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Reciprocal stream–riparian fluxes: effects of distinct exposure patterns on litter decomposition

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Abstract Resource fluxes at the stream–riparian interface are a vital contributor to both systems' energy budgets. The effect of distinct litter exposure patterns—direction of the riparia–stream movement and duration of exposure at each habitat—however, remains to be elucidated. In this field experiment, oak leaves in fine and coarse mesh bags were either exposed to a stream-to-riparia or riparia-to-stream movement sequence for distinct periods (2:6, 4:4, or 6:2 weeks). After 8 weeks, ash-free mass loss, microbial activity, and fungal biomass were compared in leaves undergoing inverse movement sequences (e.g., 2-week exposure to the riparian area at the beginning vs. end of the colonization period). Mass loss in coarse mesh bags was negatively affected when leaves were previously exposed to a short (2 weeks) terrestrial pre-conditioning period, despite higher microbial activity and fungal biomass, when compared to the inverse movement. This effect on mass loss was neutralized by longer terrestrial exposures that likely allowed for a more thorough conditioning of the leaves, through extended leaching and terrestrial microbial colonization. Our results suggest that terrestrial pre-conditioning periods of < 2 weeks lead to litter-quality legacy effects in tough leaves, to which aquatic communities respond through lower substrate degradation efficiency, hindering stream decomposition. Contrastingly, oak aquatic pre-conditioning, regardless of duration, provides riparian communities with a high-quality resource, promoting litter processing through grazing behavior. As climate-induced hydrological shifts may result in altered provision/quality of detritus subsidies at the stream–riparia interface, we suggest that assessments of decomposition dynamics should consider the entire litter conditioning history.

Keywords Hydrological oscillations · Legacy effects · Litter conditioning · Microbial-mediated decomposition · Pre-conditioning

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Introduction

Streams and riparian areas are meta-ecosystems (Loreau et al. 2003), interconnected by bilateral spatial fluxes of energy, materials, and organisms (Ballinger and Lake 2006; Lafage et al. 2019). In small forested streams, where the closed canopy limits light and primary production, subsidies from the riparian area are essential to stream productivity (Gomi et al.

2002), amounting to 80–95% of total organic carbon influx (Naiman et al. 2005). Multiple studies in the last decades have analyzed the provision of riparian particulate organic matter to streams (Richardson et al. 2010; Hart et al. 2013; Marks 2019); however, these have mostly focused on the dominant direct vertical fall, neglecting lateral connectivity. In streams experiencing flow intermittency, as occurs globally in the majority of headwaters (Messager et al. 2021), this pathway could be particularly relevant, as the deposition, retention, and displacement of leaf litter is highly modulated by heterogeneous flow contraction and resumption (Datry et al. 2018; Barthélémy et al. 2022).

Cross-ecosystem litter fluxes between the terrestrial and aquatic systems may result in partial decomposition within one environment before displacement to another. Decomposition dynamics in terrestrial and aquatic systems share important similarities regarding biotic and abiotic drivers of decomposition (García-Palacios et al. 2016, 2021; Yue et al. 2018), but experience very distinct temporal and spatial scales (Wagener et al. 1998; Treplin and Zimmer 2012), with numerous diverse microbial communities developing as a result of environmental differences between the two habitats, ultimately altering litter decomposition dynamics (Guo et al. 2022). As a result, different litter exposure patterns, defined as the sequence of movement between the riparian area and the stream, and duration of exposure at each habitat, may affect the global decomposition process (Abelho and Descals 2019). The effects of distinct litter exposure patterns remain mostly unexplored, and the limited number of studies available shows that a terrestrial pre-conditioning period may determine important litter-quality changes [e.g., decline in carbon content and increase in lignin (del Campo et al. 2021b) or increase in nitrogen content (Kochi et al. 2010)]. This is believed to be the result of abiotic decomposition processes such as photodegradation (Langhans et al. 2008). These changes, determined a priori by intrinsic initial litter quality (Abelho and Descals 2019) and environmental conditions of the riparian soil (del Campo et al. 2021b), may result in slower decomposition rates by the recipient aquatic communities (Dieter et al. 2013). The effects of an aquatic pre-exposure to the subsequent terrestrial litter degradation are even less explored; aquatic conditioning may stimulate recipient terrestrial microbial colonization and decomposition (Riedl et al. 2013), while increasing litter susceptibility to subsequent photodegradation (Amado et al. 2007). This effect seems to be ruled by aquatic exposure duration, as longer periods may lead to over-conditioning, reducing leaf litter quality (Treplin and Zimmer 2012). Different exposure patterns may therefore result in poorly defined legacy effects (Simões et al. 2021, 2022), affecting the global leaf litter decomposition process (Fellman et al. 2013).

