



# Joint effects of warming and salinization on instream leaf litter decomposition assessed through a microcosm experiment

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**Abstract** Stream ecosystem functioning is often impaired by warming and salinization, but the joint effect of both environmental stressors on key processes such as leaf litter decomposition is virtually unknown, particularly in the tropics. We experimentally explored how increased water temperature (26, 29 and 32°C) and salinity (no salt addition, 0.1, 1.0

and 10 g l<sup>-1</sup> NaCl added) affected the rates of total, microbial and detritivore-mediated decomposition, in stream microcosms containing leaf litter of *Ficus insipida* and larvae of *Chironomus* sp. collected from tropical streams. Effects of temperature were strong and consistent with previous findings: it promoted microbial decomposition and reduced decomposition mediated by detritivores, which showed greater feeding activity at 26°C. Salinity was negatively correlated with microbial decomposition at 32°C; it also had a negative influence on detritivore-mediated decomposition, which was nevertheless non-significant due to the high detritivore mortality at higher salinities. Notably, total decomposition was reduced with the joint presence of both factors (32°C and salt addition treatments, compared to 26°C and no salt addition), indicating the existence of additive effects and highlighting the relevance of multiple-stressor contexts when assessing the consequences of global change on stream ecosystems.

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## Introduction

Our planet is going through serious environmental changes as a result of anthropogenic activities, such as forest conversion into agricultural land,

urbanization, or industrial development (Sage, 2020). These environmental changes act as stressors on organisms and ecosystems, which can respond at multiple levels, from physiological alterations in individuals (Todgham & Stillman, 2013) to shifts in the rates of ecosystem processes and their capacity to provide services to humans (von Schiller et al., 2017). Within this context, multiple-stressor research is becoming prevalent because environmental changes often do not occur in isolation, and their interactions can challenge predictions of their ecological consequences (Jackson et al., 2021). The combined effects of stressors can be antagonistic, additive or synergistic depending on whether the result is lower, equal to or greater than expected (Fong et al., 2018).

Climate change is the most pervasive environmental change globally (IPCC, 2018). The rise in mean atmospheric temperature (hence in water temperature in freshwater ecosystems; Molinero et al., 2015) leads to enhanced organism metabolic rates (Brown et al., 2004) and, often, accelerated ecosystem process rates (Boyero et al., 2011b). On the other hand, changes in precipitation intensity and distribution cause the intensification of dry seasons in some regions of the planet (Park et al., 2018), which in turn interferes with water level and concentrations of pollutants in fresh waters (Rose et al., 2023). Exploring the consequences of stressors associated with climate change in freshwater ecosystems is of prime relevance because these provide fundamental ecosystem services (Richardson & Hanna, 2021) and because they are especially vulnerable to environmental changes, given that they integrate impacts produced on whole catchments (Jackson et al., 2016). Such information is particularly lacking for fresh waters located in tropical latitudes (Cornejo et al., 2019, 2020b).

In particular, stream ecosystems are highly exposed to pollutants coming from land, which are transported through runoff and can alter ecosystem processes, jointly with changes in temperature (e.g., as shown for dissolved nutrients; Ferreira & Chauvet, 2011). A type of pollutant that is common in streams, due to agricultural, industrial and mining activities, among others, and intensified by climate change, is salt (Cañedo-Arguelles et al., 2014). Salinization, however, has received little attention compared to other types of stream pollution, such as eutrophication (Cañedo-Arguelles et al., 2018), and its joint effect with warming on

ecosystem processes is virtually unknown (despite some evidence existing for organism physiological responses; e.g., Velasco et al., 2018).

Information about how the above stressors and their interactions affect stream ecosystems is particularly lacking for tropical latitudes (Cornejo et al., 2019), where climate change projections are especially critical and uncertain (Corlett, 2012). Besides, some tropical areas (such as our study area in Panama) can be susceptible to salinization for multiple reasons (Herbert et al., 2015; Castillo et al., 2018), including their high aridity (Sauer et al., 2016); their proximity to the ocean (Chui & Terry, 2013), with salt being transported by sea breezes and seawater intrusions (superficial or through aquifers); and human activities such as agriculture and cattle raising (Nack et al., 2021), with salt being used as feed supplement for livestock.

