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Litter quality modulates the effects of environmental drivers on microbial decomposition and home-field advantage in headwater streams

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Abstract

1. We investigated how microbial decomposition in headwater streams is influenced by environmental factors and litter quality, including the potential adaptation of microbes to decompose more efficiently leaf-litter species from their native range (HFA, 'home-field advantage' hypothesis).
2. We conducted a leaf-litter decomposition experiment in streams from four subregions contrasting in water chemistry and temperature regime, using cross-subregion reciprocal incubations of the dominant riparian plant species in each subregion.
3. Low-quality litters decomposed faster at their native site, supporting the HFA hypothesis for low-quality litter species. Moreover, temperature sensitivity of decomposition of low-, but not high-, quality litters was close to that predicted by the metabolic theory of ecology. Among litter traits, nitrogen content and toughness were the major predictors of decomposition. Temperature and nitrate concentration in stream water enhanced decomposition but, these two extrinsic factors did not act synergistically.
4. Together our results indicated that leaf-litter traits have a leading role as drivers of the decomposition process in headwater streams. However, this role is indirect, and occurs because low-quality litters modulate the decomposition effects of environmental drivers (temperature and N in water). Consistently with the above finding, HFA occurred only in low-quality litter.
5. Thus, if climate change leads to minor local changes in litter quality, microbial decomposition would be accelerated additively by warming and stream-water nitrate enrichment, with more pronounced effects on low-quality litters.

KEYWORDS
activation energy, global change, home-field advantage, litter quality, streams functioning

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1 | INTRODUCTION

Terrestrial-derived detritus constitutes a key functional component of many aquatic ecosystems, particularly in shaded headwater streams (Moore et al., 2004; Vannote et al., 1980). These ecosystems derive most of the energy and nutrients flowing through their food webs from terrestrial leaf litter (Marks, 2019).

Microbial decomposition of plant litter in streams is mainly driven by aquatic hyphomycetes, representing an essential link between litter resources and invertebrate consumers (Hieber & Gessner, 2002). Fungal decomposing activity depends on many factors which can be grouped into two categories: the intrinsic characteristics of leaf-litter (litter traits), to which a predominant control of decomposition has been attributed (García-Palacios et al., 2016; Zhang et al., 2019); and the extrinsic in-stream factors: abiotic (Gessner et al., 2007; Lecerf & Chauvet, 2008), and biotic (i.e. microbial community structure and functional traits; Fenoy et al., 2022; Wallenstein & Hall, 2012). Thus, decomposer assemblages and the ecological processes in which they are involved may be deeply affected by global change drivers (Fenoy et al., 2022; Ferreira et al., 2014; Martínez et al., 2014).

The forecasted changes in litter quality due to climate warming (i.e. reduced nutrient concentration, increased leaf toughness and/or silicon [Si] content; e.g. Perry et al., 2012; Rier et al., 2005; Rubio-Ríos et al., 2022; Salinas et al., 2018) could slow down fungal activity and litter decomposition (Pettit et al., 2012; Schaller et al., 2014). On the other hand, microbial decomposition of leaf litter, particularly that of low quality, is accelerated by global change-related extrinsic factors, that is, increased temperature, which accelerates metabolic rates (Amani et al., 2019; Ferreira et al., 2014; Follstad Shah et al., 2017), and moderate increases in stream-water nutrients (Biasi et al., 2017; Woodward et al., 2012).

However, the effects of the interaction between litter traits and environmental factors on litter decomposition are either controversial if abiotic (García-Palacios et al., 2021), or poorly studied when it comes to microbial decomposers. Some results suggest that, by taking nutrients from the stream water (Suberkropp, 1998), microbial decomposers reduce the metabolic cost of producing extracellular enzymes to degrade complex molecules, speeding up microbial activity and litter decomposition (e.g. Ferreira et al., 2006; Gulis et al., 2006), particularly in nutrient-poor litters (Ferreira et al., 2015). Similarly, and according to the 'temperature quality' hypothesis (Bosatta & Ågren, 1999), the role of temperature accelerating decomposition becomes more prominent with increasing litter recalcitrance. Thus, evaluating the temperature sensitivity of litters of different quality is paramount to understanding how global change may affect decomposition, which can be tackled through the metabolic theory of ecology (MTE; Brown et al., 2004). However, synergies between both environmental factors—temperature and dissolved nutrients—are also poorly understood, and evidence is limited to laboratory incubations (Fernandes et al., 2014; Ferreira & Chauvet, 2011), contrary to the additive effect found in the field (Manning et al., 2018). Thus, published results leave unresolved the effects of these interactions on ecosystem processes (Canhoto et al., 2016; Cross et al., 2015; Pérez et al., 2023).

The lack of consensus could indicate that some extrinsic factors involved in the decomposition process are being neglected, or that some cryptic feedbacks among factors have not been properly addressed. For example, the local adaptations of decomposers to their resources (Mooshammer et al., 2014), a central tenet of the home-field advantage hypothesis (HFA; Gholz et al., 2000; Hunt et al., 1988; Vivanco & Austin, 2008), have been scarcely studied in freshwater ecosystems so far. The HFA hypothesis states that decomposition rates are partially determined by the adaptations of microbial assemblages to exploit more efficiently the type of resources historically dominant at home. In terrestrial ecosystems, this hypothesis has been widely tested. However, results are conflicting and hinder generalizations across scales and ecosystems (Palozzi & Lindo, 2018). In aquatic ecosystems, few studies have evaluated HFA effects, and results are inconclusive (Franzitta et al., 2015; Jackrel & Wootton, 2014; Luai et al., 2019). The few studies that have explicitly tested this hypothesis for microbial decomposition in headwater streams, reported a limited support with some HFA effects just for recalcitrant litters (Fenoy et al., 2016; Yeung et al., 2019).

Given the simultaneous control of decomposition by numerous factors and the strong context dependency of this process (Boyero et al., 2016; Woodward et al., 2012), determining the primary drivers of litter decomposition is challenging but of paramount importance in a changing world. However, logistic constraints in most studies limit the number of environmental factors and litter species studied, which hinder the elucidation of the general drivers of decomposition in streams (Canhoto et al., 2016; Tiegs et al., 2019; Zhang et al., 2019). This emphasizes the need for simultaneously examining decomposition rates of litter species differing in key functional traits across a wide range of abiotic factors.