This dearth of studies addressing litter decomposition at the aquatic–terrestrial interface has been previously recognized (García-Palacios et al. 2021). This study attempts to provide insights into this knowledge gap by reporting on a field-manipulative experiment aimed at analyzing how decomposition dynamics are affected by distinct litter exposure patterns, by altering the movement sequence and duration of exposure to the riparian area or the streambed. Oak (*Quercus robur L.*) leaves, enclosed in fine and coarse mesh bags, were either immersed in a stream or placed in the neighboring riparian floor. After two, four, or six weeks, leaves were moved to the alternative habitat, for a total colonization length period of eight weeks. At the end of the experiment, each pair of treatments with inverse movement sequences (e.g., 2 weeks in the riparian area at the beginning versus at the end of the colonization period) was compared in terms of ash-free dry mass loss, microbial activity, and fungal biomass, for fine and coarse mesh bags. It was hypothesized that litter exposed to a terrestrial pre-conditioning period would present lower mass loss and associated microbial parameters than the inverse treatment, due to increased litter recalcitrance as a result of terrestrial pre-exposure (Abelho and Descals 2019). On the other hand, a stream-to-riparian exposure should result in higher mass loss at the end of eight weeks, mainly due to increased microbial activity and fungal biomass during the aquatic colonization period (Langhans et al. 2008), that could potentially enhance leaf litter quality to the recipient terrestrial invertebrate community, stimulating colonization and consumption in coarse mesh bags.

Materials and methods

Study site

The study was carried out during Spring 2019 in Ribeira do Candal in Lousã (Central Portugal,

40°04′48.9″ N 8°12′11.1″ W), a second-order stream that runs through a mixed deciduous forest, mostly composed of *Quercus robur* and *Castanea sativa* Mill. trees. The studied stream section was approximately 2 m wide and 26 cm deep with a mean flow of 0.50 ± 0.09 m s^{-1}. Oxygen concentration was 10.80 ± 0.40 mg L^{-1} (WTW Oxi 3310, Germany), pH was 6.4 ± 0.1 (WTW pH 3110, Germany), and conductivity was 198.00 ± 32.30 μS (Hanna HI 98192, Portugal). Throughout the experiment, no precipitation was recorded at the study site; mean soil and water temperature were 9.80 ± 0.33 °C and 8.80 ± 0.40 °C, respectively (Hobo Pendant UA-001-08; Onset Computer Corp., Cape Cod, MA, USA).

Experimental design

Quercus robur leaves, collected after abscission and air-dried in the dark at room temperature, were enclosed (2.00 ± 0.15 g) in fine (FM; 10×12 cm, 0.5 mm mesh) and coarse (CM; 10×12 cm, 10 mm mesh) mesh bags. Half of the bags of each mesh was immersed in the stream and the other half was deployed in the immediately adjacent riparian area, fixed with metal stakes, and mixed in the surface with dead fallen leaves. At the beginning of the experiment, four extra bags were immediately brought back to the laboratory, oven-dried (60 °C, 48 h), and weighed to account for mass loss due to handling.

The positioning of the bags was manually manipulated according to the different exposure patterns ($n = 4$; Fig. 1); treatment codes refer to total duration of exposure to the riparian (R) habitat in weeks (2, 4, or 6) and the timing of riparian exposure with regard to the colonization period (i: initial; f: final). All bags remained in each environment for a minimum of 2 weeks. For comparison purposes, two additional groups of eight bags (4 FM + 4 CM) were left for the entire colonization period (eight weeks) either in the stream channel (stream control, SC) or in the riparian area (riparian control, RC).

