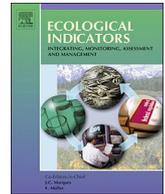




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Extreme temperature events alter stream ecosystem functioning

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ARTICLE INFO

Keywords:

Climate change
Conservation/biodiversity
Running waters/rivers/streams
Decomposition
Functional indicator
Nutrient cycling
Invertebrates

ABSTRACT

Extreme temperature events have increased in intensity, duration and frequency in the last century, with potential consequences on organisms and ecosystems. In many streams, leaf litter of terrestrial origin is a key resource for microorganisms and some detritivores, and its decomposition has a main role on ecosystem functioning and is often used as an indicator of ecological integrity. As litter is often exposed to atmospheric conditions before entering the stream, extreme warming and freezing events may alter its physicochemical structure and affect decomposition and associated detritivores. We tested this prediction in a microcosm experiment by exposing litter of three tree species (in single-species treatments and the 3-species mixture) to different temperature pre-treatments: heating (40 °C), freezing (−20 °C) and both (heating followed by freezing). We then examined changes in litter traits due to leaching (72 h), litter decomposition in the absence and presence of detritivores, and detritivore growth (28 d), with focus on mass and nutrient (nitrogen and phosphorus) changes. Nutrient leaching was promoted mostly by the heating pre-treatment, which apparently produced lower-quality litter. However, microbial activity mostly resulted in litter mass and nutrient gain, which were reinforced by the heating pre-treatment, while freezing had the opposite effect. When detritivores were present, decomposition showed high variation among litter types but, again, the heating and freezing pre-treatments tended to reduce and enhance nutrient loss, respectively. The greatest and more consistent effects occurred for detritivore growth, which was reduced by temperature pre-treatments, particularly in the highest-quality litter type. In general, the sequential application of heating and freezing pre-treatments showed no synergistic effect, and the litter mixture showed similar responses to single-species treatments. Our results demonstrate that short-term extreme temperatures can modify litter quality in riparian soils and have subsequent effects on its decomposition within the stream and associated fauna, potentially altering stream food webs, ecosystem functioning and biogeochemical cycles.

1. Introduction

Climate change involves the alteration of atmospheric conditions at different temporal scales. Thus, while the Earth's global mean surface temperature has undergone a gradual, long-term increase (IPCC, 2014), there has been a rise in both warm and cold short-term extreme climatic events (ECEs), which are now more frequent, long and intense than decades ago (Cohen et al., 2018; Coumou and Rahmstorf, 2012; Kim et al., 2017). Such ECEs have the potential to alter the structure and function of biological communities and ecosystems (De Boeck et al., 2011; Smith, 2011b) and affect human health (Di Napoli et al., 2018;

Wang et al., 2016). However, the results of different studies exploring the ecological impacts of ECEs have been highly variable, probably due to the complexity and context-dependency of such events (Smith, 2011a). Furthermore, most of these studies have focused on terrestrial plant communities and primary productivity (see references in Smith, 2011a), while other processes and ecosystems have been largely neglected.

The decomposition of terrestrial plant litter is a key process that supports food webs in both terrestrial and stream ecosystems (Gessner et al., 2010). Up to 90% of global terrestrial plant production enters the detrital pathway (Cebrian, 1999), being ultimately decomposed and

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<https://doi.org/10.1016/j.ecolind.2020.106984>

Received 23 April 2020; Received in revised form 7 September 2020; Accepted 17 September 2020

Available online 03 November 2020

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recycled into inorganic compounds such as carbon dioxide (CO₂), which is released to the atmosphere, and inorganic nutrients that are used by plants and microorganisms (Boyero et al., 2011b). In streams, leaf litter (hereafter litter) from riparian vegetation is a major basal resource (Wallace et al., 1997). The rate at which litter is decomposed is a key component of stream ecosystem functioning and often an indicator of its ecological integrity (Gessner and Chauvet, 2002), hence the importance of predicting changes in the decomposition process as a result of environmental changes (Mollá et al., 2017; von Schiller et al., 2017). The indicator value of the decomposition process relies on the large amount of existing information about its natural drivers, together with the simplicity and inexpensiveness of its measurement and its wide applicability across habitats (Young et al., 2008). Moreover, decomposition is tightly linked to other fundamental processes such as nutrient cycling and secondary production, which can be examined simultaneously and improve the capacity of indicating environmental change (López-Rojo et al., 2019).

