L.) leaves were inhibited up to ~ 50% compared with leaves kept immersed, and inhibition of microbial activities increase as the number of emersed days increased to 14 and 21 (Duarte et al., 2017). Inhibition of microbial activities under drought can result from impaired nutrient diffusion between decomposers and the surrounding medium (de Beer et al., 1996) or from a tradeoff between stress tolerance, which is energetically demanding, and metabolic activity (Pesce et al., 2016).

Although both flow reduction and drying reduce litter decomposition rates, their ecological effects at the ecosystem level can be very distinct. While slower litter decomposition during periods of low flow keeps reducing litter stocks, drying greatly halts litter decomposition and promotes the accumulation of litter on riverbeds (del Campo et al., 2021). This means that a greater amount of litter is likely available for transport to downstream reaches when flow resumes after a drying period than in cases where low flow was maintained (del Campo et al., 2021).

Reduction of litter decomposition was stronger under natural than under human-induced drought, which contradicts our hypothesis that proposed that the adaptation of aquatic communities to seasonal drought in intermittent streams would mitigate drought effects on ecosystem processes. This result may, however, be reflecting the higher proportion of cases in which litter experienced dry conditions under natural drought (68%) than under human-induced drought (59%). It is possible that human-induced drought was not as strong (e.g., flow reduction) as natural drought in the studied streams. Although human-induced drought can lead to complete desiccation of streams and rivers, this is less frequent in developed countries such as those where most studies have been performed, and where environmental regulations for environmental flows tend to be applied more stringently (Arthington et al., 2018). Additionally, human-induced experimental drought using control/impact approaches, such as when simulating drought or using mesocosms, was limited in duration and intensity, as indicated by the wet incubation conditions under drought (Dewson et al., 2007a, b; Arroita et al., 2017; Huang et al., 2018). Only in the human-induced experimental drought simulating desiccation (i.e., comparing litter samples that were immersed vs. emersed), there were litter samples incubated in (simulated) dry streambeds (Langhans & Tockner, 2006; Bruder et al., 2011). A recent study (Gruppuso et al., 2021) comparing the effects of natural drought (i.e., perennial vs. intermittent streams) with those of experimental drought simulated in artificial stream-side channels found similar patterns of both types of drought on litter decomposition, but effects were still stronger under the natural than the experimental drought. However, natural and experimental drought effects were assessed for different regions, seasons and litter species, which may confound the comparison between drought types (Gruppuso et al., 2021). Also, it is possible that studies addressing natural drought effects use preferentially intermittent streams that dry out rather than perennial streams that undergo a reduction in flow, which results in overall strong effects of natural droughts. Still, stronger effects of natural than of human-induced drought on litter decomposition may explain the greater reduction of litter decomposition found in this study (by 43%) compared with a recent meta-analysis that only considered human-induced drought (reduction by 31%; Sabater et al., 2018).

Experimental drought allows for higher control of confounding variables and it is essential to our understanding of the mechanisms behind drought effects on aquatic communities and processes. However, it may underestimate the full extent of drought effects expected under warming scenarios since effects found for experimental drought were less pronounced than those found for natural drought, likely because the former approach lacks the cumulative effects of repeated droughts captured in the latter approach (e.g., 'drying memory'; Datry et al., 2011). Alternative experiments performed over aridity gradients (i.e., using space-for-time substitution) may better inform about future drought effects on stream ecosystem functioning.

Contrary to expected, the magnitude of litter decomposition reduction under drought did not depend on the type of comparison (spatial vs. temporal) for natural drought or on the type of human-induced (experimental vs. cultural) or of experimental drought (water diversion vs. desiccation vs. mesocosms), indicating that water availability is a stronger moderating factor of litter decomposition than any potential confounding factor. However, the magnitude of litter decomposition reduction increased with drought severity as shown by the meta-regressions; as expected, reduction of litter decomposition became stronger with stronger decreases in flow and higher percentage number of emersed days. It is, nevertheless, important to note that drought severity was not consistently reported across studies, which limits a better understanding of how it affects litter decomposition. Studies have reported (or it was possible to estimate) percentage number of days litter samples were emersed during the incubation period, percentage reduction in flow, current velocity, and wet width or depth (Schlief & Mutz, 2011; Pinna et al., 2016; Solagaistua et al., 2016), which are not necessarily equivalent (no significant correlation was found based on the available data; data not shown). Efforts should therefore be made so that at least discharge (and number of days litter samples are emersed in case the streambed dries) is recorded.