After a conditioning period of eight weeks, bags from each treatment were individually placed in a plastic zip-lock bag and transported to the laboratory. Bags sampled at the stream or riparian area were rinsed with distilled water or gently cleaned with a brush, respectively, over a 500-μm mesh sieve to remove excess sediment. From each bag, 10 leaf disks were cut using a cork borer (10 mm Ø); half were
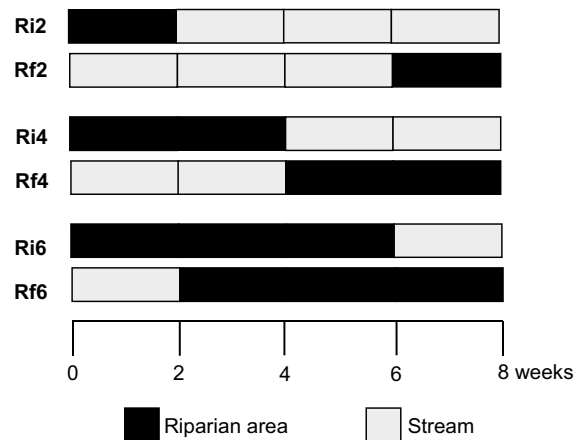

Fig. 1 Schematic representation of the different treatments. Oak leaves, enclosed in fine and coarse mesh bags, were initially placed either on the riparian area (black) or immersed in the stream (gray). After 2, 4, or 6 weeks, they were manually transported to the alternative habitat to ensure distinct exposure patterns—movement sequence and duration of exposure at each habitat. Treatment codes refer to: 2, 4, 6: total exposure to the riparian (R) habitat (weeks); i/f: timing of riparian exposure with regard to the colonization period (initial/final)

immediately used to account for microbial activity estimation and the second half was frozen (-4 °C) until fungal biomass assessment. All leaf material (disks + remaining litter) from each replicate was then dried, weighed, ashed (500 °C, 5 h), and re-weighed to obtain ash-free dry mass (AFDM) loss.

Microbial activity

Microbial activity was assessed by fluorescein diacetate (FDA) hydrolysis (Datry et al. 2011; Simões et al. 2022). Leaf disks were placed in sterile glass vials with 3 ml of phosphate buffer (pH = 7.6) and 100 μl of FDA stock solution (0.02 g FDA in 10 ml acetone). Tubes were shaken and incubated in the dark for 60–100 min until a fluorescent green color appeared, at which point the reaction was stopped with 3 ml of acetone. Absorbance was measured using a spectrophotometer (6400 Jenway, Dunmow, Essex, UK; 490 nm). Leaf disks were dried (60 °C, 48 h) and weighed. A standard curve was obtained from a sodium fluorescein salt stock solution (2000 μg of fluorescein in 100 ml of phosphate buffer), and microbial activity was expressed as μmol FDA h^{-1} g^{-1} AFDM.

Fungal biomass

Frozen leaf disks were lyophilized for 24 h (lyophilizer CHRIST, ALPHA 1–2/LD Plus, Osterode am Harz, Germany) and weighed. Ergosterol was extracted in methanol by microwave exposure, separated by pentane (Canhoto et al. 2013), and quantified through high-performance liquid chromatography (HPLC; Shimadzu Prominence UFLC, Kyoto, Japan; HPLC C18 column: Mediterranean sea18, 250×4.6 mm, 5 µm particle size; Teknokroma). Ergosterol concentration was converted into fungal biomass assuming 5.5 µg of ergosterol per milligram of fungal dry mass (Gessner and Chauvet 1993). Results were expressed as mg fungal biomass g^{-1} AFDM.

Statistical analysis

Ash-free dry mass loss, microbial activity, and fungal biomass after eight weeks were each analyzed using a two-way Analysis of Variance (ANOVA), with litter movement sequence and mesh (fine versus coarse) as categorical variables. When significant ($p < 0.05$) statistical differences were found in the interaction between both variables, planned-comparisons were performed to compare only inverse treatments [e.g., 2 weeks of riparian exposure at the beginning (Ri2) versus at the end of the colonization period (Rf2)] for each mesh. Normality and homoscedasticity assumptions were met. Statistical analyses were performed with Statistica 7 software (StatSoft, Tulsa, USA). Results from the stream and riparian controls (SC and RC) were not included in the statistical analysis as they were only used to guide the interpretation of the results.

Results

Ash-free dry mass loss

When litter was exposed to the riparian area for 2 weeks, AFDM was affected by litter movement sequence (two-way ANOVA, $F_{1,12} = 16.83$, $p < 0.001$) and mesh size ($F_{1,12} = 141.51$, $p < 0.001$), with a significant interaction between both factors ($F_{1,12} = 9.031$, $p < 0.001$; Fig. 2). AFDM loss showed no differences between treatments for fine mesh bags (planned-comparisons, $p = 0.45$); in coarse mesh bags, AFDM loss was lower when litter was exposed to the riparian area at the beginning of the colonization period. In both Ri2 and Rf2, higher AFDM loss was observed in coarse than fine mesh bags (planned-comparisons, $p < 0.001$).