Here, we measured leaf litter decomposition in microcosms in order to evaluate the combined effect of warming and salinization on stream ecosystems from a tropical dry area, the Dry Arc region in Panama. The process of leaf litter decomposition is a useful tool to assess environmental stressor impacts on stream ecosystems (Gessner & Chauvet, 2002) and it has been used to explore effects of salinization (Canhoto et al., 2021). Terrestrial leaf litter represents the major basal resource in many streams, where the riparian canopy restrains primary production, and microbial decomposers (mainly aquatic hyphomycetes) and some detritivorous invertebrates (hereafter detritivores) specialize in processing this leaf litter and incorporating it into the aquatic food web (Marks, 2019). We used all combinations of three temperatures and four sodium chloride (NaCl) concentrations, and exposed leaf litter to the action of microorganisms and detritivores collected from tropical streams for 2 weeks. We hypothesized that (1) increased temperature would enhance microbial and detritivore-mediated decomposition, as a result of higher metabolic rates (Ferreira & Chauvet, 2011); (2) increased salinity would decrease microbial and detritivore-mediated decomposition, as a result of osmotic imbalances and hence reduced rates of biological activity (Canhoto et al., 2021); and (3) effects of salinization would be more evident at lower temperatures, because the increase in decomposition rates at higher temperatures would offset the decrease caused by salinization (i.e., both

stressors would show antagonistic effects; Jackson et al., 2016).

## Materials and methods

### Collection of biological material

We used leaf litter of *Ficus insipida* Willd. (Moraceae), a species of fig tree that is commonly found in the Pacific slope of Panama. Leaves of this species have relatively good quality ( $SLA = 10.7 \pm 1.1 \text{ mm}^2 \text{ mg}^{-1}$ ;  $N = 1.09 \pm 0.09\%$ ; Cornejo et al., 2020b) and have been readily used by microbial decomposers and detritivores in previous experimental studies (Cornejo et al., 2020b; López-Rojo et al., 2020b; Pérez et al., 2021b). We collected recently fallen leaves from the forest floor of the Metropolitan Natural Park ( $8^\circ 59' 36.77'' \text{ N}$ ,  $79^\circ 32' 46.66'' \text{ W}$ ) in August 2022. Leaves were air dried and stored in the laboratory until used.

Larvae of *Chironomus* sp. (Diptera: Chironomidae) were selected as detritivores, as the species is the most abundant in the study area (the Tonosí river catchment, central Panama) and it feeds on a wide variety of types of detritus, including leaf litter (Callisto & Gonçalves Jr, 2007; Small et al., 2011). This group of organisms has shown high tolerance to alterations related to eutrophication and low concentrations of dissolved oxygen (Frouz et al., 2003), being an example of generalist tolerant (Rosin et al., 2010; Steinberg & Steinberg, 2012), and becoming the dominant detritivore in decomposing litter under altered conditions (Pérez et al., 2013).

We collected larvae in a tributary near the Tonosí Forest Reserve ( $7^\circ 14' 51.77'' \text{ N}$ ,  $80^\circ 34' 14.93'' \text{ W}$ ; 57 m asl), to ensure that they had not been previously exposed to high levels of salinity and high temperatures. For larval collection, we placed six artificial pools at the stream banks within 2 m from the stream for 21 days. The pools consisted of 9-l plastic buckets, each filled with stream water [pH: 7.8; conductivity:  $0.351 \text{ mS cm}^{-1}$ ; salinity: 0.17 PSU; dissolved oxygen (DO):  $6.1 \text{ mg l}^{-1}$ ] and containing 3 g of *Ficus insipida* leaf litter enclosed within a coarse-mesh (10 mm) bag. The collected larvae were transported to the laboratory and placed in glass containers filled with stream water and leaf litter, with constant aeration. Larvae were acclimated for  $96 \text{ h}$  at  $26.31 \pm 0.01^\circ \text{C}$ ,

fed with *F. insipida* leaf litter fragments for the first 48 h, and then fasted for another 48 h before the start of the experiment. We used 168 individuals in the experiment (2 per microcosm).

Finally, we collected mixed leaf litter at different stages of decomposition from natural leaf litter deposits in a stream tributary near the Tonosí Forest Reserve ( $7^\circ 14' 51.77'' \text{ N}$ ,  $80^\circ 34' 14.93'' \text{ W}$ ). This leaf litter was incubated in a 2.5-l aquarium filled with filtered stream water ( $100 \mu\text{m}$ ) with aeration for 48 h, with replacement every 24 h. This water was used as microbial inoculum (10 ml per microcosm) at the beginning of the experiment (day 0), providing the microcosms not only with aquatic hyphomycete conidia, but also with other microorganisms (i.e., bacteria), which might also play a role in the decomposition process.

