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Wildfires alter stream ecosystem functioning through effects on leaf litter

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Abstract

Background Wildfires have strong impacts on terrestrial and aquatic ecosystems, whose frequency, severity, and intensity are increasing with climate change. Moreover, the expansion of exotic monoculture plantations, such as those of eucalypts, increases this risk. When wildfires do not cause the disappearance of riparian vegetation, they still imply the fall of leaf litter exposed to the fire (i.e., crown scorch), which consequences for ecosystems are unknown.

Experimental design To explore how these leaf litter inputs may affect stream ecosystem functioning, we conducted a microcosm experiment where we quantified the decomposition of leaf litter from three tree species (alder, oak, and eucalypt) under two conditions (control litter simulating natural entries and litter subjected to 150 °C for 3 h mimicking exposure to fire). We also examined the interaction between this factor and a temperature rise (which is often associated to the loss of riparian vegetation caused by the wildfire) by manipulating water temperature (10, 12.5, and 15 °C). Finally, we explored the effects of these variables on the growth of a common detritivore, the caddisfly *Sericostoma pyrenaicum*.

Results Control alder presented the highest decomposition rates, which were notably reduced due to fire exposure. On the contrary, eucalypt litter decomposition was even slower than that of oak and hardly showed any effect derived from fire exposure. The different leaf litter types determined detritivore growth, to a greater extent than variation related to warming, which generally had negligible effects.

Conclusions Our study shows the negative effects of wildfires on stream ecosystem functioning even when they only involve brief exposure of leaf litter to the fire. Effects are greater on the most palatable native species, which represents the highest quality input in streams of the study area. Our results highlight the importance of protecting riparian forests, especially those composed of native species, against wildfires.

Keywords Leaf litter, Decomposition, Detritivores, Aquatic hyphomycetes, Plantations, Eucalyptus

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Resumen

Antecedentes Los incendios forestales suponen fuertes impactos sobre los ecosistemas terrestres y acuáticos cuya frecuencia, severidad e intensidad están aumentando con el cambio climático. Además, las grandes extensiones de monocultivos de especies exóticas, tales como el eucalipto, conllevan un incremento de este riesgo. Cuando los incendios no implican la desaparición completa de la vegetación ribereña, generan la caída de hojarasca expuesta al fuego, con consecuencias desconocidas para los ecosistemas.

Diseño experimental Para conocer cómo afecta la entrada de esta hojarasca al funcionamiento del ecosistema fluvial se realizó un experimento de microcosmos, comparando la descomposición de hojarasca de tres especies arbóreas (aliso, roble y eucalipto) bajo dos condiciones (hojarasca control representando entradas naturales, y hojarasca sometida a 150 °C durante 3 h simulando la exposición al fuego). Examinamos además la interacción de este factor con el calentamiento del agua (atribuido a la pérdida de vegetación riparia por el incendio), manipulando la temperatura (10, 12.5 y 15 °C). Finalmente, analizamos los efectos de estas variables sobre el crecimiento de un detritívoro común, el tricóptero *Sericostoma pyrenaicum*.

Resultados El aliso control presentó la mayor tasa de descomposición, que se redujo notablemente con la exposición al fuego. Por el contrario, la hojarasca de eucalipto, cuyo procesamiento fue aún más lento que la del roble, apenas se vio afectado por la exposición al fuego. Los diferentes tipos de hojarasca determinaron el crecimiento de los detritívoros en mayor medida que las variaciones derivadas del calentamiento del agua, que tuvieron efectos por lo general insignificantes.

Conclusiones Nuestro estudio demuestra que los incendios forestales tienen efectos nocivos sobre el funcionamiento del ecosistema fluvial, incluso cuando únicamente implican una breve exposición de la hojarasca al fuego. Los efectos fueron mayores sobre la especie nativa con hojarasca más palatable, que además constituye el aporte de mayor calidad en los ríos del área de estudio. Nuestros resultados resaltan la importancia de proteger los bosques ribereños, especialmente los compuestos por especies nativas, contra los incendios.

Palabras clave Hojarasca, Descomposición, Detritívoros, Hifomicetos acuáticos, Plantaciones, Eucalipto

Introduction

Wildfires are landscape disturbances with the potential to fundamentally alter the structure and function of forest ecosystems (Flannigan et al. 2009; Pettit and Naiman 2007; Vaz et al. 2015). Each year, fire burns nearly 650 Mha of forests around the globe, and it is expected that their frequency and extent will increase in the near future in association with factors such as climate change (Gergel et al. 2017; IPCC 2018), land abandonment, or afforestation with monocultures of fire-prone species (Moreira et al. 2011; Pausas et al. 2004), such as eucalyptus plantations (Gill 1997). According to climate change predictions, the prevalence of fires will increase due to reduced snowpack, hotter summers, and more vapor pressure deficit that will reduce soil and fuel moisture (Flannigan et al. 2013; Westerling 2016).