Extreme temperatures have the potential to alter the physico-chemical properties of riparian litter – which is generally exposed to atmospheric conditions before entering streams (Tonin et al., 2017b) – and consequently alter its within-stream decomposition by microorganisms and litter-feeding detritivores (hereafter detritivores). This question, to our knowledge, has been addressed by a single field study, which demonstrated a detrimental effect on microbial decomposition of litter that had been exposed to extreme temperatures, particularly litter subjected to freezing under wet conditions (Correa-Araneda et al., 2020). This finding is important, as it points to a potential reduction in rates of nutrient recycling and CO₂ outgassing from streams, with clear impact in global biogeochemical cycles (Raymond et al., 2013). However, the above study examined the decomposition process in isolation, with no assessment of related ecosystem processes, and did not consider the potential effects of litter identity and diversity, which can be key determinants of decomposition and nutrient cycling rates (López-Rojo et al., 2019; Robbins et al., 2019; Tonin et al., 2017a) and thus potential modulators of extreme temperature effects.

We addressed the above knowledge gaps in a laboratory experiment, where we subjected litter of three common riparian plants (in single-species treatments and the 3-species mixture) to extreme temperatures (i.e., heating, freezing, or both sequentially) and then examined their decomposition mediated by microorganisms and detritivores within microcosms. We examined litter mass loss but also nutrient dynamics during the process, as well as changes in several litter traits and detritivore growth. We hypothesised that (1) freezing would alter the physicochemical structure of litter, possibly through cell wall damage due to ice crystal growth (Charoenrein and Owcharoen, 2016), resulting in softer litter of lower quality (i.e., lower concentrations of nutrients because these would be more rapidly leached to water); (2) heating would also induce physicochemical changes in litter, possibly by promoting the breakdown and mineralization of organic compounds (Gray and Dighton, 2006), again decreasing litter quality, and reducing toughness; (3) microbial decomposition of litter subjected to extreme temperatures (freezing and/or heating) would be slower, due to the reduced nutritional value of litter, which would inhibit microbial colonization (Correa-Araneda et al., 2020); (4) in the presence of detritivores, decomposition of litter subjected to extreme temperatures would be enhanced due to increased litter softness (Correa-Araneda et al., 2020) and/or compensatory feeding (Landeira-Dabarca et al., 2018), but (5) detritivore growth would be reduced due to the lower nutritional value of litter; and (6) effects of extreme temperatures on decomposition and detritivore growth would vary among litter types (i.e., plant species), but would be lessened in litter mixtures, that is, plant diversity would mitigate such effects, as shown in other contexts (e.g., Silva Pedro et al., 2015). Additionally, our study design allowed us to compare the usefulness of different ecosystem processes (leaching, decomposition, nutrient cycling and secondary production) and compartments (microbial decomposers and detritivores) as ecological

indicators of the ecological consequences of ECEs.

2. Materials and methods

2.1. Litter and detritivore collection

We collected litter and detritivores in the Agüera stream catchment 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 mean annual temperature of 11.0 °C. Vegetation of the catchment consists of mixed native forest dominated by *Quercus robur* L. (Fagaceae), *Alnus glutinosa* (L.) Gaertn. (Betulaceae), *Castanea sativa* Mill. (Fagaceae) and *Corylus avellana* L. (Betulaceae). In autumn 2017 we collected leaves of three plant species: *A. glutinosa* (an N-fixing, rapidly decomposing species), *C. sativa* (a non-N-fixing, rapidly decomposing species) and *Q. robur* (a non-N-fixing, slowly decomposing species); hereafter *Ag*, *Cs* and *Qr*. Leaves were collected from the forest floor immediately after natural abscission, air dried to constant mass in the laboratory, and preserved in dark and stable conditions within cardboard boxes, at laboratory temperature (ca. 20 °C) and humidity (ca. 50%). Just before the start of the experiment, leaves were cut in pieces of approximately 4 cm², avoiding the basal midrib, and weighed to the nearest 0.01 mg using a precision balance.

Detritivores were larvae of *Sericostoma pyrenaicum* Pictet, 1865 (Trichoptera: Sericostomatidae), one of the most common detritivores in streams of the Agüera catchment (Martínez et al., 2016). In June 2018, larvae of similar size were manually picked from riverbed litter at one site within the catchment (Perea stream; 43.296°N, 3.254°W) and transported to the laboratory. They were acclimated in trays with constant aeration and mixed riverbed 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 mimicked stream conditions and minimized evaporation. Detritivores were starved 48 h prior to starting the experiment.

