Aquatic Sciences

RESEARCH ARTICLE

Effect of experimental and seasonal warming on litter decomposition in a temperate stream

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Abstract Litter decomposition, a fundamental ecosystem process in woodland streams, is potentially affected by the predicted increase in water temperature. Here, we assessed the effects of experimental and seasonal warming on oak litter decomposition and on the relative contributions of microbes and invertebrates to this process. Experimental warming ($\sim$3 °C) stimulated litter decomposition in the coldest, but not in the warmest, months. This may be attributed to (1) higher temperature sensitivity of decomposition at lower ambient temperature due to temperature limitation of enzymatic activity, (2) higher relative temperature increase in winter than in warmer months, (3) existence of a previous warming period in winter, and (4) stronger stimulation of the activity of detritivores by warming in winter due to the prevalence of earlier (smaller) instars than in warmer months. The low response of litter decomposition to warming may have been due to the low nutrient availability in the study stream. The 30-day litter decomposition was stimulated over the seasonal gradient (monthly mean temperature: 6–16 °C), which may be attributed to a stimulation of metabolic activities by warming and to changes in detritivore life history over the seasons. The stimulation of litter decomposition with temperature suggests that the rate of CO_2 release from freshwaters will increase under global warming. However, invertebrate-driven litter decomposition was more responsive to warming than microbial-driven litter decomposition, suggesting that a larger fraction of litter carbon may be converted into secondary production and stored in the system for longer periods.

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Introduction

Climate models predict that global mean air temperature will increase by 1.1–6.4 °C by the year 2100 (IPCC (Intergovernmental Panel on Climate Change) 2007). Water temperature of streams and rivers is expected to follow this increase by rising 0.6–1.0 °C for each degree of increase in air temperature (Morrill et al. 2005). This increase in water temperature might have strong effects on biotic communities and ecological processes (Hogg and Williams 1996; Friberg et al. 2009), since species distribution, phenology, and biological activities are temperature-dependent (Parmesan and Yohe 2003; Brown et al. 2004).

The decomposition of organic material of terrestrial origin is a fundamental ecological process in small woodland streams where primary production is generally limited by shading (Vannote et al. 1980). These woodland streams constitute the majority of watercourses in hydrological networks in temperate regions (Allan and Castillo 2007), which makes them important participants in the global carbon cycle (Battin et al. 2008). Also, the rate at which litter decomposes in these small streams, together with their headwater position in the river continuum (Vannote et al. 1980), determines the amount and form of carbon (e.g., particulate organic carbon, dissolved organic carbon) that is transported downstream, shaping food webs both locally and in larger streams and rivers (Wipfli et al. 2007). It is therefore important to study the effect of increases in water temperature on litter decomposition if we want to

predict the contribution of freshwaters to the carbon cycle, and anticipate changes in aquatic food-webs and stream functioning.

The decomposition of submerged litter is generally carried out by microbes and invertebrates (Hieber and Gessner 2002). Microbes, aquatic hyphomycetes in particular, macerate the leaf matrix by the activities of extracellular enzymes (Chamier and Dixon 1982), convert organic carbon into fungal biomass (mycelium and conidia; Gessner and Chauvet 1994; Gulis and Suberkropp 2003; Ferreira et al. 2012), and mineralize it (Gulis and Suberkropp 2003), which leads to litter mass loss (Hieber and Gessner 2002). The accumulation of fungal biomass and the maceration of litter increase the litter quality for invertebrate detritivores, whose feeding activities lead to further litter mass loss (Bärlocher and Kendrick 1975; Graça et al. 2001; Chung and Suberkropp 2009). Therefore, any changes in microbial colonization and conditioning of submerged leaf litter can be carried over to higher trophic levels, with effects on litter decomposition.