The role of wildfires in ecosystem dynamics has attracted considerable attention for extensive biomes such as grasslands and forests (Bowman et al. 2021; Miller et al. 2019). However, less attention has been devoted to other ecosystems such as riparian forests, which can also be affected (Coble et al. 2023; Cunillera-Montcusí et al. 2021; Gomez Isaza et al. 2022). Besides, altered riparian forests have the potential to impact stream ecosystems, particularly headwaters, where

allochthonous leaf litter inputs provide the primary source of energy to the aquatic food web (Vannote et al. 1980; Wallace et al. 1997). Leaf litter is decomposed in the water while its constituent elements are used by microbial decomposers, mainly aquatic hyphomycetes (AHs), and by detritivorous invertebrates (hereafter detritívoros). Thus, this terrestrial material is partly incorporated into the stream food web, and it drives other fundamental stream processes such as nutrient cycling and energy flow (Marks 2019; Swan et al. 2021). Rates of leaf litter decomposition are often used as a tool to assess stream ecosystem functioning and integrity and how these properties are altered by different stressors (Ferreira et al. 2021; Gessner and Chauvet 2002). However, there is little information to date about how instream leaf litter decomposition can be affected by wildfires occurring in their surrounding forest (Gama et al. 2007).

Wildfires can produce the total loss of the riparian forest, thus exposing streams to greater solar radiation and, as a result, increasing their temperature (Veraverbeke et al. 2012), affecting soil characteristics (Granged et al. 2011), and eliminating allochthonous leaf litter inputs (Bixby et al. 2015; Warren et al. 2022). This, in turn, can result in decreased detritivore numbers that

cascade into alterations at higher trophic levels (Mellon et al. 2008), with repercussions downstream or for the whole watershed (Piccolo and Wipfli 2002). However, in some cases, fires do not completely eliminate the forest, causing heat damage to the foliage—the so-called crown scorch (Varner et al. 2021)—and driving inputs of partially burnt leaf litter to the stream with potential effects on their decomposition and decomposer assemblages. It is known that, when leaf litter is subjected to high temperatures associated to heat waves ($\approx 40\text{ }^{\circ}\text{C}$), which can generate foliar damage (Still et al. 2023), nutrient leaching is accelerated once submerged and leaf litter quality is reduced, decreasing decomposition and, ultimately, the growth of detritivores (Pérez et al. 2021b). During wildfires, many of the fire-exposed leaves can be subjected to much higher temperatures (60–150 $^{\circ}\text{C}$), resulting in severe effects on fire-exposed leaves (Lodge et al. 2018; Manzello 2020). Consequently, this may have potentially strong but unknown effects on leaf litter decomposition.

Moreover, the magnitude and recurrence of wildfires increase due to the transformation of native forests into monoculture plantations (Heilmayr et al. 2016; Whitney et al. 2015). For example, *Eucalyptus* spp. are fast-growing evergreen species frequently planted for paper production (Ferreira et al. 2006; Graça et al. 2002) and highly flammable (Gill 1997; Jenkins et al. 2016). In general, eucalypt leaf litter inputs to streams differ in timing, quantity, and quality from those of native trees (Pozo et al. 1998), and eucalypt leaf litter decomposes more slowly and has lower quality than that of many native species. Its lower quality is due to lower N and P contents (Ferreira et al. 2006), higher secondary compound contents including oils and polyphenols, and a waxy cuticle, all of which hinder microbial colonization and degradation (Graça et al. 2002) and affects decomposers and ecosystem functioning (Canhoto and Graça 1996; Larrañaga et al. 2021; Pérez et al. 2021c).

Here, we examined the above issues through a microcosm experiment, where we subjected leaf litter of two native species differing in leaf quality as well as the exotic eucalypt, to temperatures simulating those of a wildfire. We examined the decomposition of this leaf litter compared to control leaf litter not subjected to high temperatures, because decomposition rate is a key functional metric frequently used to measure stream ecosystem integrity (Ferreira et al. 2021; Pérez et al. 2011). We predicted that (i) fire-exposed leaf litter would decompose more slowly than control leaf litter, because of alterations in their structural and chemical characteristics such as toughness, specific leaf area, and nutrient concentration (as shown for leaf litter subjected to heat waves; Pérez

et al. 2021b). However, we expected that (ii) changes in leaf quality and hence in decomposition would not be identical for different species, being more marked for leaf litter of higher quality, as shown for other impacts (Cornejo et al. 2020). Finally, we manipulated water temperature during the experiment to explore any interaction between wildfire effects on leaf litter and water warming associated to the loss of riparian vegetation, predicting that (iii) higher temperatures would accelerate the decomposition of control leaf litter more markedly than that of burnt leaf litter, due to the greater activity of microbial decomposers and detritivores in the former.

Material and methods

Leaf litter

We collected leaf litter and detritivores from the Agüera stream catchment, which is located in northern Spain (43.21° N, 3.27° W). The climate is humid oceanic, with annual mean precipitation of 1650 mm distributed regularly throughout the year and a mean annual temperature of 11.0 $^{\circ}\text{C}$. The catchment forest is dominated by several native species including *Quercus robur* L. (Fagaceae), *Alnus glutinosa* (L.) Gaertn. (Betulaceae), *Castanea sativa* Mill. (Fagaceae) and *Corylus avellana* L. (Betulaceae). In parts of the catchment, the native forest has been replaced by exotic monocultures of *Eucalyptus globulus* Labill. (Myrtaceae). We selected three species to be used in the experiment: *A. glutinosa* (a native, N-fixing, rapid decomposer; hereafter alder) and *Q. robur* (a native, non-N-fixing, slow decomposer; hereafter oak), both known to be important for stream ecosystem integrity in the study area (Alonso et al. 2022), and *E. globulus* (an exotic, non-N-fixing, slow decomposer; hereafter eucalypt). Leaf litter was collected from the forest floor immediately after natural abscission in the Agüera catchment headwaters (Nov. 2021).