Here, we aim at evaluating the intrinsic and extrinsic factors most often identified as key drivers of decomposition in streams. To this end, we studied the decomposition of four litter species belonging to four functional groups; namely deciduous N-fixer and deciduous non N-fixer plants, broad-leaves evergreen and giant gramminoid¸ differing in leaf traits reflecting potential climate-driven alterations of riparian inputs to headwater streams, caused by changes in the dominant vegetation (Salinas et al., 2018). The study was conducted in Andalusia, an environmentally diverse but relatively small Mediterranean region. We performed a reciprocal incubation experiment across four selected subregions with sharp contrasts in riparian vegetation and physico-chemical characteristics in stream waters (Casas et al., 2011; Salinas et al., 2018). This spatial scale provides a suitable framework to simultaneously evaluate target factors influenced by relatively smaller biogeographic historical constraints compared to studies at larger spatial scales (e.g. Heberling & Fridley, 2012; Leibold et al., 2010). We hypothesized that there is a preponderant role of litter traits on the decomposition process due to (i) a high temperature sensitivity of decomposition in recalcitrant leaf litter; (ii) increased concentration of dissolved nutrients favour decomposition of nutrient-poor litters; and (iii) an origin effect (home vs. away), assuming potential specialization of the local microbial community to decompose the dominant litter, the quality of which may largely vary across regions.

2 | MATERIALS AND METHODS

2.1 | Study sites

We conducted a decomposition experiment during winter 2016–2017 in four subregions of contrasting biogeoclimatic conditions within Andalusia (southern Spain), in each of which we selected four low-order streams. Streams located in Sierra Nevada (1148–1465 m a.s.l.) and Alcornocales (415–532 m a.s.l.) drain silica rocks, and those located in Sierra de Cazorla (686–1249 m a.s.l.) and Semiarid Lowland of Almería (47–300 m a.s.l.) drain calcareous rocks. The climate of the region is Mediterranean type in most of the range. However, there is substantial variation among subregions in mean annual precipitation and range of minimum–maximum annual means of air temperatures (1971–2000): Sierra Nevada, 581 mm, −1.2 to 26.9°C; Alcornocales, 1227 mm, 6.6–27.0°C; Cazorla, 913 mm, −0.5 to 30.5°C; and Semiarid Lowland, 350 mm, 4.0–30.7°C (REDIAM, http://www.juntadeandalucia.es/medioambiente/site/web/rediam). Dominant riparian species were as follows: alder (*Alnus glutinosa* [L.] Gaertn.) and grey willow (*Salix atrocinerea* Brot.) in Sierra Nevada; narrow-leaved ash (*Fraxinus angustifolia* Vahl), grey willow and black pine (*Pinus nigra* [Dunal]) in Cazorla; common rhododendron (*Rhododendron poncticum* L.), alder and Andalusian oak (*Quercus canariensis* Willd.) in Alcornocales; giant cane (*Arundo donax* L.) and common reed (*Phragmites australis* [Cav] Trin ex Steud.) in the Semiarid Lowland. Further, riparian vegetation composition and bioclimatic information of these subregions can be found in Salinas et al. (2018). Additionally, data on the quality of leaf-litter inputs to streams in these regions are provided in Salinas et al. (2018) and Fenoy et al. (2021).

2.2 | Stream-water characteristics

Electrical conductivity (conductivity, therein), pH and dissolved oxygen were measured in each stream using a multiparametric probe (HACH® model HQ-30d, Loveland, CO, USA). Water samples were collected and filtered (0.45 µm, APFC, Millipore®, Darmstadt, Germany) in the field to measure alkalinity, total dissolved nitrogen (TN) and phosphorus (TP), NO_3^--N and PO_4^{3-}-P. Total alkalinity was measured by acid titration to a pH end-point of 4.25 (Wetzel & Likens, 2000). An aliquot of 100 mL was wet mineralized for 30 min at 120°C in autoclave. After cooling to room temperature, an aliquot of 50 mL was acidified with concentrated sulphuric acid to determine TN (absorbance at 220 nm), whereas TP, mineralized to phosphate, was determined in the remaining 50 mL (Wetzel & Likens, 2000). NO_3^--N concentrations were analysed by the sodium salicylate method (APHA, 2005), and PO_4^{3-}-P concentrations by the ascorbic acid method (Wetzel & Likens, 2000). All measurements were performed twice in each stream, at the beginning and at the end of the decomposition experiment. Water temperature was recorded hourly in each stream with HOBO Pendant (Onset Computer Corporation, Bourne, MA, USA) data loggers through the entire duration of the experiment (40 days).

2.3 | Leaf litter selection and characterization

From each subregion, we selected one dominant species, resulting in a final selection of contrasting leaf-litter quality among subregions: alder from Sierra Nevada, ash from Cazorla, rhododendron from Alcornocales and giant cane from the Semiarid Lowland of Almería. Leaves in evident state of senescence (miscoloured) were collected from the riparian zones in each subregion just after abscission (alder and ash) or from branches or standing-dead shoots (rhododendron and giant cane). Litter was air dried to constant weight at room temperature (2 weeks at ca. 23°C). Silica (Si) concentration was measured using ICP mass spectrometry (iCAP 6500—ICP-OES, Thermo Scientific®). Litter toughness, SLA and chemical characteristics were determined after in-stream leaching (see below). We determined specific leaf area (SLA, $mm^2\ g^{-1}$) by measuring area (WinDIAS 3, Delta-T devices), dry mass (DM, 60°C, 78 h) and toughness using a calibrated texturometer (TA.XT2 Plus, Stable Micro Systems) as in Fenoy et al. (2021). Percentages of hemicellulose, cellulose and lignin were determined as in Fenoy et al. (2016). Litter nitrogen (N) and carbon (C) concentrations were determined using a Perkin Elmer series II CHNS/O elemental analyser (EA-Thermo DELTA V Advantage, Fisher Scientific®), with results expressed as % N and % C of litter dry mass. Phosphorus (% P) was determined following the method described in Wetzel and Likens (2000), after sample incineration (500°C, 5 h).