Under laboratory conditions, the individual activities of microbes and invertebrates have been shown to be stimulated by increases in temperature, until the optimal temperature is reached (Chauvet and Suberkropp 1998; González and Graça 2003; Azevedo-Pereira et al. 2006; Dang et al. 2009). Correlative studies have found a positive relationship between decomposition rates of litter incubated along elevation (Fabre and Chauvet 1998), latitudinal (Irons et al. 1994; Boyero et al. 2011b), or geothermal gradients (Friberg et al. 2009). Studies under different seasonal thermal regimes have also reported faster litter decomposition in warmer seasons (Swan and Palmer 2004; Ferreira et al. 2006). However, the relative sensitivity to temperature of microbial-driven and invertebrate-driven litter decomposition has rarely been discussed (but see Irons et al. 1994; Friberg et al. 2009; Boyero et al. 2011b), despite the possibility that the two groups have distinct sensitivities to temperature (Boyero et al. 2011b). In this study, we assessed the effects of experimental ($\sim$3 °C) and seasonal warming (monthly mean temperature: 6–16 °C) on oak leaf litter decomposition, and on the relative contributions of microbes and invertebrates to this process, in a small temperate mountain stream. This assessment was done monthly since the temperature sensitivity of biological processes might depend on the ambient temperature (Kirschbaum 1995). Given that biological activities are temperature-dependent within tolerance limits (Brown et al. 2004), that the experimental warming was within these limits (Chauvet and Suberkropp 1998; Dang et al. 2009), and that invertebrate detritivores feed preferentially on conditioned litter (Graça et al. 2001), microbial- and invertebrate-driven litter decomposition were expected to be stimulated by an increase in temperature, primarily during the cold months.

Fig. 1 Stream reach studied, showing the longitudinal schist division and the upstream dam with the two valves that provided water to each stream half. Pipes transported the water from two tanks (inside the wooden shelter on the stream bank) into the valves. The experimental stream half is on the left, and the control half is on the right of the schist division. Photo credit: João Rosa

Materials and methods

Experimental design and study site

Quercus robur L. leaves were incubated, exposed and protected from invertebrates, monthly over 2 years in both halves of a small mountain stream that was divided longitudinally (Fig. 1). During the first year (February 2010–March 2011; ambient year) both stream halves were at ambient water temperature, while during the second year (April 2011–February 2012; warmed year) one stream half was warmed $\sim$3 °C (experimental half) above the ambient temperature in the other half (control half) (Fig. 2). Leaf litter was not incubated during July 2010–September 2010 (ambient year) and July 2011–October 2011 (warmed year) due to very low or no discharge, which in the warmed year prevented the heating system from operating.

The study reach was located in Ribeira do Candal (Lousã Mountain, central Portugal; 40°4′44″N, 8°12′10″W, 620 m a.s.l.), a second-order stream that drains an area of 0.8 km^2 covered by mixed deciduous forest dominated by chestnut (*Castanea sativa* Mill.) and oak (*Q. robur*), and where human activity is low. A stream reach ($\sim$1 m wide and <10 cm deep) was divided longitudinally in half over a length of 22 m using local laminar schist stones. The water
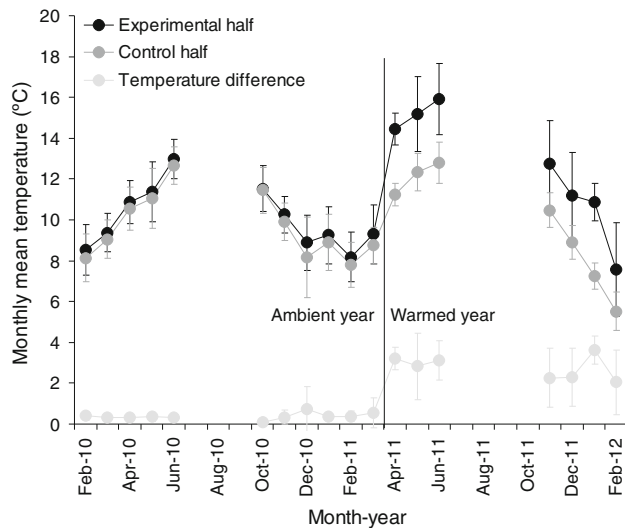
Fig. 2 Monthly mean temperature (±SD) in the control and experimental stream halves during the ambient (February 2010–March 2011) and the warmed year (April 2011–February 2012). Mean differences (±SD) in temperature between the experimental and the control halves over the study period are also shown. Water temperature was not monitored during July 2010–September 2010 (ambient year) and July 2011–October 2011 (warmed year)