In the laboratory, leaf litter was air dried to constant mass and preserved in dark and stable conditions within cardboard boxes, at laboratory temperature (ca. 20 $^{\circ}\text{C}$) and humidity (ca. 50%). Half of the leaves from each species were subjected to a high-temperature pre-treatment, which represented the occurrence of a wildfire in the near proximity; this consisted of exposing the leaf litter to 150 $^{\circ}\text{C}$ for 3 h within an oven (i.e., fire-exposed leaf litter). The other half of the leaves were kept at air temperature (i.e., control leaf litter). Both sets were cut into pieces of approximately 4 cm² avoiding the basal midrib and weighed to the nearest 0.01 mg using a precision balance. Five subsamples of each leaf litter \times pre-treatment combination were directly dried to estimate remaining humidity and to establish the pre-leaching conditions (see below).

Detritivores

Detritivores used in the experiment were larvae of the cased caddisfly *Sericostoma pyrenaicum* Pictet, 1865 (Trichoptera: Sericostomatidae; hereafter *Sericostoma*), one of the most common leaf litter consumers in streams of the Agüera catchment (Martínez et al. 2016a). In April 2022, larvae of similar size were manually picked from stream leaf litter at one site within the catchment (the Perea stream; 43.296° N, 3.254° W) and transported to the laboratory. Larvae were acclimated in trays with constant aeration and mixed riverbed leaf litter for 72 h, within a controlled-temperature room set at 10 °C (i.e., the lower end of the stream temperature range at the season when detritivores were collected), which simulated stream conditions and minimized evaporation. Detritivores were starved for 48 h prior to starting the experiment.

Leaching

We measured the leaching of soluble compounds in the leaf litter of each species (alder, oak, and eucalypt) subjected to each pre-treatment (control and fire-exposed) and water temperature (10, 12.5, and 15 °C) in 54 microcosms, with 3 replicates per combination of treatments. Five subsamples of each species × pre-treatment combination (i.e., 30 samples) were directly dried (60 °C, 72 h) in order to estimate remaining humidity (% air DM) and to establish the pre-leaching conditions (see below). Microcosms consisted of glass cups (580 mL, 8 cm diameter) that were placed in the controlled-temperature room (10 °C), constantly aerated and with a light:dark regime of 12:12 h. Each microcosm was filled with 400 mL of filtered (100 µm) stream water [dissolved inorganic nitrogen (N), $365.5 \pm 12.1 \mu\text{g L}^{-1}$; soluble reactive phosphorus (P), $3.9 \pm 2.0 \mu\text{g L}^{-1}$] and contained 0.3 g of leaf litter, which was incubated for 72 h, with water replacement after 48 h. The 100-µm filter allowed the entrance of microorganisms and microbial colonization of leaf litter, but microbial decomposition was most likely negligible during this short period (Bärlocher 2020).

After the leaching trial, leaf litter was used to measure leaf toughness [using a penetrometer, which measured the pressure (kPa) necessary to pierce the leaf tissue with a 0.79-mm diameter steel rod (Boyero et al. 2011)] and specific leaf area [SLA; the ratio of leaf area (mm²) to leaf dry mass (DM; mg)]. Then, the pre-leaching and post-leaching samples were oven-dried (60 °C, 72 h), weighed, and divided into two subsamples. The first subsample was incinerated (550 °C, 4 h) and weighed to determine ash-free dry mass (AFDM). The second subsample was ground into powder (1-mm screen) and used

to determine carbon (C) and N concentrations, using a Perkin Elmer series II CHNS/O elemental analyzer (Perkin Elmer, Norwalk, CT, USA), and P concentration, using autoclave-assisted extraction (APHA, 1998). This allowed us to calculate leaching in terms of mass, as proportional leaf mass loss [LML=(post-leaching AFDM – initial AFDM)/initial AFDM], leaf litter C, N, and P pre- and post-leaching composition, and to correct initial leaf litter AFDM data for the decomposition experiment.

Decomposition experiment

The experiment was conducted in 126 microcosms with the same characteristics and under the same conditions described above. Each microcosm contained leaf litter belonging to one of the three species (alder, oak, and eucalypt), subjected to one of the two pretreatments (control and fire-exposed), and under one of the three temperatures (10, 12.5, and 15 °C). For each combination of treatments, there were seven replicate microcosms. Two types of leaf litter were added: free leaf litter (0.9 g), which was accessible to detritivores, and enclosed leaf litter (0.3 g), which was placed within a fine mesh bag (500 µm) and thus inaccessible to detritivores, with the purpose of assessing microbial decomposition.

We first added the leaf litter to microcosms and kept it for 72 h, with water replacement after 48 h, in order to allow the leaching of soluble compounds and initial microbial conditioning (Bärlocher 2020; Findlay and Arsuffi 1989). Detritivores were acclimated to experimental conditions for 5 days (fed ad libitum with mixed litter from the same stream) and then starved for 48 h before the experiment. Detritivore case dimensions were measured (0.001 mm precision) using the ImageJ software (v. 1.46r), and considering their truncated cone shape, the case volume of experimental larvae was estimated (CV, mL). Their initial DM (mg) was estimated using a CV-DM relationship ($\text{DM} = 114.51 \times \text{CV} - 0.37$, $r^2 = 0.98$) obtained from 29 extra larvae (Additional file 1: Fig. S1), which were also used to estimate initial body N and P concentrations (see below).