2.4 | Litter decomposition

Litter portions (5.00 ± 0.05 g DM) of each species were spray moistened with distilled water and enclosed in handmade bags (15 × 20 cm; 1 mm mesh size). To avoid microbial community alteration if bags become partially buried, a mesh size slightly larger than usual was chosen, ensuring stream-water circulation within the litter bag. Litter bags—eight per species and stream—were incubated in five equidistant riffle sections along a 50-m stream reach (total $n = 512$ bags). Thus, leaf litter from one native species and three non-native species were incubated in each stream. Three bags per stream and species ($n = 192$ bags) were retrieved after 24 h in order to account for handling and leaching losses. The remaining five litter bags per species and stream ($n = 320$ bags) were collected after 40 days to estimate decomposition. Upon retrieval, litter bags were placed individually in ziplock bags and transported to the laboratory in an icebox. Leaves were carefully rinsed with filtered streamwater to exclude fine particles, oven-dried (70°C, 72 h) and weighed to the nearest 0.1 mg. Thereafter, litter was ground to pass a 1-mm screen; a portion was ignited at 500°C for 5 h to estimate mass loss (weighted to the nearest 0.1 mg) on an ash-free dry mass basis.

Decomposition was expressed as the relative ash-free litter-mass loss [$\mathrm{RLML} = (\mathrm{AFDM}_i - \mathrm{AFDMf})/(\mathrm{AFDM}_i)$] per day ($\mathrm{RLML\ d}^{-1}$) or per degree-day, that is, the sum of the mean daily temperatures for the incubation period ($\mathrm{RLML\ dd}^{-1}$).

2.5 | Fungal biomass

To estimate fungal biomass, an additional set of five litter bags per species and stream were incubated as above, and used to measure ergosterol content. In the laboratory, a half portion of each litter bag was carefully rinsed with filtered stream-water. To reduce the number of analyses to an affordable amount, portions were pooled by species/stream, frozen until needed and then freeze-dried and ground. The procedure previously described by Gessner and Chauvet (1993) was used for ergosterol extraction (200 mg per litter sample). Ergosterol, dissolved in 1 mL of methanol, was analysed using a HPLC (Finnigan Surveyor LC Pump Plus Thermo Scientific) system equipped with a DAD (Thermo Scientific) and Hypersil Gold C18 column (250 × 4.6 mm, 5 µm, Thermo Electron, Cambridge, UK). A flow rate of 1 mL/min was set. Ergosterol was separated with isocratic elution using methanol:acetonitrile (80:20 v/v). The column temperature was 25°C, and the injection volume was 20 µL. Peaks were monitored at 282 nm and identified by retention time in comparison with pure standard. Quantification of the ergosterol was made using external calibration curves obtained from a pure compound (Sigma Aldrich, St. Louis, MO, USA) in the HPLC system. Ergosterol content was converted into fungal biomass using a conversion factor of 5.5 mg ergosterol mg^{-1} fungal dry mass (Gessner & Chauvet, 1993) and the results were expressed as mg fungal biomass g^{-1} litter DM.

2.6 | Data analyses

All statistical tests were carried out using R software 3.5.2 (R Core Team, 2018). We used one-way ANOVAs to compare environmental factors among subregions and litter traits among species, and Tukey HSD tests for pairwise post hoc comparisons. Except for pH, to make the variances homoscedastic all analyses were performed on transformed variables, using $\log(x+1)$ for continuous variables and arcsine $\sqrt{(x/100)}$ for percentages. To explore relationships among subregions and litter species, we used the 'factoextra' R package and ran separate principal component analyses (PCAs) of stream environmental characteristics and litter traits. Variables were standardized (mean: 0, SD: 1) after varimax rotation. In order to avoid redundancy in the PCA, when two variables were highly correlated (Spearman's correlation >0.8), the one that was more strongly correlated to the rest was removed for analysis.

To look at the overall joint effects of extrinsic (subregion) and intrinsic (litter species) factors on each dependent variable, we fitted linear mixed-effects models (LME; lme4 package in R) to regress RLML (RLMLd^{-1} and RLMLdd^{-1}) and fungal biomass on 'subregion' and litter 'species' and their interaction as fixed factors, including 'stream' as a random factor. The significance of independent variables and their interaction were evaluated using type 'III' sum of squares ('car' package in R). When the interaction subregion-by-species was significant, we performed pairwise comparisons of level means for a given factor within each level of the other factor, using the 'multicomp' and 'lsmeans' packages in R. We also investigated which particular intrinsic or extrinsic factors, and interactions among them, were driving decomposition. To this end, the machine learning algorithm random forest (RF) (Breiman, 2001), was applied to select influential drivers (Sandri & Zuccolotto, 2006). We plotted the variables from highest to lowest importance values, and all the variables with values above the inflection point were selected for further analysis. RF performs well when facing multicollinearity, is relatively robust to overfitting, automatically fits non-linear relationships and high-order interactions, and provides a measure of the importance of each variable in a model (Pitcher et al., 2012). Second, using the resulting set of selected variables and to better understanding the nature of the interactions among the most important variables, we applied linear mixed effects models using the most important candidate drivers of decomposition; that is, those selected by RFs, as independent variables. Models were constructed with the *lmer* function in the R package 'lme4' (Bates et al., 2011), and *p*-values for both random and fixed effects tested using 'lmerTest' (Kuznetsova et al., 2015). 'Stream' was included as a random factor in all models. Fixed factors, that is, environmental and litter trait variables, were included with their second order interactions. All variables were standardized (mean subtracted and division by the SD) to make effect sizes comparable across variables measured at different scales. When necessary, we used Box-Cox transformation (RLMLd^{-1} and RLMLdd^{-1}) to approximate normality in the distribution of model residuals.

Relationships between temperature and decomposition rate were explored quantitatively based on the Metabolic Theory of Ecology (MTE) (Brown et al., 2004) for all species pooled and separately for each species. Mass loss was converted to decomposition rate (k), based on the exponential decay model $M_0 = M_t \times e^{-kt}$ (Bärlocher, 2005). To estimate activation energies, the natural logarithm of k was regressed against the inverse of absolute temperature (T) in degrees Kelvin multiplied by the Boltzmann constant (Brown et al., 2004). Models included 'region' as fixed factor and 'stream' as random factor, and were constructed with the *lmer* function in the R package 'lme4' (Bates et al., 2011), and *p*-values for random effects tested using 'lmerTest' (Kuznetsova et al., 2015). As 'region' did not improve the fit of the model, this factor was removed.