provided to both stream halves was collected upstream of the study area and transported by gravity into two 260-L stainless-steel tanks that delivered the water to the experimental stream halves at 2.1–2.6 L s^{-1} (Table 1), through two valves inserted in a dam constructed upstream of the study site. During the ambient year, both tanks supplied water at the ambient temperature, while during the warmed year, one of the tanks provided with electrical resistors and fed by a constant 42 kW warmed the water above ambient temperature. The target increase in water temperature was 3 °C, based on predictions for air temperature in Portugal by the end of this century (Miranda et al. 2002) and on the relationship between water and air temperature reported for similar streams (Morrill et al. 2005). A detailed description of the hydraulic and heating systems can be found in Canhoto et al. (2013).

Water variables

Water temperature was recorded hourly during the study period, using submersed data loggers placed at the upstream and downstream end of each stream half

Table 1 Water variables in the control and experimental stream halves during the ambient (February 2010–March 2011) and the warmed year (April 2011–February 2012)

Water variables[a]	Ambient year				Warmed year				Methods
	n	Control half	n	Experimental half	n	Control half	n	Experimental half	
Temperature (°C)	331	9.7 ± 1.9 a	331	10 ± 1.8 a	214	9.8 ± 2.6 a	214	12.6 ± 3.1 b	Data loggers (Hobo Pendant, Onset Computer Corp., Massachusetts, USA)
Discharge (L s^{-1})	36	2.3 ± 1.1 b	38	2.6 ± 1.1 a	28	2.1 ± 0.5 a	28	2.2 ± 0.5 a	Volumetric method (Gore 1996)
Electrical conductivity (µS cm^{-1})	29	26.8 ± 2.1 a	29	26.9 ± 1.6 a	30	26.5 ± 0.8 a	30	26.8 ± 0.8 a	Field probe (LF 330, WTW, Weilheim, Germany)
DO (mg L^{-1})	37	9.7 ± 1.9 a	37	9.6 ± 2.0 a	33	10.4 ± 1.4 a	33	9.9 ± 1.4 a	Field probe (Oxi 3210, WTW, Weilheim, Germany)
DO (%)	37	90.9 ± 18.4 a	37	91.1 ± 19.4 a	33	97.9 ± 8.9 a	33	98.1 ± 9.6 a	Field probe (Oxi 3210, WTW, Weilheim, Germany)
pH	35	7.2 ± 0.6 a	35	7.2 ± 0.5 a	33	7.3 ± 0.2 a	32	7.2 ± 0.2 a	Field probe (pH 3110, WTW, Weilheim, Germany)
Alkalinity (mg CaCO$_3$ L^{-1})	35	4.5 ± 0.9 a	35	4.8 ± 1.4 a	20	5.91 ± 1.21 b	20	6 ± 1.4 b	Titration with 0.02 N H$_2$SO$_4$ to endpoint of pH 4.2 (APHA 1995)
NO$_3$-N (µg L^{-1})	33	53.2 ± 33.1 a	33	52.8 ± 39.1 a	24	52.8 ± 38.0 a	18	60.3 ± 54.9 a	Ion chromatography (Dionex DX-120, Sunnyvale, California, USA)
SRP (µg L^{-1})	26	14.9 ± 13.5 a	25	11.2 ± 7.4 a	29	14 ± 20.1 a	29	6.5 ± 11.1 a	Ascorbic acid method (APHA 1995)