On day 0 of the experiment, the water was replaced in the microcosms, and detritivores were added. Subsequently, water was replaced weekly, using a 100-µm mesh filter in order to avoid losing leaf litter fragments. The experiment was terminated on day 30, when all the remaining leaf litter material in each microcosm was oven dried (60 °C, 72 h) and weighed to estimate the final DM. Each sample was divided into two subsamples, which were either incinerated (550 °C, 4 h) and used to estimate the final AFDM, or ground and used

to determine the final N and P concentration (as for the leaching trial). Detritivores were starved for 48 h within the microcosms filled with filtered stream water, and then larvae were removed from their cases, freeze-dried, weighed, and ground into powder to determine their final N and P concentrations (using the same methods as for leaf litter samples).

Response variables and data analysis

We assessed our first hypotheses (i.e., that fire exposure would reduce leaf litter quality and hence decomposition), firstly by comparing key leaf litter traits (pre-leaching, leaching, and post-leaching characteristics; humidity, ash, toughness, SLA, C, N, and P) with general linear models (the “*gls*” function on the *nlme* package in R software); we used a model selection procedure based on the Akaike Information Criterion (AIC) to include or exclude the variance function structure *varIdent* as appropriate (e.g., López-Rojo et al. 2022). Pre-leaching traits (remaining humidity, ash, C, N, and P) were compared using species (alder, oak, and eucalypt) and pre-treatment (control and fire-exposed) as fixed factors and considering their interaction. In a similar way, leaching, in terms of mass and post-leaching traits (toughness, SLA, ash, C, N, and P), was examined with species, pre-treatment, and water temperature (10, 12.5, and 15 °C) as fixed factors and considering all their interactions. Significant differences among temperatures or species ($\alpha < 0.05$) were further explored with Tukey tests (the “*ghlt*” function of the *multcomp* package).

Secondly, we assessed the effects of fire exposure on decomposition, which was quantified as leaf litter mass loss: $LML(\text{prop}) = (\text{initial mass} - \text{final mass}) / \text{initial mass}$, where initial mass is the leaching-corrected initial AFDM and final mass is the remaining AFDM after one month of incubation in the microcosms. We assessed variation in total decomposition (from free leaf litter), microbial decomposition (from enclosed leaf litter), and detritivore-mediated decomposition (the difference between the two) among species, pre-treatments, and water temperatures (all fixed factors) and all their interactions, using general linear models with model selection to account for the appropriate *varIdent* structure and Tukey tests, as explained above for leaf litter traits. Total and detritivore-mediated decomposition were standardized by mean detritivore initial DM (6.6 ± 0.3 mg) in order to avoid any possible effect of different detritivore sizes. Finally, we assessed variation in detritivore growth in terms of mass and N and P growth using the same type of model as for decomposition. Initial detritivore elemental

composition was $45.6 \pm 1.0\%$ C, $7.89 \pm 0.21\%$ N, and $0.30 \pm 0.02\%$ P.

Results

Pre-leaching leaf litter traits varied among species, and the concentration of nutrients (N and P) was higher in alder than in the other two species (Additional file 1: Fig. S2 and Table S1). Fire exposure barely affected pre-leaching traits, with negligible effects on ash, N, and P concentrations, and no evident pattern for C concentration (Additional file 1: Fig. S2). In contrast, the remaining humidity significantly decreased with fire exposure in the three species ($p < 0.0001$, Additional file 1: Table S1, Fig. 1). Leaf mass loss due to leaching was determined by water temperature and species, to a much greater extent than fire exposure (Fig. 2, Additional file 1: Table S1). Post-leaching leaf litter traits were not affected by fire exposure (Fig. 2, Additional file 1: Tables S1 and S2), differing mainly among species, with toughness and C concentration being also affected by temperature.

Total, microbial, and detritivore-mediated decomposition were affected by fire exposure, but the effect varied with species (Fig. 3, Table 1), being more evident for alder, lower for oak, and negligible for eucalypt. Water temperature enhanced total and detritivore-mediated decomposition. Most detritivores reached the end of the experiment in the active larval stage (92%), with only ten individuals having pupated, most of them at the higher temperature microcosms (2 at 10 °C, 2 at 12.5 °C, and 6 at 15 °C), and only two dead individuals. After excluding these microcosms from the analyses, detritivore growth decreased with fire exposure in terms of mass and N, which was especially evident for alder and oak (Fig. 4, Table 1). Detritivores fed eucalypt leaf litter did not grow during the experiment, and growth in terms of P was very limited in all cases, with no response observed in relation to fire exposure.