2.2. Litter pre-treatments

Before the experiment, litter was exposed to one of four temperature treatments for 12 h (following Correa-Araneda et al., 2020): (1) 20 °C (control, C); (2) 40 °C (heating pre-treatment, H); (3) –20 °C (freezing pre-treatment, F); and (4) heating and freezing pre-treatments applied sequentially (H + F; 12 h each, separated by a period of 2 h, and then 1 h after spraying with distilled water). The H and F pre-treatments simulated the exposure to very high and very low temperatures that occasionally occur at mid latitudes during late summer and autumn (heat waves) and in winter (cold waves or cold air outbreaks), respectively. The H + F pre-treatment simulated the occurrence of both ECEs within a short period of time, which is increasingly common at these latitudes due to the higher frequency of both types of event (Mitchell et al., 2016). Although the freezing temperature was well below the normal range experienced in the study area, it represents common temperature drops during cold spells in continental regions at our latitude (Cohen et al., 2018). Nonetheless, the F pre-treatment was applied for a very short time compared to the duration of freezing temperatures in the field. Prior to freezing, litter in the F and H + F pre-treatments was sprayed with distilled water, because low temperatures are usually accompanied by rain or humid conditions in the study area.

2.3. Leaching trial

We measured the leaching of soluble compounds in litter of each species (*Ag*, *Cs* and *Qr*) subjected to each pre-treatment (C, H, F and H + F) in 36 microcosms (3 replicates per species and pre-treatment). Microcosms consisted of glass cups (580-mL, 8 cm-diameter) that were placed within the above-mentioned controlled-temperature room (10 °C), constantly aerated and under a light:dark regime of 12:12 h.

Each microcosm was filled with 400 mL of filtered (100 µm) stream water (dissolved inorganic nitrogen: $365.5 \pm 12.1 \mu\text{g L}^{-1}$; soluble reactive phosphorus: $3.9 \pm 2.0 \mu\text{g L}^{-1}$) and contained 0.3 g of 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 litter, but microbial decomposition was most likely negligible during this short period (Bärlocher, 2005).

Leached litter was firstly used to measure leaf toughness [using a penetrometer, which measured the pressure (kPa) necessary to pierce the leaf tissue with a 1.55-mm diameter steel rod (Boyero et al., 2011a)] and specific leaf area [SLA; the ratio of leaf area (mm^2) to leaf dry mass (DM; mg)]. Then the material was oven dried (60 °C, 72 h), weighed, and divided in two subsamples. The first subsample was incinerated (550 °C, 4 h) and weighed to determine post-leaching ash free dry mass (AFDM); the second subsample was ground into powder (1-mm screen) and used to determine post-leaching nitrogen content [N; using a Perkin Elmer series II CHNS/O elemental analyser (Perkin Elmer, Norwalk, CT, USA)] and phosphorus content [P; using autoclave-assisted extraction (APHA, 1998)]. This allowed us to calculate leaching in terms of mass, N and P, and to correct initial litter AFDM data in the decomposition experiment.

2.4. Decomposition experiment

We conducted the decomposition experiment in 160 microcosms with the same characteristics and under the same conditions described above. In this case, each microcosm contained 0.9 g of litter belonging to one species (single-species treatments) or to the 3 species (mixture, 0.3 g per species). We first added the litter 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 (Findlay and Arsuiff, 1989). For each temperature pre-treatment (C, H, F and H + F) and litter type (Ag, Cs, Qr and mixture) there were 10 microcosms, including 7 replicates with detritivores (2 larvae per microcosm) and 3 without detritivores; the latter allowed us to assess microbial decomposition.

On the first day of the decomposition experiment the water was replaced, and detritivores (case length previously measured under a binocular microscope with an accuracy of 0.5 mm) were added. Water was again replaced on days 7, 14, and 21 using a 100-µm mesh filter in order to avoid losing litter fragments. The experiment was terminated on day 28 (4 weeks of incubation), when all the remaining litter material in each microcosm was oven dried (60 °C, 72 h) and weighed to estimate final DM. In mixtures, litter of each species was processed separately. As for the leaching trial, each sample was divided in two sub-samples, which were either incinerated (550 °C, 4 h) and used to estimate final AFDM, or ground and used to determine final N and P contents. Detritivores were starved for 48 h within the microcosms filled with filtered stream water and then removed from their cases,

freeze-dried, weighed, and ground into powder in order to determine their final N and P contents as for litter samples. Thirty-five extra larvae were used to estimate the relationship between case length (CL, mm) and body DM (mg) ($\text{DM} = 0.2265e^{\text{CL} \cdot 0.2427}$; $r^2 = 0.90$) and to estimate initial body N and P contents.