Values are means ± SD. Stream halves and years were compared by two-way ANOVA; treatments with the same letter do not differ significantly (Tukey's test, $p > 0.050$)

[a] Water variables were not monitored during July 2010–September 2010 (ambient year) and July 2011–October 2011 (warmed year). DO, dissolved oxygen; SRP, soluble reactive phosphorus. Nitrite and ammonium were below detection limit (<100 µg L^{-1} and <50 µg L^{-1}, respectively)

(Table 1). Water temperature significantly differed between the upstream and downstream end of each stream half (paired t-test, p < 0.001 for both stream halves). However, the mean difference was 0.082 °C (±0.003) and 0.255 °C (±0.003) in the control and experimental half, respectively, and therefore the values from the upstream and downstream end were averaged to produce hourly temperature records for each stream half, and hourly temperature records were averaged to produce daily (see Canhoto et al. 2013) and monthly means. Weekly or biweekly, electrical conductivity, pH, and dissolved oxygen were recorded in situ in both stream halves using portable probes. Water samples were also collected from each stream half for determination of nutrient concentrations and alkalinity. Discharge was determined volumetrically at the output of the valves that fed each stream half (Table 1).

Leaf litter decomposition

The study area was dominated by chestnut and oak trees, which contributed the most to benthic litter standing stocks. However, chestnut trees shed most their leaves earlier than oak trees (Pozo et al. 1997), and chestnut leaves decompose faster than oak leaves (Ferreira et al. 2012). Therefore, the presence of chestnut leaves in the stream bed in spring and summer is much reduced compared with that of oak. Oak leaves were thus selected for this study. Leaves were collected just after abscission in Cioga do Campo, central Portugal, in autumn 2008, air-dried at room temperature and stored in the dark until needed. Leaves (2.25–2.58 g) were placed in fine-mesh bags (FM; 10 × 12 cm, 0.5 mm mesh) to exclude invertebrates and ensure that decomposition was mostly carried out by microbes, and in coarse-mesh bags (CM; 10 × 12 cm, 10 mm mesh) to allow invertebrates to enter and decomposition to be carried out by both invertebrates and microbes. Six litter bags of each mesh size were deployed monthly in each stream half and allowed to decompose for 30 days (Nikolcheva and Bärlocher 2005). Upon collection, litter bags were placed individually in zip-lock bags, transported to the laboratory in a cooler and promptly processed. In the laboratory, leaves were rinsed with tap water over a 500 μm-mesh sieve to recover small leaf fragments. Remaining litter was oven-dried at 105 °C for 48 h, weighed (±0.1 mg), ignited at 550 °C for 4 h and reweighed (±0.1 mg) to calculate the ash-free dry mass (AFDM) remaining. On day 0, three extra litter bags for each mesh size were taken to the field, submerged for ~10 min, returned to the laboratory and treated as above to allow determination of initial AFDM. Results were expressed as AFDM lost after 30 days (%). Overall litter decomposition was given by the AFDM lost from CM bags, while microbial-driven litter decomposition was given by the AFDM lost from FM bags. Litter decomposition attributed to invertebrates alone was calculated as the difference between AFDM lost from CM bags and AFDM lost from FM bags (Woodward et al. 2012). The potential effect of physical fragmentation on litter-mass loss was assumed to be negligible since the discharge in each stream half was very low (Ferreira et al. 2006).

Data analysis

Hourly water temperature was compared between the upstream and downstream end of each stream half by a paired t-test ($\alpha = 0.050$). Water variables were compared between years and stream halves by two-way ANOVA followed by Tukey's unequal honestly significant difference test ($\alpha = 0.050$). Normality of data was assessed by the normal P plot and the homogeneity of variances was assessed by the Bartlett test.

Litter decomposition (monthly mean values) was compared between mesh sizes (CM versus FM) for each stream half and year, between stream halves (control versus experimental) for each year, and between years (ambient versus warmed) for each stream half by paired t-tests. T tests were used to compare litter mass loss between mesh sizes and between stream halves for each month. To evaluate the relationship between water temperature and litter decomposition, the monthly overall, invertebrate-driven and microbial-driven litter decomposition means across the entire study period were regressed against the monthly mean temperature (linear regression).

