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Variable temperature effects between heterotrophic stream processes and organisms

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Abstract

1. Temperature is known to stimulate metabolism with cascading effects on multiple biological processes. These effects may, however, vary across processes, types of organisms or levels of biological organisation. They can also vary with nutrient availability, with potentially stronger temperature effects when nutrients are not limiting. This context dependence of temperature effects on processes challenges our ability to anticipate their consequences on ecosystems in a changing world.
2. In headwater streams, the decomposition of allochthonous leaf litter, driven by both microbial decomposers and invertebrates, is known to respond to both temperature and nutrient availability. These food webs are highly tractable and a useful model system to investigate the variations of temperature effects on processes across types of organisms (microbes versus invertebrates), resource availability levels (nutrient concentration), and levels of biological organisation (from individual to ecosystem).
3. In a microcosm experiment, we measured the effects of temperature and nitrogen availability (four levels each) on respiration rates of litter-consuming microbes and invertebrates and their decomposition activity in different contexts of food web complexity. The latter included one treatment without invertebrate detritivore (microbial decomposers only), three single invertebrate taxa (*Gammarus*, *Potamophylax*, and *Sericostoma*) treatments, and one mixed invertebrate taxa treatment (three-species altogether).
4. Microbial processes increased nearly exponentially with temperature (Arrhenius model, activation energy (± 95% confidence interval) = 0.56 ± 0.53 and 1.00 ± 0.23 eV for litter decomposition and respiration), while invertebrate-driven processes increased (activation energy from 0.47–1.15 eV) up to a maximal value at an intermediate temperature (*c.* 11–15°C depending on species and process), above which process rates decreased. By contrast, litter consumption in mixed invertebrate species treatments was not significantly influenced by temperature, because of a negative effect of species mixing occurring above 12°C. Nitrogen had a weaker influence, only slightly stimulating litter consumption by mixed-species invertebrates, which limited the scope for synergies with temperature effects.

5. Our results raise issues about how aquatic litter consumers meet their energy requirements at high temperature and suggest that a general consequence of warming could be loss of carbon through mineralisation in headwater stream food webs. In several aspects, our results deviate from expectations based on universal relationships between temperature and individual metabolism (e.g. metabolic theory of ecology), suggesting that we may need to develop less simplistic assumptions to predict the consequence of warming on ecosystem processes.

KEYWORDS
decomposers, litter decomposition, nitrogen, respiration, temperature

1 | INTRODUCTION

Understanding the consequences of global changes for ecosystems is currently one of the major challenges for ecologists. Air temperature is expected to increase by up to 4°C by the end of the century (Collins et al., 2013). Major impacts of temperature change have been documented on virtually all levels of biological organisations, from individual to ecosystem, as temperature is a prominent driver of biological activities that sustain life and major biogeochemical cycles. Temperature effects on individual performance and their consequences on population dynamics and species distribution are relatively well understood whereas mounting evidence indicates that temperature affects carbon (C) uptake, transformation, and release by freshwaters at various spatial and temporal scales (Yvon-Durocher et al., 2012). Although these findings convey the idea that temperature response of ecological processes is predictable, both inconsistent results from different case studies or tested environmental conditions and considerable variation unexplained by temperature call for caution when extrapolating findings. We currently still lack sufficient mechanistic understanding of how temperature effect scales up across different processes, types of organisms (from micro- to macro-consumers) and levels of biological organisation (from individual to community and ecosystem).

In streams and rivers, temperature is expected to increase concomitantly with air temperature (0.6–1.0°C for each degree of increase in air temperature; Eaton & Scheller, 1996), and the trend in surface water warming may be exacerbated by local-scale hydrological alteration and land-use (e.g. riparian forest clearing, presence of dams, channelisation; Poole & Berman, 2001). Plant litter decomposition is a fundamental ecological process in river networks (Petersen & Cummins, 1974), fuelling heterotrophic ecosystems with energy in headwaters (Wallace, Eggert, Meyer, & Webster, 1997). It delivers C products downstream that are stored in sediments or incorporated into biomass, as well as C dioxide that is released to the atmosphere. Litter decomposition involves complex food webs, which typically include various consumers such as microbial decomposers (bacteria and fungi) and invertebrate detritivores (Gessner, Chauvet, & Dobson, 1999; Graça, 2001). The activity of microbial decomposers, dominated by aquatic hyphomycetes (Suberkropp, 1992), is known to increase litter palatability (digestion of refractory litter components) and to improve its nutritive value for invertebrate detritivores, both by increasing litter nutrient content and changing the nature of detritus C compounds (Krauss, Solé, & Krauss, 2011).