### Experimental procedure and sample processing

The experiment was carried out in September 2022, at the facilities of the Aquatic Ecology and Ecotoxicology Laboratory (AEEL) of the Gorgas Memorial Institute for Health Studies, located at the National Institute of Agriculture (INA:  $8^\circ 07' 43.4691'' \text{ N}$ ,  $80^\circ 41' 18.3086'' \text{ W}$ ). We used eighty-four 500-ml glass jars, which were located in a temperature-controlled room set at  $25^\circ \text{C}$ , and provided with constant aeration and a light:dark regime of 12:12 h, thus reflecting natural conditions. The jars were introduced within three 100-l tanks (with 28 microcosms per tank; 7 replicates per temperature  $\times$  salinity combination), which were used as water baths with different temperatures (26, 29 and  $32^\circ \text{C}$ ) that were reached using aquarium water heaters (HITOP 300w) and turbines (AQUANEAT average 800 GPH) for water circulation. This represented basal conditions in the study stream and two situations of warming (3 and  $6^\circ \text{C}$  increase) that could result from climate change (IPCC, 2018) and/or heat waves (Pérez et al., 2021a). Temperatures were monitored with a data logger (Thermobutton, model 22L, Plug & Track) placed within one microcosm per tank, which took a measurement every 30 min.

Each microcosm contained 400 ml of filtered ( $100 \mu\text{m}$ ) stream water and it was assigned to one of four salinity treatments depending on NaCl concentration [control (no NaCl added), low ( $0.1 \text{ g l}^{-1} \text{ NaCl}$ ), moderate ( $1.0 \text{ g l}^{-1} \text{ NaCl}$ ) and high

(10.0 g l<sup>-1</sup> NaCl)], with seven replicates per treatment at each experimental temperature. The studied salinity gradient aimed to represent successive increases of one order of magnitude, from the basal concentration (0.12–0.27 PSU, 0.15–0.40 TDS g l<sup>-1</sup>) to high salinity stress (2 orders of magnitude higher), in order to assess the effects in halotolerant taxa such as aquatic hyphomycetes (Canhoto et al., 2017). We chose to alter concentrations of NaCl because sodium represents the major cation increasing salinity in fresh waters (Cunillera-Montcusí et al., 2022), especially when the source of salt is related to seawater (Cañedo-Argüelles, 2020), using high-purity salt (ACS Grade) to reduce contamination by other components (e.g., table salt in Panama is always supplemented with iodine). Prior to the experiment, we introduced 1 g of air-dried leaf litter fragments in each microcosm and kept them for 48 h, with water exchange at 24 h. Leaf litter was collected (by filtering the water through 100 µm), oven-dried (70°C, 48 h), weighed to calculate dry mass (DM), incinerated (500°C, 4 h), and re-weighed to calculate AFDM. These data were used to calculate mass losses due to the leaching of soluble compounds (see “Data analyses” below; Bärlocher, 2020).

For the experiment, the microcosms were again filled with water with the same salinity treatments as before. This time, each microcosm received 700 ± 0.001 mg of free, air-dried *Ficus insipida* leaf litter fragments, attached with a safety pin to prevent them from floating; and another 300 ± 0.003 mg of leaf litter enclosed in mesh bags (8 × 6.5 cm size, 0.5 mm mesh opening), so they would not be accessible to detritivores. Water was exchanged after 24 and 48 h to promote leaching and, after 48 h, 10 ml of the microbial inoculum and two *Chironomus* larvae were also added. The body length of each larva was measured using a millimetre sheet. The experiment lasted 15 days, after which leaf litter was collected and processed as above, separately for free and enclosed leaf litter. The final status of each detritivore (i.e., dead, alive or emerged) was recorded and their final body length measured. During the experiment, every 2 days, several physical and chemical variables (temperature, pH, DO and salinity) were measured with a multiparametric probe (model 556 MPS, YSI Inc.).