Following a four-week exposure to the riparian area, AFDM was not affected by litter movement sequence (two-way ANOVA, $F_{1,12} = 0.39$, $p = 0.54$), but varied with mesh size ($F_{1,12} = 99.25$, $p < 0.001$); the interaction between both factors was significant ($F_{1,12} = 9.89$, $p = 0.008$). In both treatments, AFDM loss was higher in coarse than fine mesh bags

Fig. 2 Oak ash-free dry mass (AFDM) loss (mean ± SE) for fine (FM) and coarse (CM) mesh bags, exposed to two, four, or six weeks of riparian (R) exposure at the beginning (i) or at the end (f) of the colonization period. (*) represents significant differences between inverse litter movements (Ri *vs.* Rf), for each exposure duration
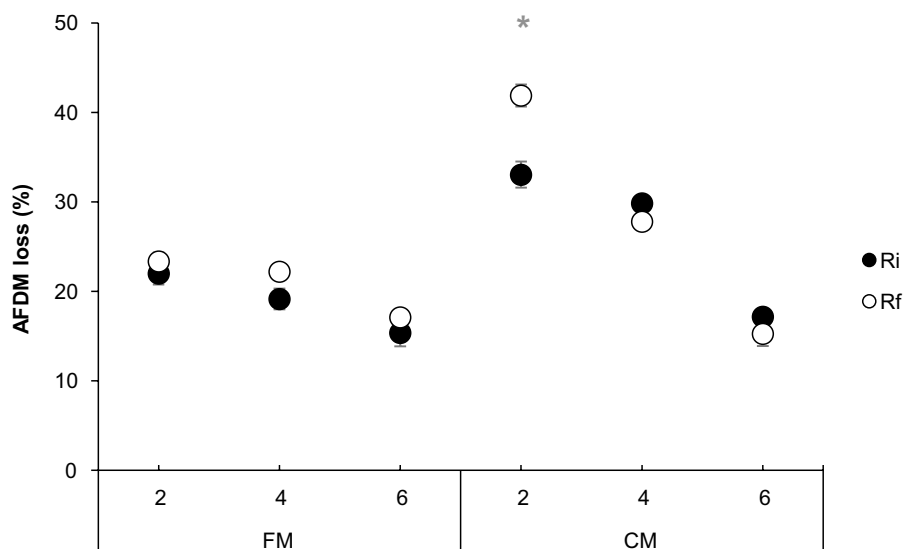
(planned-comparisons, $p < 0.001$). Similarly, after a six-week exposure to the riparian area, ash-free dry mass loss was not affected by litter movement sequence (two-way ANOVA, $F_{1,12} = 0.93$, $p = 0.35$) or mesh size ($F_{1,12} = 0.72$, $p = 0.41$), whereas the interaction between both factors was significant ($F_{1,12} = 6.15$, $p = 0.03$); no significant differences were found by planned-comparisons.

Oak leaves exposed for eight weeks in the stream channel (SC) presented $27.90\% \pm 1.53$ and $38.81\% \pm 0.44$ AFDM loss in fine and coarse mesh bags, respectively; oak leaves exposed for eight weeks in the riparian area (RC) showed $10.34\% \pm 1.41$ and $15.29\% \pm 1.53$ AFDM loss in fine and coarse mesh bags, respectively.

Microbial activity

Microbial activity was consistently higher in litter exposed to the riparian-to-stream movement sequence (two-way ANOVA, $p < 0.001$) (Fig. 3). When the riparian exposure lasted two or six weeks, mesh had no effect on microbial activity ($F_{1,8} = 1.16$, $p = 0.31$; $F_{1,8} = 1.43$, $p = 0.27$, respectively) and the interaction between factors was not significant ($F_{1,8} = 0.92$, $p = 0.37$; $F_{1,8} = 1.54$, $p = 0.25$, respectively). After an exposure of four weeks, there were a significant effect of mesh ($F_{1,12} = 54.80$, $p < 0.001$) and a significant interaction between both factors ($F_{1,12} = 13.83$, $p = 0.005$). Differences between mesh

sizes (CM > FM) occurred only for the Ri4 treatment (planned-comparisons, $p < 0.001$).