Discussion

The effects of wildfires on freshwater ecosystems encompass direct and indirect complex interactions between aquatic and terrestrial ecosystems (Carvalho et al. 2019; Gomez Isaza et al. 2022; Whitney et al. 2015). Many of these have been scarcely assessed, especially for scenarios where vegetation does not completely disappear and burnt leaf litter remains in the forest (Varner et al. 2021; Warren et al. 2022). In this study, we experimentally addressed how this altered leaf litter would influence the key process of leaf litter decomposition in stream ecosystems and the fitness of detritivorous invertebrates involved in this process. Additionally, we explored

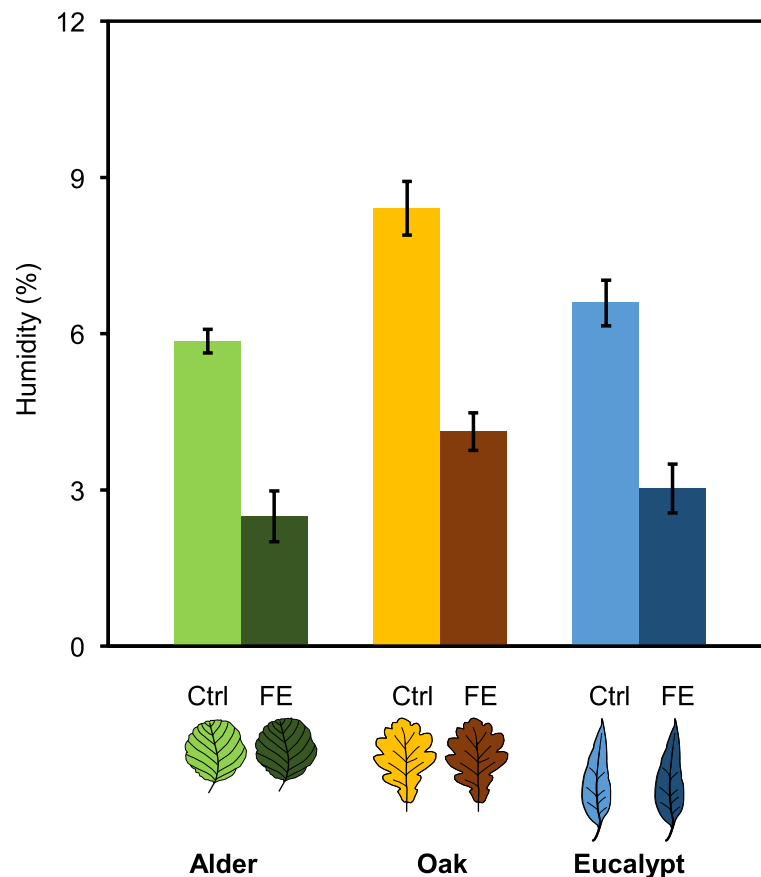


Fig. 1 Mean \pm SE of leaf litter moisture in control (Ctrl) and fire-exposed (FE) leaf litter in terms of remaining humidity (% of pre-leaching air-DM litter) of alder (*Alnus glutinosa*), oak (*Quercus robur*), and eucalypt (*Eucalyptus globulus*)

whether the effects would be intensified by warming, because the loss of canopy cover caused by wildfires exposes the stream channel to direct sunlight (Mahlum et al. 2011) and increases water temperature (Molinero et al. 2012; Warren et al. 2022) long after the wildfire event (Musetta-Lambert et al. 2020).

The decomposition of leaf litter exposed to fire was slower

Unexpectedly, we observed no significant changes in most of the studied leaf litter traits as a result of fire exposure. This agreed with a field study examining the effects of fire exposure on eucalypt leaf litter, which found no changes in litter quality (Gama et al. 2007), but contrasted with another one subjecting leaf litter to heating at a lower temperature than our experiment (40 °C), which found a decrease in leaf litter quality (i.e., increase of nutrient leaching; Pérez et al. 2021b). The only trait consistently affected in our study was remaining humidity, which was reduced approximately by half in the fire exposure treatment, where leaf litter

retained <5% moisture. This change may not seem relevant in the aquatic environment, but it may be for decomposition in soils, where humidity is a limiting factor (Leirós et al. 1999). Importantly, leaf litter conditioning by microbial decomposers (Dieter et al. 2011; Pérez et al. 2012) often starts in the forest floor or dry riverbeds (del Campo et al. 2021; Martínez et al. 2016a, 2015), being a key step for the ulterior utilization of nutrient-poor substrates by aquatic detritivores (Graça 2001; Santonja et al. 2018).

Nevertheless, despite the almost negligible changes observed in leaf chemistry, we found evident and consistent effects of fire exposure on leaf litter decomposition. Even if there were large differences in decomposition rates of the three studied species (which were greatest in the alder and lowest in the exotic eucalypt), as shown elsewhere (Graça et al. 2002; Monroy et al. 2023; Pérez et al. 2014), decomposition rates were consistently lower in leaf litter exposed to fire than in control leaf litter, and this effect was observed for both microbial and