As hypothesized, the effects of natural drought were stronger for total (mediated by both microbes and invertebrates) than for microbial-mediated litter decomposition. Aquatic macroinvertebrates, especially shredders, are key players on litter decomposition (Hieber & Gessner, 2002; Cornut et al., 2010), and may be directly and indirectly affected by drought. Shredder abundance and diversity are negatively affected by drought, which has negative impacts on litter decomposition (Datry et al., 2011; Martínez et al., 2015; Abril et al., 2016; Monroy et al., 2016). Also, impaired microbial conditioning of litter under drought may render litter less palatable for shredders (Abril et al., 2016), which prefer to feed on litter that has been softened and enriched in nutrients by microbial decomposers (Graça & Cressa, 2010). Additionally, the contribution of physical fragmentation to litter decomposition, which is more pronounced on coarse- than on fine-mesh bags, is likely reduced under drought. While high discharge promotes litter abrasion by suspended sediments and stimulates litter mass loss, low discharge facilitates the deposition of fine sediments on litter and retards litter decomposition (Canton et al., 1990; Ferreira et al., 2006b). In contrast, microbial decomposers may have high functional redundancy, as shown in the context of other environmental changes (Pascoal et al., 2005; Ferreira et al., 2006a; Martínez et al., 2020), and thus, microbial-mediated litter decomposition is less affected than total litter decomposition under drought, although reduction is still significant. However, less information is available on natural drought effects on microbial-mediated litter decomposition compared with total litter decomposition, and therefore, the lower effects of drought on the former compared with the latter need to be considered carefully. In fact, when human-induced drought was considered, both total and microbial-mediated litter decomposition were reduced to similar extents. More information on drought effects on microbial-mediated litter decomposition is needed, especially considering that invertebrate shredders are typically cold-water species and will likely become less diverse and abundant in streams experiencing increases in temperature (Boyero et al., 2021). Thus, under warming scenarios, the relative contribution of microbes to litter decomposition may increase (Boyero et al., 2011).

Contrary to expected, the reduction of litter decomposition under drought was not affected by litter type as wood and leaf litter decomposition were reduced to similar extents. This suggests that reduction of microbial contribution to wood decomposition was likely equivalent to the reduction of shredder contribution to leaf litter decomposition. As wood is a denser substrate than leaves, reduction in flow, and consequently in oxygen and nutrient diffusion in the water–substrate interface, may more strongly affect microbes associated with wood than with leaves. In addition, as shredders can also exploit wood biofilms, and therefore contribute to wood mass loss (Eggert & Wallace, 2007), decreases in shredder abundance and activity under drought may also impair wood decomposition.

The magnitude of the reduction of litter decomposition by drought depended on litter identity, but no strong conclusion about the interaction between drought and litter identity (or quality) is possible since the ranking of litter genera in our results does not match their known quality (Ostrofsky, 1997; Jabiol et al., 2019) and even litter genera with contrasting quality (e.g., from less to more recalcitrant: *Alnus* < *Populus* < *Phragmites*; Fenoy et al., 2016; Jabiol et al., 2019) were similarly affected by drought. However, understanding the interaction between drought and litter quality is crucial considering that, in the short term, drought can affect individual tree traits such as litter chemistry, with the direction and magnitude of changes depending on species identity and litter characteristics, and consequently litter decomposition (LeRoy et al., 2014; Orians et al., 2019; Wilson et al., 2022). In the long term, drought can lead to changes in plant composition as more frequent, prolonged and intense droughts will select for more drought-resistant species, often with changes in plant functional type and consequently in the characteristics of litter inputs to streams (Barba et al., 2016; Martínez-Vilalta & Lloret, 2016). Understanding the interaction between drought and litter identity/quality may also help managers in selecting the plant species to use in the restoration of degraded riparian areas in regions prone to become affected by drought.

Conclusion

Natural drought is an integral part of the functioning of streams in many regions, where it strongly reduces litter decomposition. However, as droughts become more frequent and intense with ongoing warming, many perennial streams will likely become intermittent, facing severe reductions in litter decomposition, with impacts on nutrient cycling and food webs. In contrast, the existing research shows human-induced droughts to have smaller effects on litter decomposition, likely because ecological flows are maintained. Although there is little information on other regions, we suspect that where human activities lead to total stream desiccation, its effects on litter decomposition will be strong. Effects of drought are especially strong for total litter decomposition, suggesting that streams where shredders are abundant will undergo a stronger reduction of litter decomposition under warming than streams where litter decomposition is mostly mediated by microbial decomposers. Also, reduction of litter decomposition with drought depends on litter identity, which can have management implications as the effects of drought may be exacerbated or mitigated by changes in the composition of the riparian vegetation.

Acknowledgements We thank the many authors who provided information that was not easily accessible in the primary studies and the reviewers for their insightful comments. This study was financed by the Portuguese Foundation for Science and Technology (FCT) through the research project STREAMECO (SFRH/BD/140761/2018), projects UIDP/04292/2020 and UIDB/04292/2020 granted to MARE, and project LA/P/0069/2020 granted to the Associate Laboratory ARNET, and by the Basque Government (IT1471-22). Financial support granted by the FCT to VF (CEECIND/02484/2018) is also acknowledged.

Author contributions VF contributed to conceptualization, preparation of the literature search, study selection and data extraction protocols, literature search, study selection, data extraction, data analysis, and writing. MASG contributed to conceptualization, contribution to the protocols, revision of the manuscript, and approval of its final version. AE contributed to the protocols, revision of multiple versions of the manuscript, and approval of its final version.

Funding Open access funding provided by FCT|FCCN (b-on). This study was financed by the Portuguese Foundation for Science and Technology (FCT) through the research project STREAMECO (SFRH/BD/140761/2018) and the strategic projects UIDP/04292/2020 and UIDB/04292/2020 granted to MARE and project LA/P/0069/2020 granted to the Associate Laboratory ARNET, and by the Basque Government (IT1471-22). VF was financially supported by the FCT (CEECIND/02484/2018).

Data Availability Data used in the analyses are provided in Supplementary Material.

Code availability Not applicable.

Declarations

Conflict of interest Authors have no conflicting or competing interests.