2.5. Data analysis

We assessed hypotheses 1 and 2 (i.e., that temperature pre-treatments would enhance nutrient loss during leaching and result in softer and lower-quality litter) by calculating ordinary nonparametric bootstrapped 95% confidence intervals [BCa method using the ‘boot’ function on boot R package, based on 999 bootstrap replicates (Canty and Ripley, 2016; Davison and Hinkley, 1997)] for leaching in terms of mass, N and P, and for post-leaching toughness and SLA, in each pre-treatment (C, H, F and H + F) and species (Ag, Cs, Qr). We determined whether the H, F or H + F intervals overlapped the C interval – i.e., the null expectation that the temperature pre-treatment had no effect.

We examined hypotheses 3–5 (i.e., that temperature pre-treatments would reduce microbial decomposition, enhance detritivore-mediated decomposition and reduce detritivore growth) using bootstrapped 95% confidence intervals (as above) for six variables: (1) litter mass loss [LML = (initial – final litter AFDM)/initial AFDM]; (2) litter N loss [LNL = (initial – final litter N content)/initial N content]; (3) litter P loss [LPL = (initial – final litter P content)/initial P content]; (4) detritivore mass gain [DMG = (final – initial detritivore DM)/initial DM]; (5) detritivore N gain [DNG = (final – initial detritivore N content)/initial N content]; and (6) detritivore P gain [DNG = (final – initial detritivore P content)/initial P content]. The three first variables (LML, LNL and LPL) were standardized by mean detritivore initial DM in microcosms with detritivores ($13.32 \pm 0.33 \text{ mg}$), in order to avoid a possible effect of differences in initial detritivore DM.

We examined hypothesis 6 (i.e., that temperature pre-treatment effects would vary among litter types and be less evident in the litter mixture) by comparing pre-treatment effects among the different single-species treatments and the mixture).

3. Results

The temperature pre-treatments had significant effects on nutrient leaching and post-leaching litter traits (Fig. 1). However, only the H pre-treatment consistently enhanced N and P leaching, while the F and H + F pre-treatments resulted in variable effects depending on litter type.

In microcosms without detritivores, unexpectedly, we observed microbial biomass accrual and nutrient immobilization (i.e., negative decomposition values; Fig. 2A–C), which were enhanced by the H pre-treatment, with significant effects in terms of mass (Qr), N (mixture)

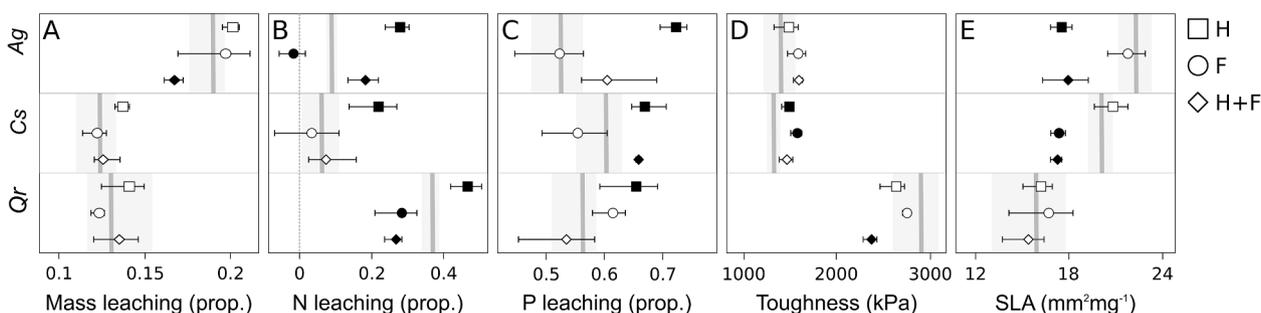


Fig. 1. Mean and 95% bootstrapped confidence intervals for leached litter mass (A), nitrogen (B) and phosphorous (C) and post-leaching toughness (D) and specific leaf area (E) in different plant species (*Alnus glutinosa*, Ag; *Castanea sativa*, Cs; and *Quercus robur*, Qr) and temperature pre-treatments (heating, H; freezing, F; and heating + freezing, H + F). Mean and 95% bootstrapped confidence intervals for controls are represented by grey lines and areas, respectively. Closed and open circles represent significant and non-significant results, respectively.