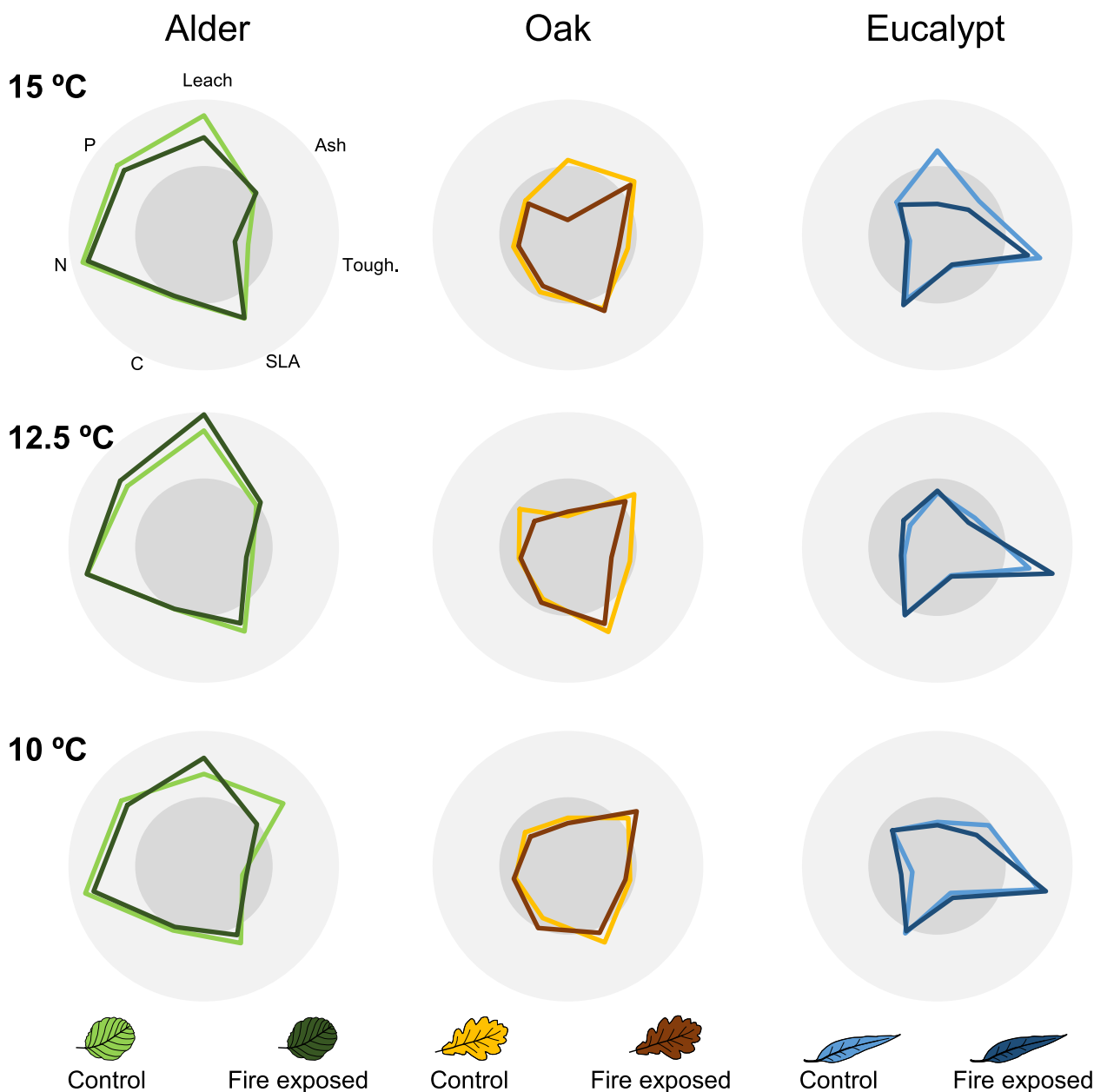


Fig. 2 Radial representation of leaching loss and different post-leaching leaf litter traits (ash concentration, toughness, specific leaf area, and C, N, and P concentrations) at different experimental temperatures for the 6 studied substrates (Additional file 1: Table S2, see Fig. 1) at 3 different temperatures (10, 12.5, and 15 °C) in 54 microcosms. The dark gray circle represents the mean value (μ) of all the considered substrata for each trait, and the light gray circle a twofold increase ($\mu \times 2$)

detrivore-mediated decomposition. While the above-mentioned study by Gama et al. (2007) found no effects of fire exposure on eucalypt leaf litter decomposition in the short term, the study by Pérez et al. (2021b) found results comparable to ours for native species, suggesting that the effects observed here could apply not only to the areas closely affected by the wildfire, but to wider areas.

Wildfire effects on decomposition might be greater in the longer term

The effect of fire exposure was surprisingly less evident for microbial than for detritivore-mediated or total decomposition. In contrast, other studies have found microbial activity to be more strongly boosted by an increase in temperature (Boyer et al. 2011; Follstad Shah