References

References marked with "*" are used in the database and are cited in the supplementary material.

*Abril, M., I. Muñoz & M. Menéndez, 2016. Heterogeneity in leaf litter decomposition in a temporary Mediterranean stream during flow fragmentation. Science of the Total Environment 553: 330–339.

Acuña, V., 2010. Flow regime alteration effects on the organic C dynamics in semiarid stream ecosystems. Hydrobiologia 657: 233–242.

Acuña, V., I. Muñoz, A. Giorgi, M. Omella, F. Sabater & S. Sabater, 2005. Drought and postdrought recovery cycles in an intermittent Mediterranean stream: Structural and functional aspects. Journal of the North American Benthological Society 24: 919–933.

Appling, A. P., J. S. Read, L. A. Winslow, M. Arroita, E. S. Bernhardt, N. A. Griffths, R. O. Jr, J. W. Hall, J. B. Harvey, E. H. Heffernan, E. G. Stanley & Stets & C. B. Yackulic, 2018. The metabolic regimes of 356 rivers in the United States. Scientific Data 5: 180292.

*Arias-Real, R., I. Muñoz, C. Gutierrez-Cánovas, V. Granados, P. Lopez-Laseras & M. Menéndez, 2020. Subsurface zones in intermittent streams are hotspots of microbial decomposition during the non-flow period. Science of the Total Environment 703: 135485.

Arias-Real, R., M. Menéndez, I. Muñoz & C. Pascoal, 2022. Drying shapes the ecological niche of aquatic fungi with implications on ecosystem functioning. Science of the Total Environment 859: 160374.

Aristi, I., M. Arroita, A. Larrañaga, L. Ponsatí, S. Sabater, D. von Schiller, A. Elosegi & V. Acuña, 2014. Flow regulation by dams shapes metabolism in Mediterranean rivers. Freshwater Biology 59: 1816–1829.

*Arroita, M., I. Aristi, J. Díez, M. Martínez, G. Oyarzun & A. Elosegi, 2015. Impact of water abstraction on storage and breakdown of coarse organic matter in mountain streams. Science of the Total Environment 503: 233–240.

*Arroita, M., L. Flores, A. Larrañaga, A. Martínez, M. Martínez-Santos, O. Pereda, E. Ruiz-Romera, L. Solagaistua & A. Elosegi, 2017. Water abstraction impacts stream ecosystem functioning via wetted-channel contraction. Freshwater Biology 62: 243–257.

Arroita, M., L. Flores, A. Larrañaga, E. Chauvet & A. Elosegi, 2018. Hydrological contingency: drying history affects aquatic microbial decomposition. Aquatic Sciences 80: 1–12.

Arthington, A. H., A. Bhaduri, S. E. Bunn, S. E. Jackson, R. E. Tharme, D. Tickner, B. Young, M. Acreman, N. Baker, S. Capon, A. C. Horne, E. Kendy, M. E. McClain, N. L. Poff, B. D. Richter & S. Ward, 2018. The Brisbane Declaration and Global Action Agenda on environmental flows (2018). Frontiers in Environmental Science 6: 1–15.

Asadieh, B. & N. Y. Krakauer, 2017. Global change in streamflow extremes under climate change over the 21st century. Hydrology and Earth System Sciences 21: 5863–5874.

Barba, J., J. Curiel Yuste, R. Poyatos, I. A. Janssens & F. Lloret, 2016. Strong resilience of soil respiration components to drought-induced die-off resulting in forest secondary succession. Oecologia 182: 27–41.

Bastias, E., M. Bolivar, M. Ribot, M. Peipoch, S. A. Thomas, F. Sabater & E. Martí, 2020. Spatial heterogeneity in water velocity drives leaf litter dynamics in streams. Freshwater Biology 65: 435–445.

*Bernal, R. R., 2010. Effects of Hydrologic Gradients on Woody Debris Breakdown and Macroinvertebrate Colonization in a Cumberland Plateau Watershed, Eastern Kentucky, USA. Master Thesis. Western Kentucky University.

Borenstein, M., L. V. Hedges, J. P. T. Higgins & H. R. Rothstein, 2009. Introduction to Meta-Analysis, John Wiley & Sons Ltd, Chichester:

*Boulton, A. J., 1991. Eucalypt leaf decomposition in an intermittent stream in south-eastern Australia. Hydrobiologia 211: 123–136.

Boyero, L., R. G. Pearson, C. Hui, M. O. Gessner, J. Pérez, M. A. Alexandrou, M. A. S. Graça, B. J. Cardinale, R. J. Albariño, M. Arunachalam, L. A. Barmuta, A. J. Boulton, A. Bruder, M. Callisto, E. Chauvet, R. G. Death, D. Dudgeon, A. C. Encalada, V. Ferreira, R. Figueroa, A. S. Flecker, J. F. Jr, J. Gonçalves, T. Helson, T. Iwata, J. M. Jinggut, C. Mathooko, C. Mathuriau, M. S. M'Erimba, C. M. Moretti, A. Pringle, L. Ramírez, J. Rincon. Ratnarajah & C. M. Yule, 2016. Biotic and abiotic variables influencing plant litter breakdown in streams: A global study. Proceedings of the Royal Society B - Biological Sciences 283: 20152664.