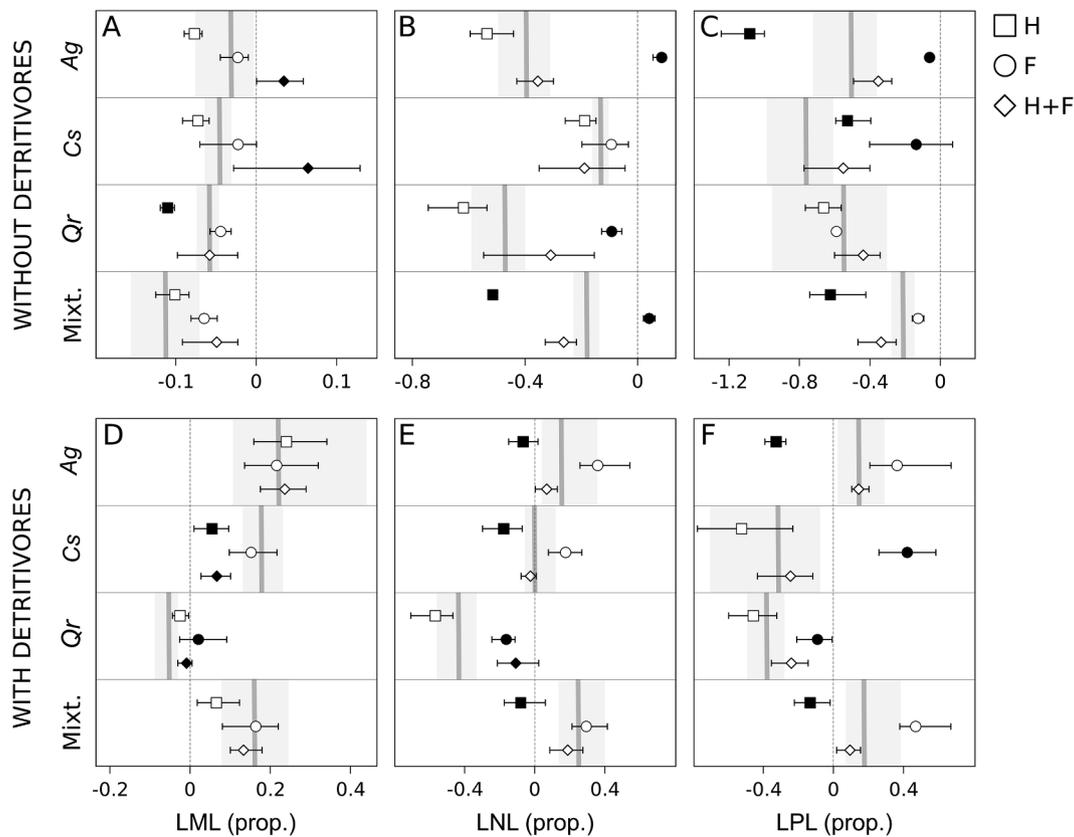


Fig. 2. Mean and 95% bootstrapped confidence intervals for the proportion of litter mass loss (LML; A, D) litter N loss (LNL; B, E) and litter P loss (LPL; C, F) in different litter types (*Alnus glutinosa*, Ag; *Castanea sativa*, Cs; and *Quercus robur*, Qr and the mixture) and temperature pre-treatments (heating, H; freezing, F; and heating + freezing, H + F) in the presence (A, B, C) and absence (D, E, F) of detritivores. Mean and 95% bootstrapped confidence intervals for controls are represented by grey lines and areas, respectively. Negative values represent mass gain and nutrient immobilization. Closed and open circles represent significant and non-significant results, respectively. Note that graphs have different scales.

and P (Ag and mixture). The F pre-treatment, on the contrary, resulted in less immobilization of N (Ag, Qr and mixture) and P (Ag and Cs) than in the control. Litter mass loss occurred only in the H + F pre-treatment, which differed significantly from the control (where there was biomass accrual and nutrient immobilization). Biomass accrual was in general greater in the litter mixture than in single-species treatments, but nutrient immobilization was lower in the former.

When detritivores were present, litter mass loss and nutrient mineralization became predominant (i.e., positive decomposition values; Fig. 2D–F), except for one litter type (Qr) that showed biomass accrual and nutrient immobilization. Litter pre-treatments had variable effects depending on litter type: the H pre-treatment reduced LML (Cs), LNL (Ag, Cs and mixture) and LPL (Ag and mixture), while the F pre-treatment enhanced LML (Qr), LNL (Qr) and LPL (Cs and Qr), and the H + F treatment reduced LML (Cs) and at the same time enhanced LML and LNL (Qr). Decomposition of the litter mixture was similar to that of the rapidly decomposing species (i.e., Ag and Cs) in control and pre-treated litter.