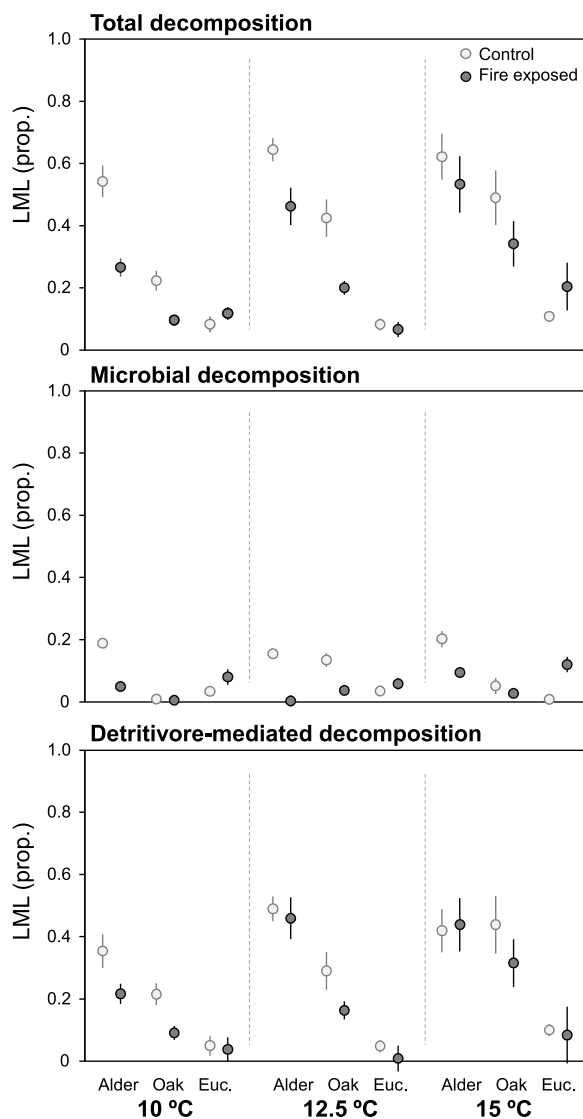


Fig. 3 Total, microbial, and detritivore-mediated leaf litter decomposition of the six studied substrates (see Fig. 1; alder, oak, and eucalypt × control and fire-exposed) at different experimental temperatures (mean ± SE)

et al. 2017). In other microcosm experiments, where a natural detritivore assemblage was lacking as in our experiment (e.g., Pérez et al. 2023), microbial and detritivore activity resulted both similarly stimulated by warming in the short term. These results do not discard other possible responses of microbial decomposers and detritivores in the longer term. For example, after a wildfire, other known long-term legacies for stream ecosystems are the reduction in the quantity and quality of terrestrial organic matter supplies (Bixby et al. 2015; Warren et al. 2022), greater solar radiation (Veraverbeke et al. 2012),

and a sustained increase in nutrient availability over time (Silins et al. 2014). All these changes could bring alterations in the structure and functioning of headwater streams (Jankowski et al. 2021; Pérez et al. 2013) that would make them more similar to mid-low reaches (Martínez et al. 2016b; Vannote et al. 1980) but that cannot be detected in a short-term microcosm experiment like the present one.

Eucalypt effects on stream ecosystems beyond wildfires

We observed that the growth of detritivores was severely limited for larvae-fed leaf litter exposed to fire. We thus observed stronger effects of fire exposure on detritivore fitness than on ecosystem processes, similar to those observed for more moderate heating (Pérez et al. 2021b). The effect was evident for detritivores fed native species (alder and oak), while for those fed eucalyptus, no net growth was observed regardless of the pre-treatment. The high nutritional quality of alder leaf litter is well documented, as well as its key role in stream ecosystem functioning (Alonso et al. 2021; Rubio-Rios et al. 2021), so the highest growth of detritivores fed control alder was expected, especially in terms of N. Eucalypt plantations, on the contrary, provides the stream ecosystem with bad-quality leaf litter inputs, which usually require a long microbial conditioning period to be a suitable food resource for detritivores (Graça et al. 2002; Pérez et al. 2014) and often alter detritivore assemblages (Canhoto et al. 2013; Larrañaga et al. 2014). Gama et al. (2007) found a lower abundance of detritivores in control compared to fire-exposed eucalyptus leaf litter and attributed this difference to the loss of chemical compounds that are known to be detrimental for detritivores (Correa-Araneda et al. 2017; Gama et al. 2014; Graça et al. 2002) during the fire exposure.

Implications for riparian forest management

Previous studies demonstrated that alder leaf litter is a better resource for stream decomposers and detritivores than other leaf litter types, being especially important in terms of N cycling (Rubio-Ríos et al. 2023). Our results confirm this pattern and further show that it continues to be true after fire exposure, with burnt alder leaf litter being a better resource than unaffected eucalypt leaf litter. Given that alder leaf litter is a key resource for stream food webs and for supporting ecosystem functioning (Pérez et al. 2021a), and that alder trees present a high prevalence after wildfires, the presence of this species might mitigate wildfire effects on stream ecosystems (Coble et al. 2023). The benefits of maintaining

Table 1 General linear model results for decomposition (leaf mass loss (LML)) and detritivore performance variables (DF: degrees of freedom of the F; numerator | denominator)

Function	Response variable	Factor	DF	F-value	p-value
Decomposition	Total LML	Temperature (T)	2 102	4.3	0.0154
		Litter species (L)	2 102	158.3	<0.0001
		Fire (F)	1 102	15.2	0.0002
		T×L	4 102	15.1	<0.0001
		T×F	2 102	0.6	0.5419
		L×F	2 102	18.5	<0.0001
		T×L×F	4 102	0.9	0.4852
	Microbial LML	Temperature (T)	2 102	2.5	0.0886
		Litter species (L)	2 102	29.9	<0.0001
		Fire (F)	1 102	29.7	<0.0001
		T×L	4 102	7.3	<0.0001
		T×F	2 102	5.5	0.0053
		L×F	2 102	41.0	<0.0001
		T×L×F	4 102	1.2	0.3344
	Detritivore-mediated LML	Temperature (T)	2 102	10.9	0.0001
Litter species (L)		2 102	71.9	<0.0001	
Fire (F)		1 102	11.6	0.0010	
T×L		4 102	3.9	0.0056	
T×F		2 102	0.4	0.6994	
L×F		2 102	1.7	0.1837	
T×L×F		4 102	0.5	0.7230	
Detritivore performance	Growth	Temperature (T)	2 89	1.3	0.2833
		Litter species (L)	2 89	179.5	<0.0001
		Fire (F)	1 89	55.0	<0.0001
		T×L	4 89	3.2	0.0173
		T×F	2 89	1.4	0.2600
		L×F	2 89	4.1	0.0195
		T×L×F	4 89	1.3	0.2752
	N growth	Temperature (T)	2 89	2.7	0.0725
		Litter species (L)	2 89	124.0	<0.0001
		Fire (F)	1 89	45.4	<0.0001
		T×L	4 89	1.0	0.3893
		T×F	2 89	1.4	0.2417
		L×F	2 89	8.5	0.0004
		T×L×F	4 89	1.1	0.3842
	P growth	Temperature (T)	2 82	12.1	<0.0001
		Litter species (L)	2 82	33.3	<0.0001
		Fire (F)	1 82	2.3	0.1299
		T×L	4 82	1.7	0.1656
T×F		2 82	0.3	0.7208	
L×F		2 82	4.3	0.0170	
T×L×F		4 82	1.8	0.1309	