Boyero, L., R. G. Pearson, M. O. Gessner, L. A. Barmuta, V. Ferreira, M. A. S. Graça, D. Dudgeon, A. J. Boulton, M. Callisto, E. Chauvet, J. E. Helson, A. Bruder, R. J. Albariño, C. M. Yule, M. Arunachalam, J. N. Davies, R. Figueroa, A. S. Flecker, A. Ramírez, R. G. Death, T. Iwata, J. M. Mathooko, C. Mathuriau, J. F. Jr, M. S. Gonçalves, T. Moretti, S. Jingut, C. Lamothe, L. M'Erimba, M. H. Ratnarajah, J. Schindler, L. M. Castela, Buria A. Cornejo, V. D. Villanueva & D. C. West, 2011. A global experiment suggests climate warming will not accelerate litter decomposition in streams but may reduce carbon sequestration. Ecology Letters 14: 289–294.

Boyero, L., N. López-Rojo, A. M. Tonin, J. Pérez, F. Correa-Araneda, R. G. Pearson, J. Bosch, R. J. Albariño, S. Anbalagan, L. A. Barmuta, A. Basaguren, F. J. Burdon, A. Caliman, M. Callisto, A. R. Calor, I. C. Campbell, B. J. Cardinale, J. J. Casas, A. M. Chará-Serna, E. Chauvet, S. Ciapala, C. Colón-Gaud, A. Cornejo, A. M. Davis, M. Degebrodt & E. S. Dias M. E. Díaz, M. M. Douglas, A. C. Encalada R. Figueroa, A. S. Flecher, T. Fleituch, E. A. García, G. García, P. E. García, M. O. Gessner, J. E. Gómez, S. Gómez, J. F. Jr. Gonçalves, M. A. S. Graça, D. C. Gwinn, R. O. Jr. Hall, N. Hamada, C. Hui, D. Imazawa, T. Iwata, S. K. Kariuki, A. Landeira-Dabarca, K. Laymon, M. Leal, R. Marchante, R. T. Martins, F. O. Masese, M. Maul, B. G. McKie, A. O. Medeiros, C. M. M'Erimba, J. A. Middleton, S. Monroy, T. Muotka, J. N. Negishi, A. Ramírez, J. S. Richardson, J. Rincón, J. Rubio-Ríos, G. M. Santos, R. Sarremejane, F. Sheldon, A. Sitati, N. S. D. Tenkiano, S. D. Tiegs, J. R. Tolod, M. Venarsky, A. Watson & C. M. Yule, 2021. Impacts of detritivore diversity loss on instream decomposition are greatest in the tropics. Nature Communications 12: 3700.

*Bruder, A., E. Chauvet & M. O. Gessner, 2011. Litter diversity, fungal decomposers and litter decomposition under simulated stream intermittency. Functional Ecology 25: 1269–1277.

*Burrows, R. M., H. Rutlidge, N. R. Bond, S. M. Eberhard, A. Auhl, M. S. Andersen, D. Valdez & M. J. Kennard, 2017. High rates of organic carbon processing in the hyporheic zone of intermittent streams. Scientific Reports 7: 1–11.

Canhoto, C., F. Bärlocher, M. Cañedo-Argüelles, R. Gómez & A. L. Gonçalves, 2021. Salt modulates plant litter decomposition in stream ecosystems. In Swan, C. M., L Boyero & C. Canhoto (eds), The Ecology of Plant Litter Decomposition in Stream Ecosystems. Springer Nature, Switzerland: 323–345.

Canton, S. P. & R. J. Martinson, 1990. The effects of varying current on weight loss from willow leaf packs. Journal of Freshwater Ecology 5: 413–415.

*Carey, N., E. T. Chester & B. J. Robson, 2021. Flow regime change alters shredder identity but not leaf litter decomposition in headwater streams affected by severe, permanent drying. Freshwater Biology 66: 1813–1830.

Cornut, J., A. Elger, D. Lambrigot, P. Marmonier & E. Chauvet, 2010. Early stages of leaf decomposition are mediated by aquatic fungi in the hyporheic zone of woodland streams. Freshwater Biology 55: 2541–2556.

*Corti, R., T. Datry, L. Drummond & S. T. Larned, 2011. Natural variation in immersion and emersion affects breakdown and invertebrate colonization of leaf litter in a temporary river. Aquatic Sciences 73: 537.

Chen, C. C., L. C. Wang, X. Z. Cao & J. Song, 2013. Environmental flows legislation and regulations in foreign countries and the enlightenment to China. Applied Mechanics and Material 295: 2181–2186.

*Datry, T., R. Corti, C. Claret & M. Philippe, 2011. Flow intermittence controls leaf litter breakdown in a French