Statistical analyses were performed with Statistica 7 software (StatSoft Inc., Tulsa, Oklahoma, USA).

Results

Water variables

Water temperature was significantly higher in the experimental stream half during the warmed year than in the control half during the same year and in both stream halves during the ambient year (Tukey's test, p < 0.001; Table 1; Fig. 2). Experimental warming increased the monthly mean water temperature of the experimental stream half by 2.0 °C (February) to 3.6 °C (January) over that of the control half during the warmed year, and by 1.6 °C (January) to 3.8 °C (May) over that of the experimental half during the ambient year (Fig. 1). Water variables were similar between stream halves; during the study period, the stream water was soft, well oxygenated, circumneutral and oligotrophic (Table 1).
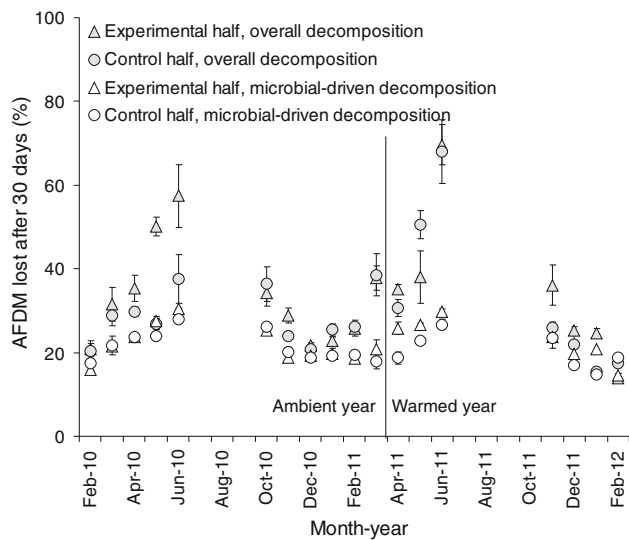
Fig. 3 AFDM lost due to overall litter decomposition (CM bags) and microbial-driven litter decomposition (FM bags) after 30 days incubation in the control and experimental stream halves during the ambient (February 2010–March 2011) and the warmed year (April 2011–February 2012). Litter was not incubated during July 2010–September 2010 (ambient year) and July 2011–October 2011 (warmed year). Values are means ± SE

Leaf litter decomposition

Litter generally lost 20–40 % of their initial mass in 30 days (Fig. 3). Overall litter decomposition (in CM bags) was higher than microbial-driven litter decomposition (in FM bags) for both stream halves during the ambient year (paired t-test, p = 0.002 and 0.015 for control and experimental half, respectively; Fig. 3); during the warmed year, differences between mesh sizes were found only in three (control half) or four (experimental half) months (t-test, p < 0.011), which resulted in an absence of significant differences between meshes across the year (paired t-test, p = 0.085 and 0.058 for control and experimental halves, respectively; Fig. 3). Overall, microbial-driven and invertebrate-driven litter decomposition did not significantly differ between stream halves for both years (paired t-test, p > 0.092), and between years for either stream half (p > 0.180) (Table 2), although differences in overall litter decomposition between halves occurred in 3 months (Nov, Jan, Feb), and differences in microbial-driven litter decomposition occurred in five months (Apr, May, Dec, Jan, Feb) during the warmed year (t-test, p < 0.034) (Fig. 3).