We estimated Home Field Advantage (HFA) for each species in its native subregion, using the Additional Decomposition at Home of species *i* (ADH_i) of Ayres et al. (2009), which departed from a method originally developed to calculate HFA in sports. We adapted ADH_i for the four species used, calculated in each of the four streams per subregion. The equation for ADH_i calculation is as follows: $\mathrm{ADH}_i = \mathrm{HDD}_i - \mathrm{ADD}_i - \mathrm{H}$, where HDD_i was calculated as $\mathrm{HDD}_i = (\mathrm{D}_{iI} - \mathrm{D}_{jI}) + (\mathrm{D}_{iI} - \mathrm{D}_{kI}) + (\mathrm{D}_{iI} - \mathrm{D}_{lI})$; ADD_i was calculated as $\mathrm{ADD}_i = (\mathrm{D}_{iJ} - \mathrm{D}_{jJ}) + (\mathrm{D}_{iK} - \mathrm{D}_{kK}) + (\mathrm{D}_{iL} - \mathrm{D}_{lL})$; and $\mathrm{H} = (\mathrm{HDD}_i + \mathrm{HDD}_j + \mathrm{HDD}_k + \mathrm{HDD}_l)/(N - 1)$. ADH_i is the additional decomposition at home for species *i*, *j* *k* and *l*; *i*, *j*, *k* and *l* are litters derived from plant species; *I*, *J*, *K* and *L* are areas dominated by species *i*, *j*, *k* and *l*, respectively; D is a measure of decomposition; HDD and ADD represent home decomposition difference and away decomposition difference, respectively; H represents the total HFA for all species combined; and N represents the number of species (Ayres et al., 2009). Thus, ADH_i results are the mean ADH for the species *i* in the four streams of its subregion of origin. We calculated ADH_i using data of decomposition in terms of ash-free RLML per day (d^{-1}) and per degree-day (dd^{-1}). A positive HFA effect, that is, faster decomposition than expected at home, occurred if $ADH_i>0$; if $ADH_i<0$, litter decomposition at home would be slower than predicted, the opposite prediction of the HFA; and no HFA effect would exist if $ADH_i=0$. We used Student *t*-tests to determine whether mean ADH_i values ($n=4$ streams per subregion) differed significantly from zero.

3 | RESULTS

3.1 | Stream-water characteristics

Environmental characteristics of streams showed wide ranges of variation across subregions (Table S1), the most prominent were those of mean water temperature (3.44–22.32°C), electric conductivity (62–3215 $\mu S\,cm^{-1}$) and TN (150–2096 $\mu g\,L^{-1}$). Water chemistry strongly reflected rock type. The calcareous subregions (Cazorla and Semiarid Lowland) showed higher values of pH, total alkalinity, electrical conductivity (EC), TN and NO_3^--N, but lower content of phosphorus compared to subregions rich in silica rocks (Alcornocales and Sierra Nevada) (Table S1). The first two rotated components (RCs) of the PCA accounted for 74% of the total variance. RC1 (38% expl. var.) showed positive loadings of water temperature (0.92) and TN (0.86). Alkalinity (0.71) and NO_3^--N (0.61) showed the highest positive load on RC2 (36% expl. var.), which clearly segregated siliceous (negative) and calcareous (positive) subregions (Figure 1). Phosphate showed the highest negative load (−0.91) on RC2, where streams from silica rocks subregions (Alcornocales and Sierra Nevada) were segregated (Figure 1).

3.2 | Leaf litter traits

Giant cane showed significantly lower C, P and lignin, but higher cellulose, hemicellulose and Si contents compared to other species (leaf-litter traits after leaching, Table S2). N concentration significantly differed across all litter species: alder >> ash > rhododendron > giant cane (Table S2). The higher concentration of fibres and, particularly, of Si in leaf blades of giant cane likely determined its significantly higher toughness (Table S2). Total variance explained by the first two components was 91.1%. RC1 (55.2% expl. var.) showed high positive load of N (0.96), P (0.75) and lignin (0.75), and negative of toughness (−0.88) and cellulose (−0.83). This dimension segregated giant cane and rhododendron (left) from alder and ash (right), the latter two much softer and richer in nutrients (Figure 2). RC2 (35.9% expl. var.) clearly segregated giant cane from other litter species due to its high content in hemicellulose (0.97) and silica (0.80) (Figure 2).

3.3 | Leaf litter decomposition and fungal biomass

Average leaf mass loss of alder and ash (both ≈35%) was higher compared to rhododendron and giant cane (13% and 21%, respectively). Relative leaf mass loss (RLML, d^{-1}, Table S3), corrected for leaching, was mainly affected by the litter species × subregion interaction ($\chi^2=99.1$, $df=9$, $p<0.001$), suggesting that decomposition of each species responded distinctively to the set of environmental characteristics in each subregion (Figure 3a, Table S4). In the warmest subregion, Semiarid Lowland, all species except