temporary alluvial river: The "drying memory." Aquatic Sciences 73: 471–483.
*Death, R. G., Z. S. Dewson & A. B. James, 2009. Is structure or function a better measure of the effects of water abstraction on ecosystem integrity? Freshwater Biology 54: 2037–2050.
de Beer, D., P. Stoodley & Z. Lewandowski, 1996. Liquid flow and mass transport in heterogeneous biofilms. Water Research 30: 2761–2765.
del Campo, R., A. Foulquier, G. Singer & T. Datry, 2021. Plant litter decomposition in intermittent rivers and ephemeral streams. In Swan, C. M., L Boyero & C. Canhoto (eds), The Ecology of Plant Litter Decomposition in Stream Ecosystems. Springer Nature, Switzerland: 73–100.
Dewson, Z. S., A. B. W. James & R. G. Death, 2007a. Invertebrate community responses to experimentally reduced discharge in small streams of different water quality. Journal of the North American Benthological Society 26: 754–766.
Dewson, Z. S., A. B. James & R. G. Death, 2007b. Invertebrate responses to short-term water abstraction in small New Zealand streams. Freshwater Biology 52: 357–369.
*Dewson, Z. S., A. B. James & R. G. Death, 2007. Stream ecosystem functioning under reduced flow conditions. Ecological Applications 17: 1797–1808.
*Di Sabatino, A., L. Coscieme & G. Cristiano, 2021. Effects of antecedent drying events on structure, composition and functional traits of invertebrate assemblages and leaf-litter breakdown in a former perennial river of Central Apennines (Aterno River, Abruzzo, Central Italy). Ecohydrology: e2358.
Döll, P., K. Fiedler & J. Zhang, 2009. Global-scale analysis of river flow alterations due to water withdrawals and reservoirs. Hydrology and Earth System Sciences 13: 2413–2432.
*Duarte, S., J. Mora-Gómez, A. M. Romaní, F. Cássio & C. Pascoal, 2017. Responses of microbial decomposers to drought in streams may depend on the environmental context. Environmental Microbiology Reports 9: 756–765.
Duval, S. & R. Tweedie, 2000. A nonparametric "trim and fill" method of accounting for publication bias in meta-analysis. Journal of the American Statistical Association 95: 89–98.
Eggert, S. L. & J. B. Wallace, 2007. Wood biofilm as a food resource for stream detritivores. Limnology and Oceanography 52: 1239–1245.
Fenoy, E., J. J. Casas, M. Díaz-López, J. Rubio, J. L. Guil-Guerrero & F. J. Moyano-López, 2016. Temperature and substrate chemistry as major drivers of interregional variability of leaf microbial decomposition and cellulolytic activity in headwater streams. FEMS Microbiology Ecology 92: fiw169.
Ferreira, V. & M. A. S. Graça, 2006. Do invertebrate activity and current velocity affect fungal assemblage structure in leaves? International Review of Hydrobiology 91: 1–14.
Ferreira, V., A. Elosegi, V. Gulis, J. Pozo & M. A. S. Graça, 2006a. Eucalyptus plantations affect fungal communities associated with leaf litter decomposition in Iberian streams. Archiv Für Hydrobiologie 166: 467–490.
Ferreira, V., M. A. S. Graça, J. L. M. P. de Lima & R. Gomes, 2006b. Role of physical fragmentation and invertebrate activity in the breakdown rate of leaves. Archiv Für Hydrobiologie 165: 493–513.
Ferreira, V., B. Castagneyrol, J. Koricheva, V. Gulis, E. Chauvet & M. A. S. Graça, 2015. A meta-analysis of the effects of nutrient enrichment on litter decomposition in streams. Biological Reviews 90: 669–688.
*Font, R. A., K. Khamis, A. M. Milner, G. H. S. Smith & M. E. Ledger, 2021. Low flow and heatwaves alter ecosystem functioning in a stream mesocosm experiment. Science of the Total Environment 777: 146067.
*Foulquier, A., J. Artigas, S. Pesce & T. Datry, 2015. Drying responses of microbial litter decomposition and associated fungal and bacterial communities are not affected by emersion frequency. Freshwater Science 34: 1233–1244.
Gessner, M. O. & E. Chauvet, 1994. Importance of stream microfungi in controlling breakdown rates of leaf litter. Ecology 75: 1807–1817.
Gonçalves, A. L., A. V. Lírio, M. A. S. Graça & C. Canhoto, 2016. Fungal species diversity affects leaf decomposition after drought. International Review of Hydrobiology 101: 78–86.
Gonçalves, A. L., S. Simões, F. Bärlocher & C. Canhoto, 2019. Leaf litter microbial decomposition in salinized streams under intermittency. Science of the Total Environment 653: 1204–1212.
González, J. M. & M. A. S. Graça, 2003. Conversion of leaf litter to secondary production by a shredding caddis-fly. Freshwater Biology 48: 1578–1592.
Graça, M. A. S. & C. Cressa, 2010. Leaf quality of some tropical and temperate tree species as food resource for stream shredders. International Review of Hydrobiology 95: 27–41.
*Gruppuso, L., A. Doretto, E. Piano, E. Falasco, M. C. Bruno, F. Bona & S. Fenoglio, 2021. Effects of flow intermittence on ecosystem processes in mountain streams: Are artificial and field experiments comparable? Fundamental and Applied Limnology 195: 39–59.
*Gruppuso, L., A. Doretto, E. Falasco, S. Fenoglio, M. Freppaz, M. E. Benbow & F. Bona, 2022. Flow intermittency affects leaf decomposition and benthic consumer communities of alpine streams: A case study along the Po River. Water 14: 258.
Gulis, V., V. Ferreira & M. A. S. Graça, 2006. Stimulation of leaf litter decomposition and associated fungi and invertebrates by moderate eutrophication: Implications for stream assessment. Freshwater Biology 5: 1655–1669.
Gusenbauer, M. & N. R. Haddaway, 2020. Which academic search systems are suitable for systematic reviews or meta-analyses? Evaluating retrieval qualities of Google Scholar, PubMed, and 26 other resources. Research Synthesis Methods 11: 181–217.
Hedges, L. V., J. Gurevitch & P. S. Curtis, 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80: 1150–1156.
*Herbst, G. & S. R. Reice, 1982. Comparative leaf litter decomposition in temporary and permanent streams in semi-arid regions of Israel. Journal of Arid Environments 5: 305–318.