## Data analyses

We explored the variation of the measured physical and chemical variables (temperature, pH, DO and salinity) through experimental time with general linear models (GLMs), where temperature treatment, salinity treatment and time were fixed factors. Our data did not meet the assumptions of normality and homoscedasticity required for parametric models (i.e. ANOVAs), but general linear models (GLMs) included a link function and a variance function that improved the fit of the model to the data structure (Nelder & Wedderburn, 1972). We used the `gls` function on the *nlme* package in R software, and a model selection procedure based on the Akaike information criterion (AIC) in order to include or exclude the variance function structure `varIdent` as appropriate (e.g., see López-Rojo et al., 2022). Leaf litter decomposition was measured through (1) the proportion of leaf litter mass loss [LML (prop.) = (final AFDM – initial AFDM)/initial AFDM] and (2) linear decomposition rates based on days ( $b_d$ ) and degree-days ( $b_{dd}$ ), the latter to standardize by temperature (Barlocher, 2020). We quantified total (free leaf litter), microbial (enclosed leaf litter) and detritivore-mediated decomposition (difference between free and enclosed leaf litter). Initial AFDM was corrected for leaching losses, multiplying by the proportion of leaf litter mass remaining in the set of leaf litter fragments used prior to the experiment. Total and detritivore-mediated decomposition were standardized using the mean initial body size (mm) of larvae in each microcosm (3.8 ± 0.06 mm; mean ± S.E., N = 168), to avoid variability due to differences in larval size. Additionally, in order to consider effects of detritivore loss (due to mortality and/or emergence) on decomposition, we corrected the initial body size according to detritivore presence at the end of the experiment. Thus, we used a correction factor of “1” when both detritivores were present at the end of the experiment, “0.75” if only one survived, or “0.5” if none of them were present.

We used general linear models (`gls` function, *nlme* package) to explore variation in the response variables (total, microbial and detritivore-mediated LML) with temperature treatments (26, 29 and 32°C), salinity treatments (control, low, moderate and high) and their interactions, with both factors being fixed. Again, model selection based on AIC was used for `varIdent` inclusion or exclusion. Differences among

treatment levels were explored with Tukey tests (ghlt function, *multcomp* package). When the interaction between temperature and salinity resulted significant, we further explored their joint effects on LML with Tukey tests of all possible combinations. Finally, to help visualize these combined effects, we examined relationships between LML and physical and chemical variables (temperature, pH, DO and salinity) at the different temperature and salinity treatments and for all treatments combined, using Pearson correlations.

## Results

Average temperature was 26.2, 28.55 and 31.67°C respectively, in the different temperature treatments, and average salinity was 0.18, 0.28, 1.21 and 10.42 mg l<sup>-1</sup>, respectively, in the different salinity treatments (Table 1). All variables showed variation with time (Table S1), but temperature and salinity mostly remained constant throughout the experiment (Fig. S1). Larval mortality was 54% overall, and it tended to increase with salinity (26%, 57%, 55% and 100% in the control, low, moderate and high salinity treatments, respectively) but not with temperature (64%, 50% and 66% at 26, 29 and 32°C, respectively). The 40% of surviving larvae emerged during the experiment, and emergence tended to decrease with

salinity (19%, 10%, 10% and null in the control, low, moderate and high salinity treatments, respectively) and to increase with temperature (9%, 17% and 14% at 26, 29 and 32°C, respectively). Considering these relatively high frequencies, our design prevented discerning between lethal and sublethal effects in the subsequent results.

Total decomposition varied with temperature and salinity and the interaction was significant (Table 2; Fig. 1), with Tukey tests indicating that decomposition was higher at the lowest temperature and control salinity than at the highest temperature and low, moderate and high salinities (Fig. S2). Microbial decomposition, however, was enhanced by temperature (26°C < 29°C < 32°C) but did not vary among salinities, and detritivore-mediated decomposition also differed only among temperatures (26°C > 29°C = 32°C). Linear decomposition rates showed similar patterns in terms of time (% d<sup>-1</sup>) or accumulated heat (% dd<sup>-1</sup>), featuring the same trends as LML in relation to stressors (Fig. S3). Decomposition rates corrected by detritivore loss showed similar trends in response to stress factors (Fig. S4).

Overall, total and detritivore-mediated decomposition were positively correlated with DO and negatively with temperature, and microbial decomposition showed the opposite pattern (Fig. 2). When examined separately for different temperature treatments, total

**Table 1** Average values (±SD) of water physical and chemical variables [temperature, °C; pH; conductivity, mS cm<sup>-1</sup>; salinity, PSU; total dissolved solids (TDS), g l<sup>-1</sup>; dissolved oxygen (DO), mg l<sup>-1</sup>] measured in microcosms subjected to

different temperature (26°C, 29°C and 32°C) and salinity treatments [control (C), no NaCl addition; low (L), NaCl concentration 0.1 g l<sup>-1</sup>; moderate (M), 1 g l<sup>-1</sup>; and high (H), 10 g l<sup>-1</sup>]