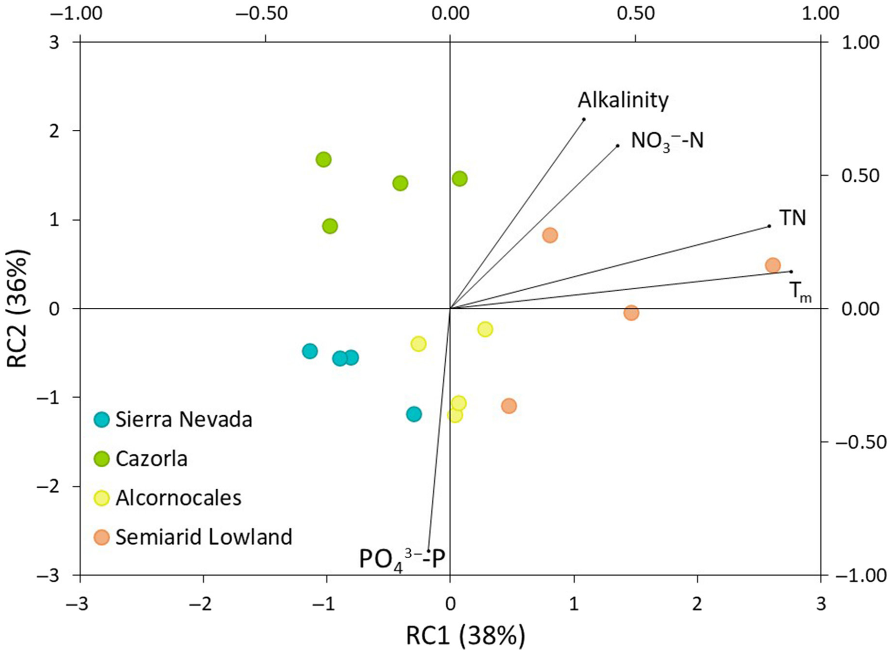
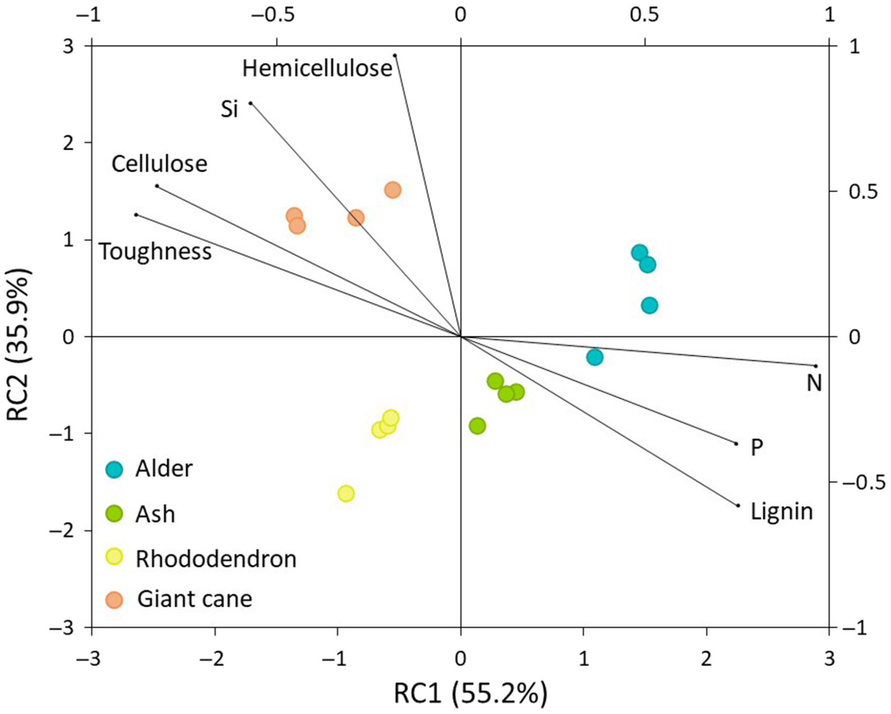


FIGURE 1 PCA ordination of streams and subregions (four streams per subregion) based on selected environmental conditions, and after varimax rotation. The scale of the right and upper axes indicates variable loadings. Alk, alkalinity; NO_3^--N, nitrates; PO_4^{3-}-P, phosphates; TN, total dissolved nitrogen; T_m, mean winter temperature of stream-water.

FIGURE 2 PCA ordination of the litter dominant species in each of the four subregions based on their litter traits (after leaching), and after varimax rotation. Points represent the mean value per region of each litter species after leaching. The scale of the right and upper axes indicates variable loadings.



rhododendron decomposed equally fast. In contrast, leaf quality largely shaped the magnitude of decomposition in other subregions, with alder and ash decomposing faster than the other two low-quality litters. Moreover, differences in decomposition of low-quality litters—rhododendron and giant cane—were higher in the cold subregions of Cazorla and Sierra Nevada (Figure 3a, Table S4).

RLML computed on a thermal sum basis (dd^{-1}) also showed a highly significant interaction species × subregion ($\chi^2=128.9$, $df=9$, $p<0.001$; Figure 3b, Table S4). Alder and ash showed a decreasing trend of mass loss with increasing temperature whereas greater similarity in mass loss across subregions was observed for the more recalcitrant species. However, giant cane showed the slowest decomposition in Alcornocales (Figure 3b).

Similarly to decomposition, litter species showed different fungal biomass variation across subregions (species × subregion: $\chi^2=434.4$, $df=9$, $p<0.001$; Figure 3c, Table S4). Ash showed the highest, and alder the lowest, fungal biomass in all subregions, particularly in the Semiarid Lowland. For all litter species, fungal biomass increased gradually with subregion temperature (Figure 3c, Table S4), and showed a positive relationship with RLML (d^{-1}), for all species pooled ($r=0.53$, p-value <0.001), and for each species separately (*Alnus:* $r=0.69$, p-value$=0.004$; *Rhododendron*: $r=0.71$, p-value$=0.003$; *Arundo*: $r=0.49$, p-value$=0.057$), except in the case of *Fraxinus* ($r=0.14$, p-value$=0.609$).

3.4 | Intrinsic and extrinsic drivers of decomposition

The Random Forest (RF) regression trees selected litter C:N ratio as the most influential variable on RLML (d^{-1}), followed by temperature, litter toughness, NO_3^--N concentration in water and litter C:P ratio (Figure S1). The linear mixed-effects model, including the independent variables selected by the RF model, marginal R^2 (i.e. variance explained by fixed factors) equalled 0.70, representing 94.8% of the conditional R^2 (0.75) (i.e. variance explained by fixed factors and the random factor stream). Temperature and its interaction with litter toughness had the strongest effect on RLML (d^{-1}), followed by the interactions (in decreasing strength): C:N × temperature, NO_3^--N × toughness, NO_3^--N × C:N and C:P × temperature (Table 1; Figure S2). Temperature accelerated decomposition more strongly as litter N, P and toughness increased (Figure S2). Also, when litter nitrogen was the lowest, there was a decomposition enhancing effect of environmental N (Figure S2d). Finally, environmental N enhanced decomposition only in the least tough litter (Figure S2e).

3.5 | Temperature sensitivity of decomposition

The activation energy (E_a) of litter decomposition of all species pooled was 0.53 ± 0.08 eV, representing 81.6% of the value (0.65 eV) predicted by metabolic theory (MTE). Litter quality clearly influenced E_a. Species with higher nutrient content and lower toughness showed E_a values from two third to half of those predicted by MTE (0.45 ± 0.06 and 0.35 ± 0.05 eV, for alder and ash, respectively), while species of low litter quality (higher toughness) showed E_a close to the predicted values (0.58 ± 0.11 and 0.73 ± 0.19 eV, for rhododendron and giant cane, respectively).