Hieber, M. & M. O. Gessner, 2002. Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. Ecology 83: 1026–1038.

*Hill, B. H., T. J. Gardner & O. F. Ekisola, 1988. Breakdown of gallery forest leaf litter in intermittent and perennial prairie streams. The Southwestern Naturalist 33: 323–331.

*Huang, W., X. Liu, W. Peng, W. Ma & J. Zhang, 2018. Quantitative response of leaf-litter decomposition rate to water abstraction in a gradient: Implications for environmental flow management. Ecohydrology 11: e1919.

Izagirre, O., U. Agirre, M. Bermejo, J. Pozo & A. Elosegi, 2008. Environmental controls of whole-stream metabolism as depicted from continuous monitoring of Basque streams. Journal of the North American Benthological Society 27: 252–268.

Jabiol, J., A. Lecerf, S. Lamothe, M. O. Gessner & E. Chauvet, 2019. Litter quality modulates effects of dissolved nitrogen on leaf decomposition by stream microbial communities. Microbial Ecology 77: 959–966.

Lajeunesse, M. J., 2013. Recovering missing or partial data from studies: A survey of conversions and imputations for meta-analysis. In Koricheva, J., J. Gurevitch & K. Mengersen (eds), Handbook of Meta-Analysis in Ecology and Evolution. Princeton University Press: 195–206.

Lake, P. S., 2003. Ecological effects of perturbation by drought in flowing waters. Freshwater Biology 48: 1161–1172.

*Langhans, S. D. & K. Tockner, 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: 501–509.

Lecerf, A. & E. Chauvet, 2008. Intraspecific variability in leaf traits strongly affects alder leaf decomposition in a stream. Basic and Applied Ecology 9: 598–605.

LeRoy, C. J., A. S. Wymore, R. Davis & J. C. Marks, 2014. Indirect influences of a major drought on leaf litter quality and decomposition in a southwestern stream. Fundamental and Applied Limnology 184: 1–10.

*Magoulick, D. D., 2014. Impacts of drought and crayfish invasion on stream ecosystem structure and function. River Research and Applications 30: 1309–1317.

*Maamri, A., H. Chergui & E. Pattee, 1997. Leaf litter processing in a temporary Northeastern Moroccan river. Archiv Für Hydrobiologie 140: 513–531.

*Maamri, A., F. Bärlocher, E. Pattee & H. Chergui, 2001. Fungal and bacterial colonisation of *Salix pedicellata* leaves decaying in permanent and intermittent streams in Eastern Morocco. International Review of Hydrobiology 86: 337–348.

Marks, J. C., 2019. Revisiting the fates of dead leaves that fall into streams. Annual Review of Ecology, Evolution, and Systematics 50: 547–568.

*Mariluan, G. D., V. D. Villanueva & R. J. Albariño, 2015. Leaf litter breakdown and benthic invertebrate colonization affected by seasonal drought in headwater lotic systems of Andean Patagonia. Hydrobiologia 760: 171–187.

Martínez, A., A. V. Lírio, I. Febra, J. Rosa, A. L. Gonçalves & C. Canhoto, 2020. Functional redundancy in leaf-litter-associated aquatic hyphomycetes: Fine sediment alters community composition but hardly decomposer activity. International Review of Hydrobiology 105: 44–51.

Martínez-Vilalta, J. & F. Lloret, 2016. Drought-induced vegetation shifts in terrestrial ecosystems: The key role of regeneration dynamics. Global and Planetary Change 144: 94–108.

*Martínez, A., J. Pérez, J. Molinero, M. Sagarduy & J. Pozo, 2015. Effects of flow scarcity on leaf-litter processing under oceanic climate conditions in calcareous streams. Science of the Total Environment 503: 251–257.

*Matthaei, C. D., J. J. Piggott & C. R. Townsend, 2010. Multiple stressors in agricultural streams: Interactions among sediment addition, nutrient enrichment and water abstraction. Journal of Applied Ecology 47: 639–649.

Medeiros, A. O., C. Pascoal & M. A. S. Graça, 2009. Diversity and activity of aquatic fungi under low oxygen conditions. Freshwater Biology 54: 142–149.

*Menéndez, M., E. Descals, T. Riera & O. Moya, 2012. Effect of small reservoirs on leaf litter decomposition in Mediterranean headwater streams. Hydrobiologia 691: 135–146.

Messager, M. L., B. Lehner, C. Cockburn, N. Lamouroux, H. Pella, T. Snelder, K. Tockner, T. Trautmann, A. Watt & T. Datry, 2021. Global prevalence of non-perennial rivers and streams. Nature 594: 391–397.

Meybeck, M., 2003. Global analysis of river systems: from Earth system controls to Anthropocene syndromes. Philosophical Transactions of the Royal Society of London. Series b: Biological Sciences 358: 1935–1955.