Fungal biomass

Fungal biomass, measured by ergosterol, was only affected by movement sequence following a two-week exposure to the riparian area (two-way ANOVA, $F_{1,8} = 20.10$, $p = 0.002$), with higher fungal biomass when such exposure occurred at the beginning of the colonization process (Ri2). For the other exposure durations (i.e., 4 and 6 weeks), litter movement sequence was not significant (two-way ANOVAs, $F_{1,8} = 0.44$, $p = 0.44$, and $F_{1,8} = 0.09$, $p = 0.78$, respectively). For all riparian exposure durations tested (i.e., 2, 4, or 6 weeks), fungal biomass was not affected by mesh ($F_{1,8} = 0.12$, $p = 0.74$; $F_{1,8} = 0.23$, $p = 0.65$; and $F_{1,8} = 1.06$, $p = 0.33$, respectively), and the interaction between both treatments was not significant ($F_{1,8} = 1.81$, $p = 0.22$; $F_{1,8} = 4.44$, $p = 0.07$; and $F_{1,8} = 0.40$, $p = 0.54$, respectively; Fig. 4).

Fungal biomass following eight weeks in the stream (SC) was 71.88 ± 5.08 mg fungal biomass g^{-1} AFDM in fine mesh bags and 57.94 ± 7.59 mg g^{-1} AFDM in coarse mesh bags; on the other hand, after eight weeks in the riparian area (RC), fungal biomass varied between 10.13 ± 0.45 mg g^{-1} AFDM in fine mesh bags and 9.40 ± 0.51 mg g^{-1} AFDM in coarse mesh bags.

Fig. 3 Microbial activity (mean $\pm$ SE) from oak leaves, enclosed in fine (FM) or coarse (CM) mesh bags, exposed to two, four, or six weeks of riparian (R) exposure at the beginning (i) or at the end (f) of the colonization period. (*) represents significant differences between inverse litter movements (Ri vs. Rf), for each exposure duration
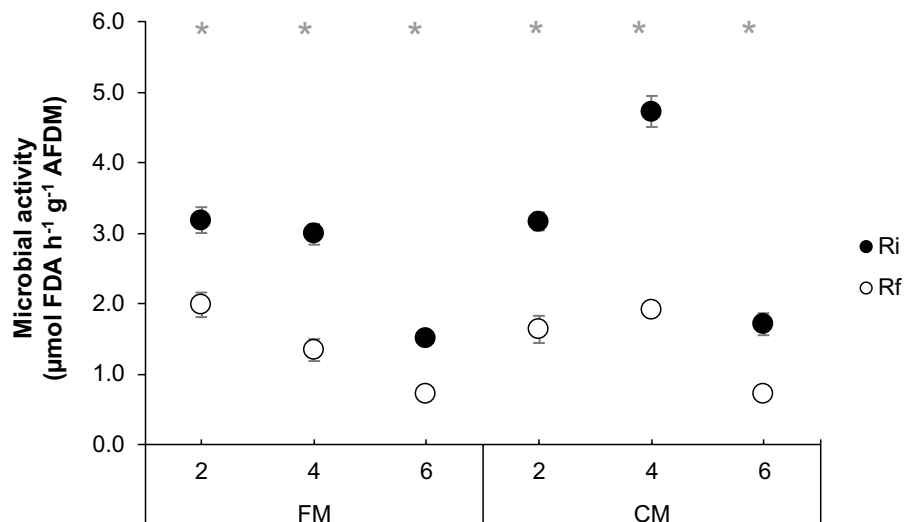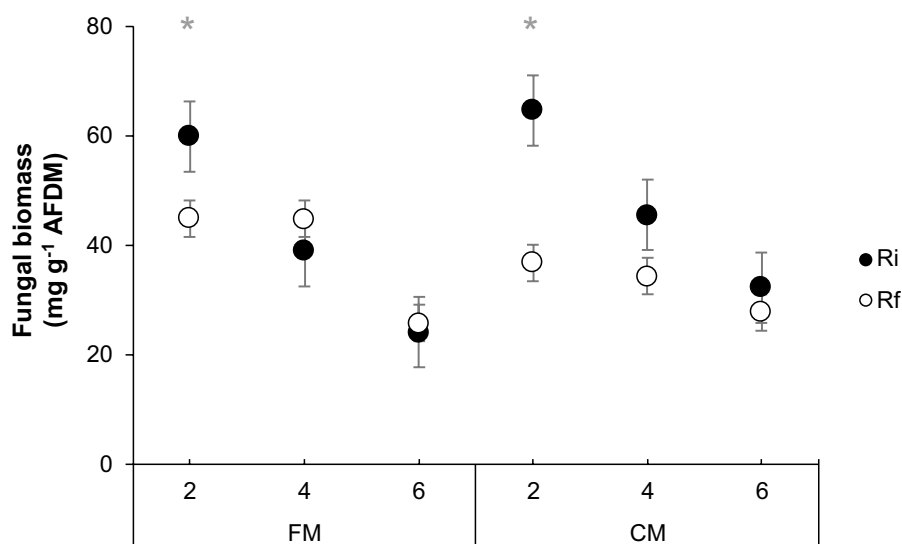
Fig. 4 Fungal biomass (mean ± SE) associated with oak leaves enclosed in fine (FM) or coarse (CM) mesh bags, exposed to two, four, or six weeks of riparian (R) exposure at the beginning (i) or at the end (f) of the colonization period. (*) represents significant differences between inverse litter movements (Ri vs. Rf), for each exposure duration