3.6 | Home field advantage

Additional decomposition at home (ADH) calculated on a time basis (RLML d^{-1}) was lower than 1% for the four litter

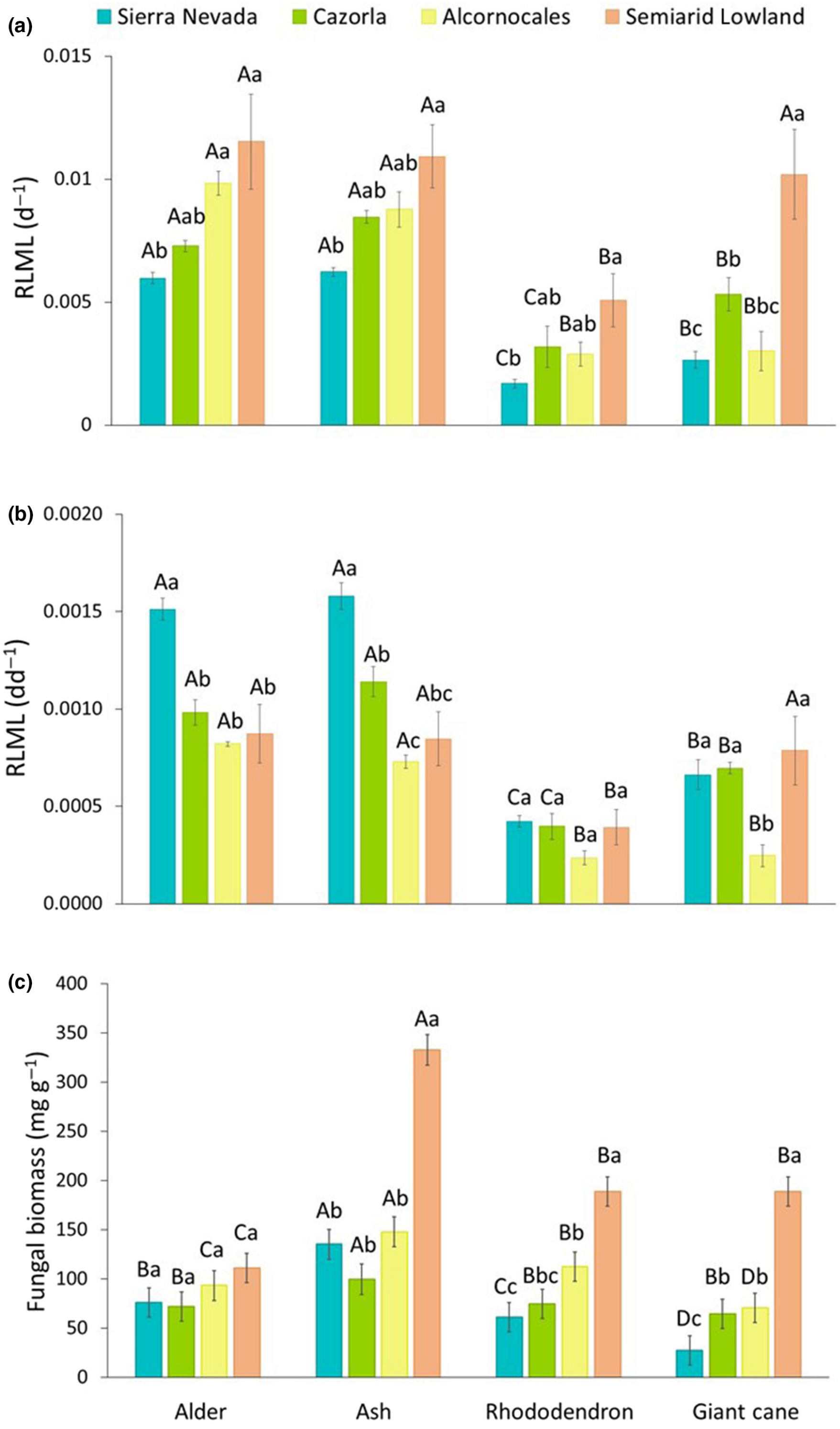


FIGURE 3 Relative leaf mass loss (RLML, mean ± SE) computed on the basis of days (a) and degree-days (b) for the four species incubated in the four subregions. (c) Fungal biomass after the incubation period (40 days). Capital letters indicate significant differences among species decomposition (intra-regional comparisons), and lowercase letters indicate intraspecific differences (inter-regional comparisons) ($p < 0.05$).

species (Figure 4a, Table S5), but significant and negative for alder. Moreover, ADH was only marginally significant for giant cane, although RLML of this species at home (Semiarid Lowland) was on average 3.1 times higher than elsewhere (Figure 4a). ADH calculated on a degree-day basis (RLML dd^{-1}) was lower than 0.2% for all species, but significantly higher than zero for the low-quality species rhododendron and giant cane (Figure 4b, Table S5).

4 | DISCUSSION

Leaf litter decomposition, a key ecosystem process in forested streams, is controlled by litter traits (including micronutrients), the environment and possible functional specializations of decomposers, with complex scale-dependent interactions which make process rates greatly context-dependent (Boyero et al., 2016; Bradford et al., 2016; García-Palacios et al., 2016; Woodward et al., 2012). Thus, determining the main biotic and abiotic factors controlling litter decomposition, their relative influence and interactions, is challenging but critical in the face of ongoing global changes.

Our findings support the general hypothesis of a leading role of litter traits on decomposition, in accordance with other studies on streams (Casas et al., 2013; Four et al., 2019; Zhang et al., 2019), soil (Cornwell et al., 2008; Makkonen et al., 2012; Zhang et al., 2008) and comparisons of terrestrial and aquatic ecosystems (García-Palacios et al., 2016). Overall, these studies conclude that high N (and related low C:N or N:P ratios) and/or low lignin (Fernandes et al., 2012; Jabiol et al., 2019; Pérez et al., 2021; Schindler & Gessner, 2009), are the main litter traits boosting decomposition. Our results highlight a major role for litter N, but not for lignin, likely due to deciduous and evergreen species, which differ more in N than in lignin, and the inclusion of lignin-poor but cellulose-rich giant gramminoid species, a functional group rarely considered in litter decomposition studies in streams (Zhang et al., 2019; but see Fenoy et al., 2016). Thus, litter N content, and particularly the related C:N molar stoichiometric ratio, seem to be more suitable and widespread traits to predict decomposition in a diverse array of plant functional types, for which the level of recalcitrance may depend on different structural compounds (e.g. lignin, cellulose, Si, etc.).