Milliman, J. D., K. L. Farnsworth, P. D. Jones, K. H. Xu & L. C. Smith, 2008. Climatic and anthropogenic factors affecting river discharge to the global ocean, 1951–2000. Global and Planetary Change 62: 187–194.

Mollá, S., J. J. Casas, M. Menéndez, A. Basaguren, C. Casado, E. Descals, J. M. González, A. Larrañaga, M. Lusi, A. Martínez, C. Mendoza-Lera, O. Moya, J. Pérez, T. Riera, N. Roblas & J. Pozo, 2017. Leaf-litter breakdown as an indicator of the impacts by flow regulation in headwater streams: Responses across climatic regions. Ecological Indicators 73: 11–22.

*Monroy, S., M. Menéndez, A. Basaguren, J. Pérez, A. Elosegi & J. Pozo, 2016. Drought and detritivores determine leaf litter decomposition in calcareous streams of the Ebro catchment (Spain). Science of the Total Environment 573: 1450–1459.

*Mora-Gómez, J., A. Elosegi, E. Mas-Martí & A. M. Romaní, 2015. Factors controlling seasonality in leaf-litter breakdown in a Mediterranean stream. Freshwater Science 34: 1245–1258.

*Mora-Gómez, J., S. Duarte, F. Cássio, C. Pascoal & A. M. Romaní, 2018. Microbial decomposition is highly sensitive to leaf litter emersion in a permanent temperate stream. Science of the Total Environment 621: 486–496.

Mosley, L. M., 2015. Drought impacts on the water quality of freshwater systems: review and integration. Earth-Science Reviews 140: 203–214.

*Muehlbauer, J. D., C. J. LeRoy, J. M. Lovett, K. K. Flaccus, J. K. Vlieg & J. C. Marks, 2009. Short-term responses of decomposers to flow restoration in Fossil Creek, Arizona, USA. Hydrobiologia 618: 35–45.

*Northington, R. M. & J. R. Webster, 2017. Experimental reductions in stream flow alter litter processing and consumer subsidies in headwater streams. Freshwater Biology 62: 737–750.

Orians, C. M., R. Schweiger, J. S. Dukes, E. R. Scott & C. Müller, 2019. Combined impacts of prolonged drought and warming on plant size and foliar chemistry. Annals of Botany 124: 41–52.

Ostrofsky, M. L., 1997. Relationship between chemical characteristics of autumn-shed leaves and aquatic processing rates. Journal of the North American Benthological Society 16: 750–759.

Pascoal, C., M. Pinho, F. Cássio & P. Gomes, 2003. Assessing structural and functional ecosystem condition using leaf breakdown: Studies on a polluted river. Freshwater Biology 48: 2033–2044.

Pascoal, C., F. Cássio & L. Marvanová, 2005. Anthropogenic stress may affect aquatic hyphomycete diversity more than leaf decomposition in a low-order stream. Archiv Für Hydrobiologie 162: 481–496.

*Pérez-Calpe, A. V., I. de Guzman, A. Larrañaga, D. von Schiller & A. Elosegi, 2022. Organic matter processing on dry riverbeds is more reactive to water diversion and pollution than on wet channels. Frontiers in Environmental Science 9: 817665.

Pesce, S., O. Zoghlami, C. Margoum, J. Artigas, A. Chaumot & A. Foulquier, 2016. Combined effects of drought and the fungicide tebuconazole on aquatic leaf litter decomposition. Aquatic Toxicology 173: 120–131.

*Pinna, M., F. Sangiorgio, A. Fonnesu & A. Basset, 2003. Spatial analysis of plant detritus processing in a Mediterranean River type: the case of the River Tirso Basin, Sardinia, Italy. Journal of Environmental Sciences 15: 227–240.

*Pinna, M., A. Fonnesu, F. Sangiorgio & A. Basset, 2004. Influence of summer drought on spatial patterns of resource availability and detritus processing in Mediterranean stream sub-basins (Sardinia, Italy). International Review of Hydrobiology 89: 484–499.

*Pinna, M., G. Marini, G. Cristiano, L. Mazzotta, P. Vignini, B. Cicolani & A. Di Sabatino, 2016. Influence of aperiodic summer droughts on leaf litter breakdown and macroinvertebrate assemblages: testing the drying memory in a Central Apennines River (Aterno River, Italy). Hydrobiologia 782: 111–126.

Ponsatí, L., V. Acuña, I. Aristi, M. Arroita, E. García-Berthou, D. von Schiller, A. Elosegi & S. Sabater, 2015. Biofilm responses to flow regulation by dams in Mediterranean rivers. River Research & Applications 31: 1003–1016.

*Richardson, W. B., 1990. A comparison of detritus processing between permanent and intermittent headwater streams. Journal of Freshwater Ecology 5: 341–357.

*Riedl, H. L., L. B. Marczak, N. A. McLenaghan & T. M. Hoover, 2013. The role of stranding and inundation on leaf litter decomposition in headwater streams. Riparian Ecology and Conservation 1: 3–10.

Roberts, B. J., P. J. Mulholland & W. R. Hill, 2007. Multiple scales of temporal variability in ecosystem metabolism rates: results from 2 years of continuous monitoring in a forested headwater stream. Ecosystems 10: 588–606.

Rolls, R. J., C. Leigh & F. Sheldon, 2012. Mechanistic effects of low-flow hydrology on riverine ecosystems: ecological principles and consequences of alteration. Freshwater Science 31: 1163–1186.