Overall, microbial-driven and invertebrate-driven litter mass loss across the entire study period was stimulated along the seasonal gradient (monthly mean temperature: 6–16 °C) (linear regression, p < 0.001; Fig. 4). This stimulation was stronger for the invertebrate-driven (slope = 2.796, R^2 = 0.39) than for the microbial-driven litter

Table 2 Litter decomposition (monthly mean AFDM remaining) was compared between stream halves (control versus experimental) for the ambient and for the warmed year, and between years (ambient versus warmed) for each stream half by paired t-tests (df = 12 for all comparisons)

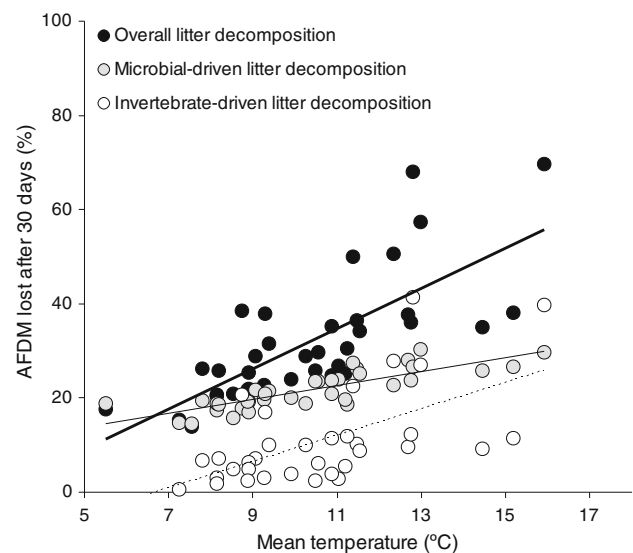| Litter decomposition	Control versus experimental half		Ambient versus warmed year	
	Ambient year	Warmed year	Control half	Experimental half
Overall litter decomposition	0.105	0.567	0.374	0.976
Microbial-driven litter decomposition	0.320	0.111	0.180	0.712
Invertebrate-driven litter decomposition	0.092	0.786	0.260	0.923

p values are given

Fig. 4 Relationship between overall, microbial-driven and invertebrate-driven litter decomposition across the study period and the monthly mean temperature (n = 36). The linear regression equation, R^2 and p values are as follows: overall litter decomposition (*bold line*), y = 4.281x − 12.401, R^2 = 0.56; microbial-driven litter decomposition (*solid line*), y = 1.490x + 6.253, R^2 = 0.69; invertebrate-driven litter decomposition (*dashed line*), y = 2.796x − 18.654, R^2 = 0.39; p < 0.001 for all regressions. Similar patterns were found when each stream half was considered individually

decomposition (slope = 1.490, R^2 = 0.69), which resulted in a stronger stimulation of overall litter decomposition (slope = 4.286, R^2 = 0.56). This changed the relative contributions of microbes and invertebrates to overall litter decomposition as temperature increased over the year; at low water temperature, microbes contributed more than macro-invertebrates, while at higher temperature, the contributions of the two communities were similar (Fig. 4).

Discussion

Litter decomposition in freshwaters significantly contributes to the global carbon cycle (Battin et al. 2008), and it is therefore important to understand how it responds to the increase in temperature as predicted for this century. Our results demonstrated that the experimental warming of stream water by ∼3 °C did not consistently affect litter processing over the study period. This contradicts a model simulating an increase in water temperature by 2 °C that predicted larger amounts of litter processed by microbes and invertebrates under warmer conditions, with invertebrates responding more strongly than microbes (Buzby and Perry 2000). Experimental warming stimulated litter decomposition in the coolest, but not in the warmest, months. This was anticipated since the temperature sensitivity of litter decomposition is higher at lower ambient temperature due to temperature limitation of enzymatic activities (Kirschbaum 1995; Janssens and Pilegaard 2003; Koch et al. 2007). The higher temperature sensitivity of litter decomposition in the colder months might also be attributed to the fact that the relative temperature increase was higher in winter than in warmer months. Winter was also the only season that was preceded by a warming period (autumn), which might have allowed the aquatic communities to acclimatize to warmer water temperature in the experimental stream half (Bárcenas-Moreno et al. 2009). Moreover, the stimulation of the (feeding) activity of detritivores by warming may be stronger in winter than in warmer months due to the prevalence of earlier (smaller) instars in the colder months and later (larger) instars in spring. Detritivore density is usually higher in the autumn/winter (although there can be high spatial and annual variability), and consumption rate and growth rate are higher for smaller than larger instars (González and Graça 2003; Azevedo-Pereira et al. 2006). Nevertheless, the low nutrient concentration of the study stream might help explain the generally limited response of litter decomposition to experimental warming. Litter decomposition is usually lower under oligotrophic conditions (Gulis et al. 2006; Woodward et al. 2012) and the effect of warming might have been limited by the low nutrient availability (Ferreira and Chauvet 2011a). In addition, the short duration (1 year) and the lack of replication, which is often associated with ecosystem-scale manipulations (e.g., Hogg and Williams 1996; Gulis and Suberkropp 2003), need to be taken into account. Our results are therefore highly conservative, which suggests that stronger effects of small increases in temperature might be found in streams that experience extended periods of warming and/or are not nutrient limited (Ferreira and Chauvet 2011a).