Our results point to significant effects on decomposition from two major global change drivers—temperature and stream water nitrate—but negligible effects from conductivity or alkalinity. The latter being stream-water environmental factors that depend on the basin rock lithology. Perhaps, the levels of these two factors were not sufficiently elevated to reduce decomposer activity substantially, as already concluded in other studies examining similar gradients of water mineral content (Casas et al., 2011; Fenoy et al., 2016; Vander Vorste et al., 2019). As expected, elevated temperature significantly accelerated decomposition, likely due to increased (i) metabolic rates of microbial decomposers (e.g. Dang et al., 2009), and (ii) fungal biomass, since it was positively related to litter decomposition (this study; Gessner & Chauvet, 1994; but see Bärlocher et al., 2013), or a combination of the two. Furthermore, in full support of our first hypothesis, temperature sensitivity of decomposition depended on litter quality (Amani et al., 2019; Follstad Shah et al., 2017). The 'temperature-quality' hypothesis posits that temperature sensitivity of decomposition is inversely related to litter quality (Bosatta & Ågren, 1999; Davidson & Janssens, 2006). The temperature sensitivity for all species pooled ($E_a = 0.53 \pm 0.08$ eV; mean ± SE) was closer to the E_a predicted by the MTE (E_a between 0.6–0.7 eV; Allen et al., 2005; Brown et al., 2004) than values reported by other studies at global scale (alder, 0.46 ± 0.21 eV; Boyero et al., 2011; pooled data of different litter species, 0.34 ± 0.04 eV; Follstad Shah et al., 2017). However, when we calculated E_a by species, the most recalcitrant ones—rhododendron and giant cane—showed E_a values in the range of the MTE prediction. High temperature sensitivity of low-quality litters (Fierer et al., 2005) is likely related with elevated E_a of enzymes involved in lignocellulose degradation (Sinsabaugh & Follstad Shah, 2012). The rationale behind this is that enzymatic reactions required to metabolize complex macromolecules have higher E_a than enzymatic reactions that metabolize chemically simpler litter constituents (Bosatta & Ågren, 1999; Conant et al., 2008).

TABLE 1 Results of linear mixed-effects model on litter mass loss (d^{-1}, $n = 294$), including litter quality and environmental factors as independent variables.

	Estimate ± SE	χ^2	*df*	*p*-value
Fixed factors				
Intercept	0.024 ± 0.062	0.14	1	0.705
Temperature	*0.503 ± 0.084*	*35.76*	1	<0.001
NO_3^--N	0.076 ± 0.084	0.82	1	0.366
C:N	*−0.772 ± 0.064*	*143.63*	1	<0.001
C:P	*−0.452 ± 0.051*	*79.18*	1	<0.001
Toughness	*0.589 ± 0.071*	*69.81*	1	<0.001
Temperature × C:N	*−0.450 ± 0.085*	*28.19*	1	<0.001
Temperature × C:P	*−0.184 ± 0.066*	*7.67*	1	0.006
Temperature × Toughness	*0.678 ± 0.088*	*59.76*	1	<0.001
NO_3^--N × C:N	*0.210 ± 0.085*	*6.10*	1	0.014
NO_3^--N × C:P	0.098 ± 0.064	2.38	1	0.123
NO_3^--N × Toughness	*−0.258 ± 0.098*	*6.96*	1	0.008
Random factor				
Stream		*18.51*	1	<0.001

Note: *Marginal $R^2 = 0.70$; Conditional $R^2 = 0.75$.*

In our study, low-quality litters from rhododendron and giant cane are particularly rich in cellulose, in addition to other complex substances, such as thick waxy cuticles in rhododendron (Salasoo, 1983) or cell walls rich in silica content in giant cane (this

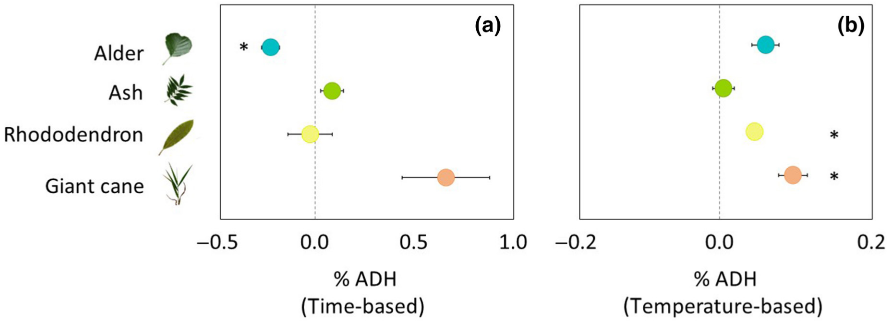


FIGURE 4 Additional decomposition at home (ADH) calculated on time-based (a) and temperature-based (b) decomposition for each litter species (mean ± SE). $n = 4$ in all cases. Asterisks indicate values significantly different from zero ($p < 0.05$).

study; Ma & Yamaji, 2006), all of which increase litter recalcitrance. The waxy cuticle of rhododendron represents a barrier to fungal colonization (Bruder et al., 2016) which is slowly degraded (Gallardo & Merino, 1993). The high Si content in Poaceae species strongly binds to cellulose in the form of polymerized silicic acid (silica gel), determining a silico-cellulose cell membrane (Ma & Yamaji, 2006) that could restrict the accessibility of enzymes to cellulose fibres (Fenoy et al., 2016). These substances, and the complex physical structure, were likely implicitly included in the variable toughness in our model of litter decomposition. Toughness interacted with temperature: the relationship between decomposition and temperature becomes steeper with increasing toughness (see Figure S2c), in agreement with the hypothesis of higher temperature sensitivity. Decomposition results expressed on a thermal-sum basis further support the relatively stronger effect of temperature on recalcitrant litters, in accord with our general hypothesis. A complementary explanation for high E_a of the most recalcitrant litters, might reside in evolutionary shifts in genotypic composition of microbial assemblages with rising temperature, which would select for genotypes that preferentially use recalcitrant C (Biasi et al., 2005), thereby becoming adapted to warmer conditions (Bárcenas-Moreno et al., 2009; Bradford et al., 2010). This specialization might, in turn, have lowered decomposition efficiency in warmer sites (Fenoy et al., 2022).

Synergistic effects of temperature and in-stream dissolved nutrients (e.g. N) on litter microbial decomposition (Ferreira & Chauvet, 2011; Martínez et al., 2014; Moghadam & Zimmer, 2016) have been attributed to the increased nutrient-use efficiencies by decomposers at higher temperatures (Fernandes et al., 2014). We found interactive effects of temperature and NO_3^--N, separately, with litter quality, that is, C:nutrients ratios and toughness (Table 1). This supports our first and second hypotheses: both factors exerted more influence on recalcitrant litters (higher toughness). Moreover, our results suggest increasing N-limitation in decomposition, compared to P-limitation, as temperature rises (based on a comparison of the standardized coefficients of the interactions on Table 1). Therefore, one could predict that as global change proceeds with a subsequent increase in stream-water temperature and NO_3^--N concentration, microbial decomposition will accelerate. This will be particularly the case in streams receiving litter inputs of relatively low quality, namely in warmer regions (Boyero et al., 2017; Salinas et al., 2018). Thus, the effect of extrinsic (i.e. acceleration) and intrinsic (i.e. slow down) factors affecting microbial decomposition in streams might be counterbalanced to some extent.