Discussion

Oak leaf mass loss and associated parameters after eight weeks were highest in litter continuously exposed to the stream, lowest in litter exclusively exposed to the riparian area, and intermediate in litter subjected to a combination of riparian/stream exposure. These trends have been consistently observed in studies comparing submerged with dry litter conditions (Treplin and Zimmer 2012; Yue et al. 2018; Viza et al. 2022; Costello et al. 2022), and in leaves subjected to a riparian-to-stream pathway (Abelho and Descals 2019), this is, to our knowledge, the first study to also point to this effect in stream-to-riparia litter movements. Our results confirm that litter decomposition dynamics are dependent on exposure patterns (i.e., movement sequence and duration of exposure at each habitat): While a short terrestrial pre-conditioning period resulted in a negative legacy effect for recipient aquatic communities, litter extensively conditioned in-stream seems to promote litter processing through foraging of fungi by terrestrial invertebrates.

In partial agreement with our first hypothesis, oak mass loss was significantly affected by litter movement sequence, with a short (2 weeks) riparian exposure leading to lower mass loss in coarse mesh bags transported from the riparia to the stream, compared to the inverse movement. During our study period, terrestrial low temperatures, humidity, and limited precipitation may have hindered leaching, microbial

colonization, and terrestrial invertebrates' processing (Langhans et al. 2008; Treplin and Zimmer 2012; Annala et al. 2022; Costello et al. 2022). Photodegradation was also likely limited by the local closed canopy, inhibiting the loss of labile organic matter (Datry et al. 2018; Abelho and Descals 2019; del Campo et al. 2021b). This negative impact of a terrestrial pre-conditioning period seems to have prompted legacy effects on the recipient aquatic microbial communities. In fact, higher leaf-associated fungal biomass and microbial activity at the end of eight weeks were not paralleled by higher mass loss in fine or coarse mesh bags. In accordance with del Campo et al. (2021b), this may be related to a higher energetic investment in enzyme production that does not translate into higher decomposition of terrestrially pre-conditioned oak leaves (i.e., lower degradative efficiency). Whether the increase in fungal biomass occurred at the expense of fungal reproductive effort was not confirmed but is plausible, considering previous studies with litter pre-exposed to terrestrial conditions (Abelho and Descals 2019). If confirmed, the presence of high inputs of leaves terrestrially pre-conditioned for short periods (< 2 weeks) may limit—or at least delay—spore production and dispersal ability of aquatic hyphomycetes, limiting fungal-mediated leaf degradation in local and downstream reaches.

Notwithstanding, this effect of movement sequence on mass loss only occurred in coarse mesh bags. A short (i.e., 2 weeks) pre-conditioning terrestrial period followed by stream exposure contributed to a

higher fungal biomass; although this is usually determinant of high leaf consumers' activity (Canhoto and Graça 2008), in our case it was likely not enough to surpass or compensate oak's inherent low leaf quality (e.g., thick cuticle, high lignin content, and leaf toughness) (Gulis et al. 2006; Jabiol and Chauvet 2012; Robbins et al. 2023), resulting in lower detritivore consumption. Likely, the potentially delayed leaching and microbial conditioning that occurred during the terrestrial pre-conditioning period may have delayed and restricted the optimal time window for aquatic detritivore activity. The lower feeding plasticity of aquatic (versus terrestrial) invertebrates (Rota et al. 2022) may have determined their preferential use of higher quality substrata, abundantly present in the stream (e.g., chestnut; pers. observation).