The 30-day litter decomposition in CM and FM bags was stimulated over the seasonal temperature gradient (monthly mean temperature: 6–16 °C). This stimulation was expected since the activities of most temperate fungi and invertebrate species are stimulated by warming within the temperature range observed (Azevedo-Pereira et al. 2006; Dang et al. 2009; Ferreira and Chauvet 2011a, b). This stimulation is also in agreement with metabolic theory (Brown et al. 2004) and with studies where litter was incubated along natural thermal gradients (Irons et al. 1994; Fabre and Chauvet 1998; Swan and Palmer 2004; Friberg et al. 2009; Boyero et al. 2011b). Although an increase in water temperature by 10 °C is over that expected for temperate woodland streams solely due to global warming (IPCC (Intergovernmental Panel on Climate Change) 2007; Morrill et al. 2005), increases of this magnitude may occur under global-warming scenarios that include removal of riparian vegetation, water abstraction, or warm-water discharge from power plants (Poff and Mathews 1986; Stefan and Sinokrot 1993).

The relative contributions of microbes and invertebrates to litter decomposition determines the amount of carbon that is mineralized, released into the atmosphere, incorporated into secondary production, and stored in the system for longer periods (Boyero et al. 2011b). In this study, invertebrate-driven litter decomposition was more strongly stimulated (∼2×) over the 10 °C temperature gradient than microbial-driven litter decomposition. This result contrasts with those of previous studies. Friberg et al. (2009), using a geothermal gradient, found that invertebrate-driven litter decomposition (as defined in this study) was less stimulated by warming than microbial-driven litter decomposition. Irons et al. (1994), using three streams located over a latitudinal range from Alaska to Costa Rica, found decreased detritivore biomass associated with decomposing litter with a decrease in latitude, while the percentage of litter-mass loss attributable to microbes increased in the same direction. This suggests that microbes contribute most to litter decomposition at low latitudes, while invertebrates are more important at higher latitudes. Boyero et al. (2011a, b), using 22 streams along a latitudinal gradient, observed that microbial-driven litter decomposition increased, while invertebrate-driven litter decomposition proportionally decreased, with a decrease in latitude (increase in temperature).

These studies found low detritivore numbers or biomass in warmer streams, which may explain why there was little if any increase of invertebrate-driven versus microbial-driven litter decomposition with temperature. At our study site, however, the number of detritivores in the benthos varied between 97 and 2,143 individuals m^{-2} (author pers. obs.). Most detritivore species belong to the orders Trichoptera and Plecoptera (also in our study), which evolved in cold environments, have low upper-thermal-tolerance-limits, and are therefore negatively affected by increases in

temperature (Gaufin and Hern 1971; Pearson and Boyero 2009). The maximum temperature observed in this study (16 °C) was lower than that observed in the three correlative studies mentioned above (23.5–26 °C), and was well within the tolerance limits for most invertebrates (Gaufin and Hern 1971). The low abundance/biomass of detritivores at low latitudes (Irons et al. 1994; Boyero et al. 2011a) might also be due to low litter quality (e.g., high concentration of structural and secondary compounds, low concentration of nutrients, thick cuticle), since resident plants may be better defended against herbivory than at higher latitudes. These defenses may persist after senescence (Graça and Cressa 2010; Marquis et al. 2012).