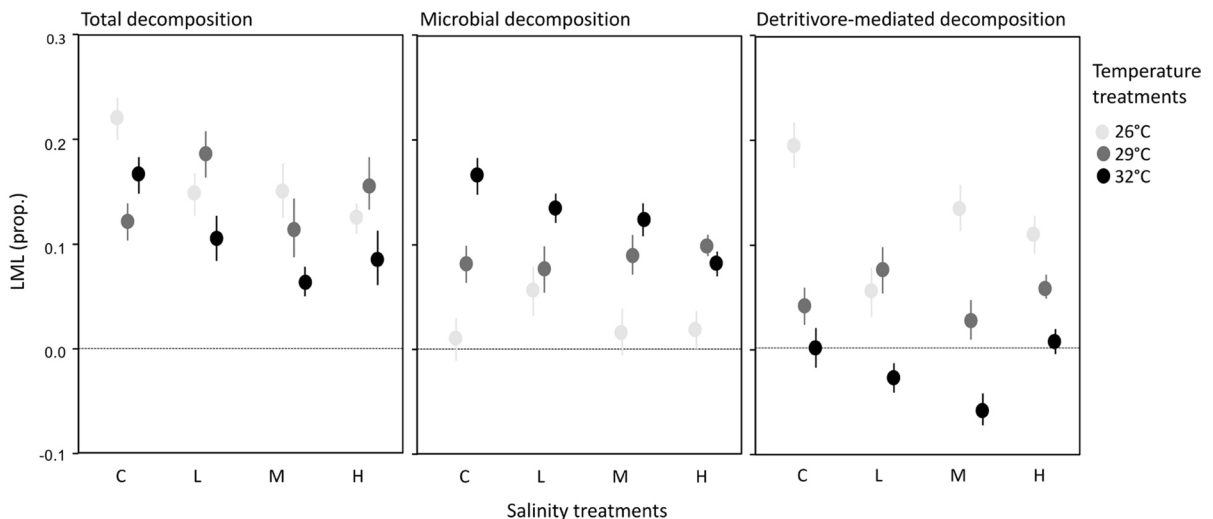
Treatments		Physical and chemical variables					
Temperature (°C)	Salinity	Temperature	pH	Conductivity	Salinity	TDS	DO
26	C	26.08±0.05	8.30±0.02	0.37±0.01	0.18±0.00	0.19±0.00	7.26±0.08
	L	26.13±0.01	8.25±0.02	0.58±0.01	0.28±0.00	0.29±0.00	7.20±0.04
	M	26.17±0.02	8.26±0.01	2.31±0.03	1.18±0.02	1.19±0.04	7.12±0.03
	H	26.15±0.02	8.20±0.02	17.24±0.15	10.15±0.09	8.60±0.09	6.80±0.05
29	C	28.73±0.05	8.26±0.02	0.38±0.01	0.18±0.00	0.19±0.00	6.31±0.16
	L	28.74±0.03	8.26±0.03	0.56±0.01	0.27±0.00	0.28±0.00	6.64±0.12
	M	28.69±0.03	8.28±0.02	2.26±0.01	1.15±0.03	1.13±0.03	6.60±0.08
	H	28.66±0.03	8.26±0.02	17.25±0.14	10.22±0.06	8.63±0.08	6.40±0.06
32	C	31.78±0.08	8.23±0.04	0.41±0.01	0.19±0.01	0.21±0.01	5.54±0.25
	L	31.84±0.05	8.32±0.03	0.60±0.01	0.29±0.01	0.30±0.01	6.19±0.08
	M	31.79±0.05	8.34±0.02	2.52±0.04	1.29±0.02	1.26±0.02	6.10±0.10
	H	31.77±0.08	8.31±0.02	18.49±0.27	10.89±0.13	9.22±0.11	5.94±0.05

**Table 2** Results of linear models testing the effects of temperature (26, 29 and 32°C), salinity (0, 0.01, 0.1 and 10 g l<sup>-1</sup>) and their interaction on total, microbial and detritivore-mediated decomposition

Response variable	Factor	df	<i>F</i>	<i>P</i>
Total decomposition	Temperature (T)	2	6.52	<b>0.003</b>
	Salinity (S)	3	3.66	<b>0.016</b>
	T×S	6	2.74	<b>0.019</b>
Microbial decomposition	T	2	29.01	<b>&lt;0.001</b>
	S	3	0.94	0.427
	T×S	6	1.98	0.080
Detritivore-mediated decomposition	T	2	39.62	<b>&lt;0.001</b>
	S	3	2.41	0.074
	T×S	6	1.98	0.081