Detritivore growth (in terms of mass, N and P) tended to be lower in pre-treated litter than in control litter, and this reduction was significant in many cases (Fig. 3). In single-species microcosms, the H pre-treatment reduced growth in all cases except for DNG in Cs; the F pre-treatment reduced DMG (Ag), DNG (Ag) and DPG (Cs); and the H + F pre-treatment reduced DMG (Ag and Qr), DNG and DPG (Ag and Cs in both cases). In litter mixtures, growth also tended to be lower in pre-treated litter than in control litter, with reductions that were similar to those of non-N fixing species (i.e., Cs and Qr) and much lower than those of the N-fixing species (i.e., Ag); however, differences were not significant in any case for the mixture.

4. Discussion

Our results provide novel evidence about how ECEs (i.e., heat waves and cold spells) can alter the functioning of stream ecosystems, through effects on litter decomposition (mediated by microorganisms and detritivores), nutrient cycling and detritivore secondary production. Many streams are heterotrophic systems, where allochthonous litter inputs exceed within-stream primary production and fuel the aquatic food web (Wallace et al., 1999), hence the importance of understanding how litter decomposition and associated processes are affected by environmental change drivers. Our findings add to previous work demonstrating that ECEs can alter primary production and nutrient cycling in terrestrial ecosystems (Ciais et al., 2005; Jentsch et al., 2011; Kim et al., 2017), with potential indirect effects on streams through altered litter inputs. Furthermore, as litter decomposition is often used as an indicator of stream ecosystem functioning and integrity (Gessner and Chauvet, 2002; Young et al., 2008), our results are comparable to those of other studies exploring how this process is altered by different environmental stressors (e.g., Benstead et al., 2009; Duarte et al., 2016; López-Rojo et al., 2019).

4.1. Pre-heating promotes nutrient leaching from litter

We found little effect of temperature pre-treatments on leaching in terms of mass loss, which was variable among species and within the common range described for broadleaves (i.e., 10–20%; Bärlocher, 2005; Ferreira et al., 2010; Gessner, 1991). This contrasts with results of a field study, which found significantly higher leaching in pre-treated litter, particularly when subjected to freezing (Correa-Araneda et al.,

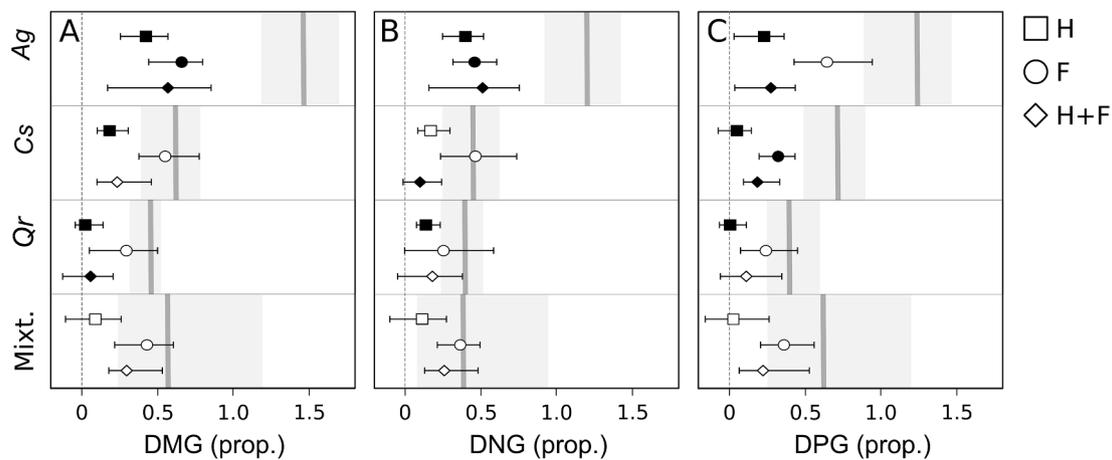


Fig. 3. Mean and 95% bootstrapped confidence intervals for detritivore mass gain (DMG), detritivore N gain (DNG) and detritivore P gain (DPG) for different litter types (*Alnus glutinosa*, Ag; *Castanea sativa*, Cs; and *Quercus robur*, Qr and the mixture) and temperature pre-treatments (heating, H; freezing, F; and heating + freezing, H + F). Mean and 95% bootstrapped confidence intervals for control detritivores are represented by grey lines and areas, respectively. Closed and open circles represent significant and non-significant results, respectively.