Our third hypothesis suggesting higher decomposition rates in the native range of each leaf litter species—'HFA' hypothesis—was supported just for some species. Although the increase in decomposition that occurs due to HFA seems to be quite small, it implies that there is indeed a certain degree of adaptation of the microbiota. A gradient of HFA strength was identified between both extremes of litter quality species used in this experiment, when calculated using time-based decomposition. It ranged from negative HFA for alder, the higher quality litter (low C:N ratio, low toughness), to positive HFA values for giant cane, the lowest quality litter (high C:N ratio, high toughness, high Si concentration). This contradicts the conclusion of the meta-analysis in Veen, Freschet, et al. (2015), where no effect of litter quality on HFA was detected. However, positive HFA has been previously detected for low-quality litters in terrestrial ecosystems (e.g. Veen et al., 2019), in contrast to studies that found either no HFA effect or in which results were inconclusive (e.g. Perez et al., 2013; Veen, Sundqvist, et al., 2015). In aquatic ecosystems, controversial results have been found as well, with positive or partially supported HFA effects (Fenoy et al., 2016; Franzitta et al., 2015; Lopes et al., 2013; Yeung et al., 2019), or even a home-field disadvantage (Luai et al., 2019). *Alnus*, being high-quality litter, could be decomposed indiscriminately by almost all decomposers, possibly explaining a lack of HFA, or even a HF disadvantage, under some circumstances. For example, when incubated in environments dominated by low-nutrient litter, alder could have faster decomposition out of *home*. Moreover, alder originates from the coldest subregion, where decomposition rates were lower, thereby probably adapted to having slow decomposition rates at *home*. Although in Veen, Freschet, et al. (2015) a weak effect of macroclimate was found, we cannot rule out that our results may reflect, in fact, the parallelism between the thermal and the litter quality gradient in our experimental design (higher quality litter from the coldest subregion, and low-quality litter from the warmest subregion). Thus, due to the great sensitivity to temperature of decomposition of low-quality litter (see E_a results), we studied HFA using temperature-based decomposition as well. With this approach, only rhododendron and giant cane, the species with lowest quality, decomposed fast at home, that is, positive HFA (Alcornocales and Semiarid Lowland subregions, respectively). This could be related to a specialized microbial community decomposing more efficiently low-quality litters in their subregions of origin, in accordance with many studies concluding that HFA is stronger for more recalcitrant litter because it requires decomposers with a higher degree of specialization (Fanin et al., 2016; Keiser et al., 2014; Milcu & Manning, 2011; see a review in Palozzi & Lindo, 2018). Although significant, our HFA estimates are considerably lower than those reported in other studies of aquatic ecosystems (e.g. Luai et al., 2019; Yeung et al., 2019). Since HFA estimates depend on species selection and abiotic conditions, this underscores the necessity for further investigation into the influence of the interaction between these two factors on the decomposition process. To this end, a more comprehensive selection of litter traits and abiotic variables should be considered, including different stages of decomposition as a source of variation.

One of the main tenets of the HFA hypothesis is that increasing dissimilarity in plant community and litter traits is a fundamental driver of HFA outcomes (Palozzi & Lindo, 2018), suggesting a substrate quality-matrix quality interaction (Freschet et al., 2012). This hypothesis predicts an increasing positive interaction (facilitating microbial decomposition) between a given litter species and its decomposer community, as the tested litter species and the litter layer of the home (target) ecosystem become increasingly similar in quality. Following this argument, and considering that HFA may be measured as a continuous variable differing in strength, it seems logical having found HFA effects in giant cane, whose 'native' range are streams with riparian vegetation overwhelmingly dominated by this invasive species along with other Poaceae species such as common reed (*Phragmites australis*) and ravenna grass (*Tripidium ravennae* [L.] H. Scholz) (Casas et al., 2011; Fenoy et al., 2021; Salinas et al., 2018), all rich in Si and cellulose. However, this type of recalcitrance seemed not to be the only cause of the observed HFA, since it was observed also in the recalcitrant rhododendron (only for the temperature-based approximation), rich in lignin and wax. Similarly, rhododendron decomposes faster at home when surrounded by riparian species that presumably evolved from tropical-like environments as well (Salinas et al., 2018). Our results add to the growing evidence than in stream ecosystems, selective pressures, such as the relative difficulty of breaking recalcitrant molecules, promote decomposer specialization when a low-quality litter species dominates at home. Thus, the greater the differences in quality between the litters at 'home' and 'away', the greater the magnitude of the HFA effect (Veen, Freschet et al., 2015). The native ranges of the other two species (alder and ash) are more similar to each other, dominated by trees/shrubs whose level of litter recalcitrance greatly depend on lignin:N (i.e. weak contrast in litter quality and matrix quality between them).

5 | CONCLUSIONS

Results of our regional-scale study suggest that litter quality strongly influences the magnitude of effects of environmental factors, mimicking processes at global scale. Thus, statistical interactions involving litter quality and environmental factors are highlighted as the main drivers of litter decomposition across scales. Stream-water temperature and nitrate concentration were the major extrinsic drivers of decomposition, although they did not act synergistically. Temperature sensitivity of decomposition of low-, but not high-, quality litters followed the predictions of the Metabolic Theory of Ecology. Moreover, our results highlight the importance of accounting for environmental variability in HFA studies, since when ADH was calculated on a degree-day basis, microbial adaptation to decompose leaf litter of low quality emerged as a relevant decomposition factor. Future research accounting for other environmental factors is needed to avoid false, positive or negative results when the HFA hypothesis is tested (Palozzi & Lindo, 2018).

AUTHOR CONTRIBUTIONS

EF: Data curation, formal analysis, investigation, methodology, writing—original draft, writing—review and editing and visualization. JM: Formal analysis, visualization and writing – review and editing. JRR: Visualization and writing—review and editing. FJM: Visualization and writing—review and editing. JJC: Conceptualization, funding acquisition and methodology, Supervision, visualization and writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the authors upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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