We show the degrees of freedom (df) of the numerator (denominator df = 71), *F*-statistic and *P*-value

Significant ones (*P* < 0.05) are highlighted in bold

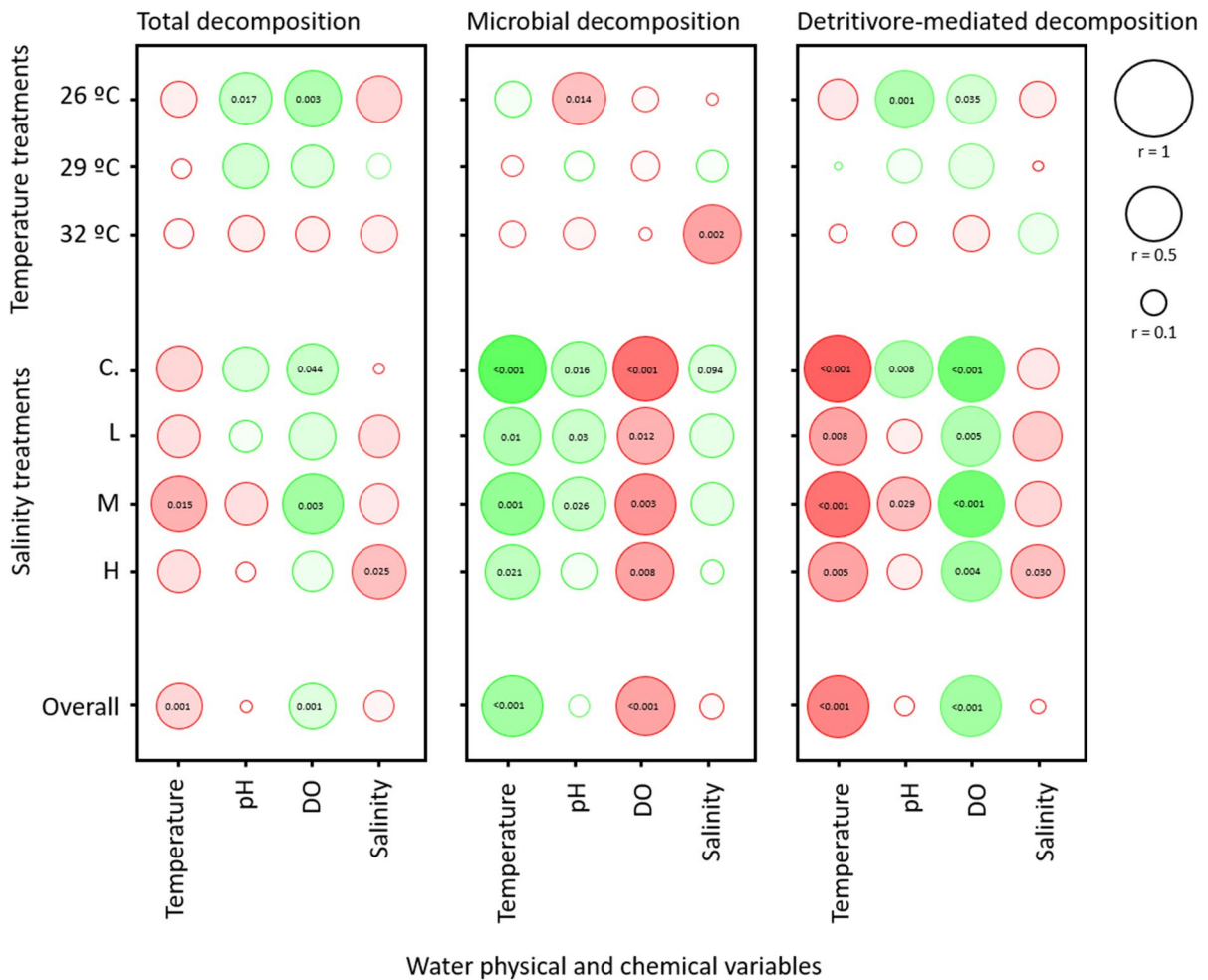
**Fig. 1** Total, microbial and detritivore-mediated decomposition (proportion of leaf litter mass loss, LML) in microcosms exposed to different temperature (26°C, 29°C and 32°C) and