2020). Such inconsistency of results is similar to that found for litter subjected to drying, which has shown a range of responses depending on the studied species (Taylor and Bärlocher, 1996). Nevertheless, we found a strong and consistent effect of pre-heating on nutrient losses during leaching, which in all cases exceeded 20% for N and 60% for P, and were higher than in control litter. The effect of pre-freezing was less clear, as it reduced N and P immobilization but not in all species. It is likely that the high temperature promoted nutrient loss by facilitating the breakdown of chemical bonds and by cell structural damage, allowing the release of mineral ions (Gray and Dighton, 2006). Moreover, pre-heating reduced among-species variability in litter structural traits (i.e., toughness and SLA). All these changes as a whole indicate that litter entering streams after a heat wave could be more homogeneous and of poorer quality, which agrees with a study showing a homogenization of litter decomposition rates after exposition to extreme temperature and solar radiation conditions (Mora-Gómez et al., 2019).

4.2. Effects of ECEs on litter decomposition are variable

In the decomposition experiment we observed variable patterns of change in terms of litter mass and nutrients, which included losses and gains. In microcosms without detritivores, which represented microbial activity, litter mass and nutrient contents mostly increased, indicating the occurrence of microbial biomass accrual (Benstead et al., 2009; Manning et al., 2015). This has been observed elsewhere in initial stages of litter decomposition (ca. 1 week; e.g., Pérez et al., 2018) as microbial colonization can start immediately after litter immersion. However, the increment in mass and nutrients is usually detectable after the initial leaching losses and lasts for a short period of time, as afterwards it is surpassed by decomposition losses (Suberkropp, 1991). In our experiment, in contrast, we observed net increments for a longer period (4 weeks), possibly due to microcosm conditions (e.g., limited water movement and lighting), which may have promoted the interplay between microbial decomposers (i.e., fungi and, to a lesser extent, bacteria; Duarte et al., 2016) and primary producers (i.e., bacillariophytes, chlorophytes, rhodophytes and cyanobacteria; Leira and Sabater, 2005; Pan et al., 1999). These two groups of microorganisms can enhance each other through priming effects (Danger et al., 2013) and both conform a biofilm on the surface of litter that increases its nutritional value (France, 2011) and reduces the nutritional imbalance between litter and detritivores (Cross et al., 2005).

We expected microbial decomposition to be reduced in pre-treated litter because of enhanced nutrient leaching, which would reduce quality and thus limit microbial colonization (Correa-Araneda et al.,

2020). However, we observed that pre-heating promoted microbial biomass accrual and/or nutrient immobilization, suggesting biofilm growth and nutrient uptake from the water. This could be related to the breakdown of complex compounds, whose elements would otherwise be unavailable to microorganisms, and would not support the idea that pre-heated litter is of poorer quality than control litter (despite its lower content of N and P). Other studies have shown that nutrients other than N and P can be important drivers of decomposition (e.g., Ca and Mg; García-Palacios et al., 2016; Makkonen et al., 2012). Pre-freezing, in contrast, tended to promote nutrient mineralization, and the same occurred in some cases when both pre-treatments were applied, although results were highly variable among species.

Decomposition in the presence of detritivores was considerably greater than in their absence, especially for fast-decomposing litter (i.e., *A. glutinosa*), as shown elsewhere (e.g., Tonin et al., 2017a). However, effects of ECEs on decomposition in the presence of detritivores were variable among species, and trends were similar to those found in the absence of detritivores, contrary to our expectation. This contrasts with previous work reporting higher detritivore-mediated decomposition in pre-treated litter, which was attributed to the loss of toxic compounds (e.g., tannins) as a result of pre-treatments (Correa-Araneda et al., 2020). In our study, the fact that pre-heating tended to cause nutrient immobilization despite the net mass loss (except for the slow-decomposing species, *Q. robur*) is remarkable and merits further exploration.

4.3. Detritivore growth is strongly reduced when litter has been subjected to ECEs

We found that the variable most affected by ECEs was detritivore growth, which was consistently lower in pre-treated litter of all species. While we had predicted a reduction in growth, we would have expected large effects on decomposition that would propagate upward to detritivores (Wallace et al., 1997), but being lessened rather than amplified (as in Correa-Araneda et al., 2020). The fact that detritivore growth responded more strongly and consistently to litter pre-treatments than leaching, microbial decomposition and detritivore-mediated decomposition (i.e., consumption) suggests that physiological variables of consumers may be more sensitive indicators of environmental change than decomposition rates, because they integrate multiple changes occurring at different levels of the food web (see also Landeira-Dabarca et al., 2018).