native buffer strips (sensu Barton and Davies 1993) in the context of exotic plantations (Larrañaga et al. 2021) have been well documented and include positive effects on biodiversity and multiple ecosystem services (Dainese

et al. 2017; Little et al. 2015; Renouf and Harding 2015). In addition to this, and given that monoculture plantations increase the frequency and dangerousness of

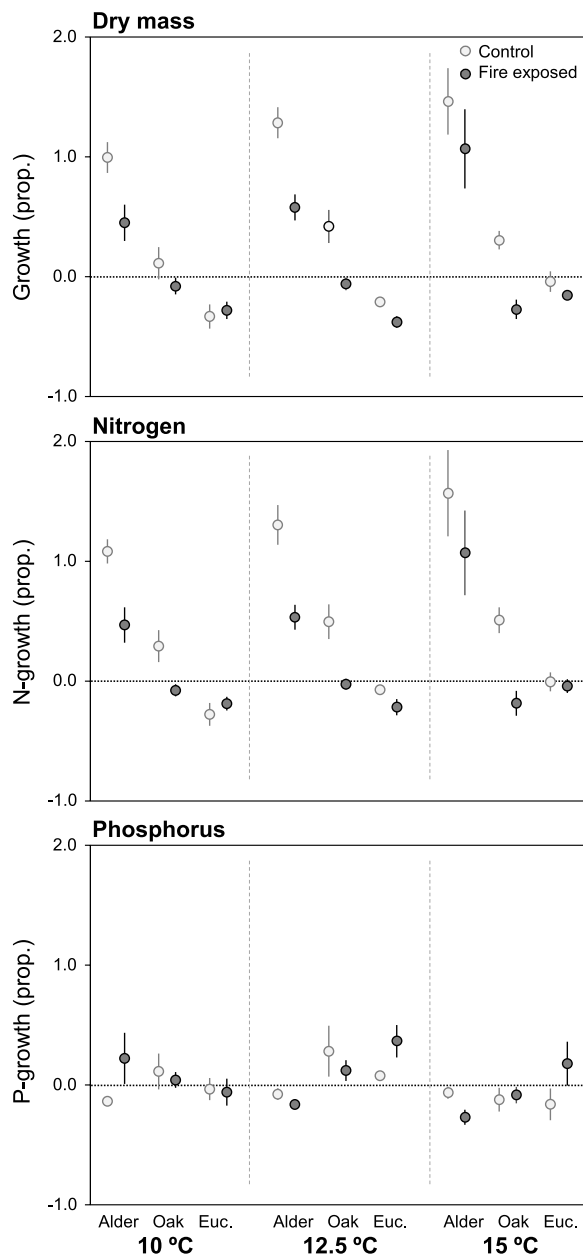


Fig. 4 Detritivore growth in terms of mass, N, and P after being fed with the six studied substrates (see Fig. 1; alder, oak, and eucalypt × control and fire-exposed) at different experimental temperatures (mean ± SE)

wildfires (Gill 1997), the use of buffer strips seems key to promote the resistance of stream ecosystems to these perturbations and their ulterior recovery. Forest management plans should thus comprehensively consider the concomitant effects of exotic plantations and wildfire intensity and severity (Heilmayr et al. 2016; Jenkins et al. 2016; Sun et al. 2019) and develop strategies to minimize

the effects of wildfires on freshwater communities and ecosystems.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-024-00268-w>.

Additional file 1: Fig. S1. Four different size-mass relations of *Sericostoma pyrenaicum* at the beginning of the experiment from 29 extra larvae. **Fig. S2.** Pre-leaching concentrations of ash, C, N and P (% DM; mean ± SE, $n = 5$) of the three litter species (Alder, Oak & Eucalypt) after both pre-treatments (Control and Fire exposed). **Table S1.** General linear model results on leaching (mass loss) and pre- and post-leaching traits of the six studied substrates (see Fig. 1). **Table S2.** Mean values of the litter traits after the leaching assay of the six studied substrates (see Fig. 1) at three different temperatures.

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Authors' contributions

JP: conceptualization, methodology, investigation, validation, formal analysis, data curation, visualization, and writing—review and editing. CB: conceptualization, resources, investigation, data curation, visualization, and writing—review and editing. AA: investigation, methodology, formal analysis, writing—original draft, and writing—review and editing. AS: investigation and writing—review and editing. DR: investigation and writing—review and editing. FC-A: investigation and writing—review and editing. LB: conceptualization, methodology, investigation, resources, writing—review and editing, supervision, and funding acquisition.

Availability of data and materials

Data will be made available upon request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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