salinity treatments [control (C), no NaCl addition; low (L), NaCl concentration 0.1 g l<sup>-1</sup>; moderate (M), 1 g l<sup>-1</sup>; and high (H), 10 g l<sup>-1</sup>]

and detritivore-mediated decomposition were positively correlated with pH and DO at the lower temperature, and microbial decomposition was negatively correlated with pH at the lower temperature and with salinity at the higher temperature (Fig. 2). When examined separately for different salinity treatments, total and detritivore-mediated decomposition were mostly positively correlated with DO (only at some salinities for total decomposition and at all salinities for detritivore-mediated decomposition), and the same occurred with temperature with negative relationships;

detritivore-mediated decomposition was positively related to pH and negatively to salinity at some salinities; and microbial decomposition was negatively related to DO and positively to temperature at all salinities, and positively related to pH and salinity in some cases (Fig. 2).





**Fig. 2** Graphical representation of Pearson ( $r$ ) correlations between rates of total, microbial or detritivore-mediated decomposition and several physical and chemical variables measured in microcosms (temperature, pH, dissolved oxygen and salinity) for all microcosms and separately for different

treatments of temperature and salinity. Green and red circles represent positive and negative correlations, respectively; circle size indicates the strength of the correlation, as shown in the legend, and the values inside the circles indicate significant  $P$ -value ( $P < 0.05$ )

## Discussion

Freshwater ecosystems are highly vulnerable to climate change (Woodward et al., 2010) and pollutants (Carpenter et al., 2011). In particular, streams flowing through agricultural catchments receive runoff that often contains organic nutrients and pesticides, as well as high levels of salinity (Schafer et al., 2012). However, while joint effects of climate warming and eutrophication on streams have received considerable attention (e.g., Ferreira & Chauvet, 2011), the effects of salinization in combination with other stressors are virtually unknown (Canhoto et al., 2021). This is

especially true for tropical regions, where water temperatures are high and detritivore assemblages differ substantially from those of temperate zones (Boyero et al., 2011a, 2021). In our microcosm experiment, we explored how warming and salinization in tropical streams jointly affected the key process of leaf litter decomposition, which often is a good indicator of how stream ecosystem integrity is impaired (Gessner & Chauvet, 2002).

Overall, we found a strong effect of temperature, which altered leaf litter decomposition driven by microorganisms and detritivores separately, as well as total decomposition. As previously mentioned, we

were unable to distinguish between lethal and sublethal effects, both of which were most likely responsible for the observed effects on the decomposition process, as occurred in other studies (e.g., Cornejo et al., 2020a; López-Rojo et al., 2020a). Importantly, our results remained the same when we corrected our data based on detritivore loss as a result of mortality or emergence. Microbial decomposition rates increased with temperature, reflecting the well-known direct relationship between temperature and metabolic rates (Brown et al., 2004), which has been shown in many other decomposition studies (e.g., Boyero et al., 2011b; Ferreira & Chauvet, 2011; Follstad Shah et al., 2017). In contrast, our results contradicted the generally positive relationship between DO and microbial decomposition (Medeiros et al., 2009), possibly in relation to the inverse relationship between DO and water temperature. Detritivore-mediated decomposition decreased with temperature, being higher at 26°C than at higher temperatures. It is well known that the role of detritivores on decomposition in tropical areas tends to be of minor importance compared to microbial activity (Boyero et al., 2011b), as most typical leaf litter consumers (i.e., shredders) are adapted to colder conditions (Danks, 2007; Strickland et al., 2015). There is, however, little information about leaf litter feeding rates of *Chironomus* species, which is a facultative leaf litter-feeding detritivore in tropical and temperate streams (Callisto & Gonçalves Jr, 2007; Pérez et al., 2013), acting as leaf-miners (Boyero et al., 2020). Other leaf litter consumers have shown different patterns of variation in their feeding activity with temperature. For example, the caddisfly *Sericostoma vittatum* Rambur, 1842 showed higher feeding rates at 10°C than 15°C (Landeira-Dabarca et al., 2018), while the amphipod *Gammarus pulex* (Linnaeus, 1758) showed higher rates at 24°C than at lower temperatures (Foucreau et al., 2016). These differences could be related to species-specific requirements or to the different temperature treatments used in experiments, or to a combination of both factors.