An aquatic-to-riparia movement sequence likely allowed a quick aquatic leaf processing by invertebrates, supported by the fast establishment of a mature aquatic hyphomycete community (Gessner et al. 1993; Gonçalves et al. 2016), which may also have then stimulated terrestrial invertebrate–mediated degradation (Tordoff et al. 2008). Detritivores are increasingly being recognized as key control factors for terrestrial decomposition (García-Palacios et al. 2021), and grazers (i.e., collembola) were abundant in the leaf samples of this treatment (pers. observation). This group shows preferential grazing activity on fungal hyphae, justifying the decreased fungal biomass and, therefore, microbial activity (A'Bear et al. 2012), and accelerating decomposition (Martins et al. 2013; Nascimento et al. 2019). Although microbial activity and fungal biomass were lower in Rf2 than Ri2 in both FM and CM bags, differences were more pronounced in the latter, suggesting a strong contribution of detritivores.

Mass loss was not affected by movement sequence when exposed to longer periods of riparian exposure (i.e., R4 and R6), contrary to our hypothesis. On leaves subjected to the riparia-to-stream movement, their intrinsic lower quality seems to be overruled by longer (>2 weeks) microbial conditioning periods, increasing detritus quality. Nutrient leaching from leaves is known to constitute an external supply of nutrients to terrestrial microbes, facilitating their extracellular enzyme production (Berg and McClaugherty 2020; Costello et al. 2022). Once in the stream, colonizing aquatic hyphomycete (AH) species may have to compete with established,

more developed terrestrial microbial communities. Although litter-associated terrestrial fungi were thought to become inactive upon submersion (Krauss et al. 2011), recent reports show that some may be able to maintain growth in submerged conditions (Hayer et al. 2022). Their contribution to decomposition under such environments is still unclear (Graça and Ferreira 1995; Nikolcheva et al. 2005) but should not be ruled out (Kuehn 2016; Liu et al. 2023). As potential antagonistic interspecific interactions occur at a metabolic cost (Hiscox et al. 2015), this may explain a higher microbial activity (but similar fungal biomass) found in leaves initially maintained for longer periods in the riparian area. Even so, similar decomposition at the end of eight weeks suggests that AH species are able to out-compete established terrestrial microbial communities and proceed with the decomposition process (Bärlocher 1992; Nikolcheva et al. 2003). On leaves subjected to the opposing movement (stream-to-riparia), early aquatic conditioning is likely to have triggered immediate decomposition. Regardless of exposure duration, this may have facilitated subsequent detritivore terrestrial degradation. It is, however, interesting to notice that no effect of mesh was found after a six-week exposure to the riparian area (Ri6 vs. Rf6), which may suggest that such longer periods of terrestrial exposure may buffer the effect of litter movement sequence across environments for the detritivore community.

The present results were likely modulated by the leaf species and environmental conditions; litter species-specific responses to distinct exposure patterns have been suggested in previous works (Dieter et al. 2013; Abelho and Descals 2019; Gruppuso et al. 2023). Even though the recalcitrance of lignin-rich and N-poor substrata can be reduced by terrestrial exposure (through photodegradation decomposing lignin and increasing nitrogen content) (Pu et al. 2014), in our work the dense canopy and the abundance of litter on the ground seems to have clearly limited light exposure. Whether the effects promoted by short (in this case, 2 weeks) pre-conditioning periods on oak applies to the spectrum of litter quality available in a temperate forested stream remains to be confirmed.

The results presented here evidence the need to recognize the entire conditioning history when considering processing dynamics, as litter initially deposited in a particular environment will be affected by

specific abiotic and biotic characteristics, with potential important consequences for posterior decomposition at the recipient system—a result of streams' lateral connectivity. Although cross-ecosystem research focuses mostly on riparian subsidies to the channel, an attempt was made here to consider and reinforce the importance of bilateral movements. If confirmed, our results suggest that shifts from perennial to intermittent flow regimes, or altered timing and duration of the dry periods, may result in altered provision of detritus subsidies at the stream–riparia interface—a mostly unexplored consequence of climate change on the natural flow regimes of streams and rivers (del Campo et al. 2021a; Jonsson and Sponseller 2021).

Data availability The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no relevant financial or non-financial interests to disclose.

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