RStudio, 2012. RStudio: Integrated Development Environment for R (Version 2.15.2) (Computer Software). Boston, MA. http://www.rstudio.com/

Sabater, S. & K. Tockner, 2009. Effects of hydrologic alterations on the ecological quality of river ecosystems. In Sabater, S. & D. Barceló (eds), Water Scarcity in the Mediterranean: Perspectives Under Global Change Springer, Berlin: 15–39.

Sabater, S., X. Timoner, C. Borrego & V. Acuña, 2016. Stream biofilm responses to flow intermittency: from cells to ecosystems. Frontiers in Environmental Science 4: 14.

Sabater, S., F. Bregoli, V. Acuña, D. Barceló, A. Elosegi, A. Ginebreda, R. Marcé, I. Muñoz, L. Sabater-Liesa & V. Ferreira, 2018. Effects of human-driven water stress on river ecosystems: a meta-analysis. Scientific Reports 8: 11462.

*Schlief, J. & M. Mutz, 2009. Effect of sudden flow reduction on the decomposition of alder leaves (*Alnus glutinosa* [L.] Gaertn.) in a temperate lowland stream: a mesocosm study. Hydrobiologia 624: 205–217.

*Schlief, J. & M. Mutz, 2011. Leaf decay processes during and after a supra-seasonal hydrological drought in a temperate lowland stream. International Review of Hydrobiology 96: 633–655.

*Smeti, E., D. von Schiller, I. Karaouzas, S. Laschou, L. Vardakas, S. Sabater, E. Tornés, L. S. Monllor-Alcaraz, N. Guillem-Argiles, E. Martinez, D. Barceló, M. L. de Alda, E. Kalogianni, A. Elosegi & N. Skoulikidis, 2019. Multiple stressor effects on biodiversity and ecosystem functioning in a Mediterranean temporary river. Science of the Total Environment 647: 1179–1187.

*Solagaistua, L., M. Arroita, I. Aristi, A. Larrañaga & A. Elosegi, 2016. Changes in discharge affect more surface than subsurface breakdown of organic matter in a mountain stream. Marine and Freshwater Research 67: 1826–1834.

Soria, M., C. Leigh, T. Datry, L. M. Bini & N. Bonada, 2017. Biodiversity in perennial and intermittent rivers: a meta-analysis. Oikos 126: 1078–1089.

Stubbington, R., M. T. Bogan, N. Bonada, A. J. Boulton, T. Datry, C. Leigh & R. Vander Vorste, 2017. The biota of intermittent rivers and ephemeral streams: Aquatic invertebrates. In Datry, T., N. Bonada & A. Boulton (eds), Intermittent Rivers and Ephemeral Streams. Academic Press: 217–243.

*Tate, C. M. & M. E. Gurtz, 1986. Comparison of mass loss, nutrients, and invertebrates associated with elm leaf litter decomposition in perennial and intermittent reaches of tallgrass prairie streams. The Southwestern Naturalist 31: 511–520.

*Truchy, A., R. Sarremejane, T. Muotka, H. Mykrä, D. G. Angeler, K. Lehosmaa, A. Huusko, R. K. Johnson, R. A. Sponseller, B. G. McKie & G., 2020. Habitat patchiness, ecological connectivity and the uneven recovery of boreal stream ecosystems from an experimental drought. Global Change Biology 26: 3455–3472.

*Vanlandingham, A. L., R. H. Walker, A. Alford & S. A. Entrekin, 2021. Intermittency mediates macroinvertebrate and crayfish effects on leaf breakdown in temperate headwater streams. Freshwater Science 40: 21–38.

Viechtbauer, W., 2010. Conducting meta-analyses in R with the metafor package. Journal of Statistical Software 36: 1–48.

*Viza, A., I. Muñoz, F. Oliva & M. Menéndez, 2022. Contrary effects of flow intermittence and land uses on organic matter decomposition in a Mediterranean river basin. Science of the Total Environment 812: 151424.

von Schiller, D., V. Acuña, D. Graeber, E. Martí, M. Ribot, S. Sabater, X. Timoner & K. Tockner, 2011. Contraction, fragmentation and expansion dynamics determine nutrient availability in a Mediterranean forest stream. Aquatic Sciences 73: 485–497.

Wallace, J. B., S. L. Eggert, J. L. Meyer & J. R. Webster, 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277: 102–104.

Wallace, B. C., M. J. Lajeunesse, G. Dietz, I. J. Dahabreh, T. A. Trikalinos, C. H. Schmid & J. Gurevitch, 2017. Open MEE: Intuitive, open-source software for meta-analysis in ecology and evolutionary biology. Methods in Ecology and Evolution 8: 941–947.

Wilson, A. M., J. C. Burtis, M. Goebel & J. B. Yavitt, 2022. Litter quality and decomposition responses to drought in a northeastern US deciduous forest. Oecologia 200: 247–257.

Yue, K., P. De Frenne, K. van Meerbeek, V. Ferreira, D. A. Fornara, Q. Wu, X. Ni, Y. Peng, D. Wang, P. Heděnec, Y. Yang, F. Wu & J. Peñuelas, 2022. Litter quality and stream physicochemical properties drive global invertebrate effects on instream litter decomposition. Biological Reviews 97: 2023–2038.