Effects of salinity were more variable than those of temperature, and non-significant for microbial decomposition, as some bacteria and aquatic hyphomycetes are highly tolerant to salt (Canhoto et al., 2021). Also, microbial decomposer assemblages can be resilient to salinization due to species functional redundancy (Canhoto et al., 2017). However, it is known that aquatic hyphomycete sporulation can

be suppressed and biomass reduced and, as a consequence, microbial decomposition can decrease with salt addition, although this is not always the case (Canhoto et al., 2021). For example, an experiment using *Eucalyptus camaldulensis* Dehnh. leaf litter observed a significant reduction in microbial decomposition when conductivity was increased from 1 to 10 mS cm<sup>-1</sup> (Sauer et al., 2016). In contrast, microbial decomposition rates of *Quercus robur* L. were not affected by increased salinity in two experiments (Gonçalves et al., 2019; Martínez et al., 2020). These inconsistent results could be partly related to differences in leaf litter traits; this hypothesis was not supported by a study conducted with *Q. robur* and *Castanea sativa* Mill., but these two species do not differ greatly in their nutrient contents and toughness (Almeida Júnior et al., 2020), so the influence of leaf traits cannot be discarded.

Detritivore-mediated decomposition did not vary with salinity in our experiment, but their activity tended to decrease; *P*-values were only slightly above the  $\alpha=0.05$  threshold, and the lack of significance was most likely due to the high mortality of *Chironomus* sp. at higher salinities (which was total at the 10 mg l<sup>-1</sup> treatment). Previous studies have found, again, inconsistent results, with reduced feeding rates due to increased salinity for some detritivores such as the tipulid *Tipula abdominalis* (Say, 1823) and the caddisfly *Schizopelex festiva* (Rambur, 1842), and the opposite pattern for others such as the isopod *Lirceus* sp. (Tyree et al., 2016; Martínez et al., 2020). These differences could be due to the different salts and salinity gradients used, but also to intrinsic differences among species. Increased salinity may affect the osmoregulatory capacity of invertebrates (i.e., their ability to actively regulate osmotic pressure), and the required energy expenditure may become too high, or osmoregulatory mechanisms may collapse resulting in cellular damage and death (Cañedo-Arguelles et al., 2013). In agreement with this, we observed a trend towards less survival of *Chironomus* sp. with increased salinity, being the highest salinity treatment lethal for all the individuals tested. However, we did not anticipate such lethal effects on *Chironomus* sp. given the known cross-tolerance of this group (Gama et al., 2014), being common in multi-stressed ecosystems (Popović et al., 2022). The inconsistent negative values in detritivore-mediated decomposition might be the result of a promoted biofilm accrual in absence



of detritivores, as previously suggested (Pérez et al., 2021a).

When total decomposition was quantified altogether, salinity influenced the process and interacted with the effect of temperature: decomposition was higher in microcosms exposed to the lower temperature and control salinity than in those exposed to the higher temperature and any of the salt addition treatments. Previous experiments have also found reductions in total decomposition with high (but not with moderate) salinity treatments; e.g., at 15 mS cm<sup>-1</sup> for *Populus nigra* L., with no effect at 5 and 10 mS cm<sup>-1</sup> (Cañedo-Argüelles et al., 2014); or at 15.3 mS cm<sup>-1</sup> for *Alnus glutinosa* (L.) Gaertn., with the opposite effect at 3.3 and 5.5 mS cm<sup>-1</sup> (Abelho et al., 2021). Our results agree with their findings, but they further show that temperature can modulate the effect of salinity, with additive effects of both factors: total decomposition was reduced by 39% due to high salinity, 21% due to high temperature and 60% due to both factors simultaneously. The effect was probably driven by detritivores, which might be more vulnerable to salt toxicity at high temperatures, as observed for other invertebrates in acute toxicity tests (Jackson & Funk, 2018). Despite the limitations of our analyses and others (Piggott et al., 2015; Tekin et al., 2020) to explore interactions between stressors, we provide evidence suggesting that such interactions should be taken into account as much as possible in experimental studies.

## Conclusions

Our experiment demonstrates that the simultaneous presence of warming and salinization can interact to inhibit leaf litter decomposition in streams. This novel result supports those of previous experiments showing positive interactions between different environmental stressors, such as the joint presence of warming and eutrophication enhancing microbial decomposition (Ferreira & Chauvet, 2011). Overall, our results reinforce the idea that a multiple-stressor context should be prioritized when examining effects of global environmental change on stream ecosystem functioning.

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**Data availability** All data generated or analysed during this study are included in this published article [and its supplementary information files]. Raw data will be made available on request.

## Declarations

**Competing interests** 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.

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