The greatest reductions in growth and nutrient gain due to pre-treatments occurred in those detritivores with the highest growth under control conditions, that is, those consuming litter of *A. glutinosa*. The

high nutritional quality of this species and its palatability for detritivores are well known, due to its high nutrient content and relatively soft cuticle (Abelho and Graça, 1996; Graça et al., 2001; Hladysz et al., 2009), and other studies have found higher growth in detritivores fed litter of this species compared to that of other species (e.g., Correa-Araneda et al., 2017; López-Rojo et al., 2019). Likewise, the reduction in growth and nutrient gain in detritivores consuming *C. sativa* was higher than in those consuming *Q. robur*, the latter being the lowest-quality litter. Thus, effects of ECEs on aquatic food webs could be stronger in streams where high-quality litter resources dominate, compared to streams where lower-quality litter is more abundant (e.g., broadleaf vs. conifer forests, or native forests vs. eucalypt plantations; Kominoski et al., 2013).

Growth of detritivores fed the mixture were more similar to those fed low-quality litter (*Q. robur*), indicating the possible existence of negative complementary effects (see Handa et al., 2014), such as chemical interference (Eisenhauer, 2011; Loreau and Hector, 2001). Interestingly, the reduction in growth was non-significant for detritivores in the litter mixture treatment, suggesting the existence of mitigation of ECE's effects, as we predicted. The same did not occur for decomposition, because the mixture decomposed at rates that were more similar to those of the highest-quality litter (*A. glutinosa*).

5. Conclusions and insights

Scientific and social concern about ECEs has increased due to their growing frequency and intensity (Coumou and Rahmstorf, 2012), but knowledge on their ecological consequences is still incipient, particularly for freshwater ecosystems. Our study reveals important indirect effects of ECEs on stream food webs, which start at changes in the quality of leaf litter before it enters the stream, and are magnified upward the food web. The strong negative effects on detritivore growth found here have the potential to significantly reduce invertebrate secondary production, particularly in streams where litter-feeding detritivores are important in terms of abundance or biomass (Boyer et al., 2011a; Cheshire et al., 2005). Moreover, such effect could be further translated into reduced secondary production at higher trophic levels, including vertebrates (Wallace et al., 1997).

The results of our microcosm experiment support the idea that ECEs affect stream ecosystem functioning, which was shown by a field study conducted in one stream (Correa-Araneda et al., 2020). However, the patterns described here differ from those found in the field study, suggesting that this issue merits further exploration in the field. Moreover, ECEs are associated to global warming, which also has direct effects on decomposition through higher water temperature (which enhances microbial decomposition and limits detritivore-mediated decomposition; Boyer et al., 2011b) and increased flow intermittency (which alters patterns of decomposition and nutrient cycling; Datry et al., 2018; von Schiller et al., 2019). Thus, potential interactions between different components of climate change should be considered in future studies, in order to be able to forecast changes in stream ecosystem functioning and food webs. Such interactions are also of crucial importance when trying to assess ecosystem integrity by means of functional indicators, which have been often neglected (von Schiller et al., 2017). We highlight the importance of exploring nutrient dynamics in decomposition studies, as some effects may not be evident when considering litter mass loss only (as shown here) and because of the fundamental role of ecological stoichiometry in understanding ecosystem functioning (Woodward, 2009), as well as physiological variables of consumers, which seem to be efficient indicators of environmental change effects on ecosystems.

CRedit authorship contribution statement

Javier Pérez: Conceptualization, Investigation, Methodology, Data curation, Validation, Visualization, Writing - original draft, Writing -

review & editing. **Francisco Correa-Araneda:** Conceptualization, Investigation, Methodology, Formal analysis, Writing - original draft, Writing - review & editing. **Naiara López-Rojo:** Investigation, Formal analysis, Visualization, Writing - review & editing. **Ana Basaguren:** Investigation, Methodology, Writing - review & editing. **Luz Boyero:** Conceptualization, Funding acquisition, Investigation, Methodology, Supervision, Writing - original draft, Writing - review & editing.

Declaration of Competing Interest

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

Acknowledgements

This study was funded by the Spanish Ministry for Science, Innovation and Universities and FEDER (project BioLoss, Ref. RTI2018-095023-B-I00), Basque Government funds (Ref. IT951-16) and Initiation Fondecyt Project (Ref. 11170390). I. Díaz and U. Apodaka-Etxebarria contributed to the sample processing.

Data availability statement

Data underlying all reported figures are shared as supplementary material.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.106984>.

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