The temperature-induced increased invertebrate contribution to litter decomposition in this study can be attributed to an interaction between stimulated detritivore metabolism (Brown et al. 2004) and enhanced microbial conditioning of litter (Graça et al. 2001; Graça and Cressa 2010). A co-variation between increased temperature (due to transition between cold and warmer months) and detritivore biomass might have also occurred (Richardson 2001). González and Graça (2003) showed that *Sericostoma vittatum* population (a common detritivore in central Portugal and also at the study site) in a nearby stream had higher total biomass and a higher proportion of larger individuals from March to May. Also, some detritivores change their feeding preferences from fine particulate organic matter in young instars (usually more abundant in autumn/winter) to coarse particulate organic matter (e.g., leaf litter) in older instars (usually more abundant in spring/summer) (Basaguren et al. 2002). In addition, the small size of the selected stream reach, the short study sections, and the hydraulic modifications that had to be introduced to regulate discharge (e.g., upstream dam, channelization of water, constant flow) might have affected the inflow of colonists and therefore the aquatic communities at the study reach. However, the decomposition of oak litter in this study was in the range previously observed for oak litter in non-altered sections upstream of the study site and in other mountain streams in the same area (Gulis et al. 2006; Ferreira et al. 2012), which suggests that microbial and invertebrate activities were not affected by methodological constraints.

In temperate regions, the major litter input to streams occurs during autumn (Swan and Palmer 2004). Accelerated litter decomposition due to warming might therefore result in higher rates of nutrient transfer and in reduced litter availability in the benthos later in the year, if no change in litter input occurs (Buzby and Perry 2000). The disappearance of litter from the benthos may be faster in streams with higher nutrient availability; in this case, the stimulatory effect of warming will not be hampered by nutrient limitation of microbial activity (Ferreira and Chauvet 2011a).

Accelerated litter decomposition has obvious consequences for the food webs, as a mismatch between consumers and their resources might occur (Durant et al. 2007). Reducing the amount of leaf litter available in detrital-based systems may lead to decreases in the abundance of detritivores and changes in the structure of food webs, which may translate into reduced secondary production and impaired ecosystem functioning (Richardson 1991; Wallace et al. 1999). On the other hand, a doubling in atmospheric CO_2 concentration may lead to increased terrestrial primary production and decreased litter quality (e.g., due to higher investment in structural compounds) (Stiling and Cornelissen 2007), which may compensate for faster litter decomposition due to increased temperature. Larger amounts of benthic litter may lead to a decrease in litter decomposition rate due to lower invertebrate density in the increased amount of submerged litter (Tiegs et al. 2008). The decrease in litter quality (increase in the carbon/nutrient ratio) may lower decomposition rates due to lower colonization and activity of microbes and detritivores, which prefer soft, nutrient rich litter (Gessner and Chauvet 1994; Graça and Cressa 2010; Ferreira et al. 2012). Future research addressing the effect of warming on litter decomposition should take into account the simultaneous changes in other environmental variables as these can affect the response of litter decomposition to warming (Ferreira and Chauvet 2011a, b).

The stimulation of microbial-driven litter decomposition with temperature suggests that the rate of CO_2 release from freshwaters will increase under global warming (Boyero et al. 2011b). However, the greater stimulation of invertebrate-driven litter decomposition suggests that a larger fraction of litter carbon might be invested in secondary production and be retained in the system for longer periods than at present, with largely unknown potential consequences for food-web dynamics (O'Connor et al. 2009). Whether higher CO_2 released from microbial activities is counterbalanced by higher carbon retention in secondary production under global warming remains to be evaluated.

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