Positive effects of water temperature on leaf decomposition have been widely reported in headwater streams over broad (*c.* 5–15°C) temperature gradients (e.g., Ferreira & Canhoto, 2014; Martínez, Larrañaga, Pérez, Descals, & Pozo, 2014). Temperature effects on decomposer biomass and per capita activity should result in changes in litter decomposition rate (Dang, Schindler, Chauvet, & Gessner, 2009). Biological activity of fungal decomposers and invertebrate detritivores is likely to increase with temperature, reaching a stress level above which individual performance declines (cf. thermal performance curves; Dang et al., 2009; Galic & Forbes, 2017). The scarcity of invertebrate detritivores in tropical areas and clear trends for cold-adaptation (Boyero et al., 2012; Irons, Oswood, Stout, & Pringle, 1994) suggest that rising part of the temperature-decomposition relationship occurs over a narrow temperature range and the scope for negative warming effect on decomposition by invertebrate detritivores is large. This hypothesis is supported by results from Friberg et al. (2009) who found the lowest invertebrate detritivore densities in the warmest streams investigated (temperature range 6–23°C). Dominant fungal decomposer communities often comprise both warm- and cold-adapted species, notably in temperate streams (Gessner, Thomas, Jean-Louis, & Chauvet, 1993), suggesting that species replacement along temperature gradient will lead to enhancement of temperature effect over a large temperature range. In tropical streams, aquatic fungal decomposers tend to be as scarce as invertebrate detritivores (Duarte, Bärlocher, Pascoal, & Cássio, 2016; Seena et al., 2019), but could be substituted by a higher biomass of litter associated bacteria (Graça, Hyde, & Chauvet, 2016).

Individual metabolic rate sets the pace at which energy and materials flow in and out organisms, providing a straightforward rationale for linking physiological responses of litter consumers to temperature and its effect on litter decomposition. A universal temperature dependence of metabolic rates demonstrated over a broad range of taxa (Brown, Gillooly, Allen, Savage, & West, 2004; Gillooly, Brown, West, Savage, & Charnov, 2001) should sustain a consistently predictable temperature effect on plant

litter decomposition rate. However, mixed empirical support from streams indicates that metabolic constraints over litter consumers may not be the unique driver of temperature–decomposition relationship (Boyero et al., 2011; Follstad Shah et al., 2017; Gossiaux, Jabiol, Poupin, Chauvet, & Guérold, 2019). Boyero et al. (2011) suggested that adaptation of stream invertebrate detritivores to cold environments may dampen temperature dependence of litter decomposition rate through compensation of microbial versus invertebrate activity as temperature changes. Follstad Shah et al. (2017) further reported temperature dependence of decomposition rate lower than expected based on metabolism but similar to that reported for exoenzyme activity, which would ultimately mediate temperature effects on microbial decomposition and conditioning. The latter study further indicates that temperature change might differentially affect litter decomposition rate depending on the quality of leaf litter prior incubation or the climatic region where decomposition occurs (Follstad Shah et al., 2017). These findings together with several other results point toward the fact that response of litter decomposition to temperature might be more complex and less predictable than generally expected based on individual metabolic response.

Mounting evidence indicates that temperature increase challenges the ability of consumers to meet their nutritional requirement (Lemoine & Burkepile, 2012). Resource availability and quality to microbial decomposers and invertebrate detritivores should be therefore important in mediating the temperature sensitivity of litter decomposition rate (e.g. Ott, Rall, & Brose, 2012). Microbial decomposers strongly rely on dissolved nutrients to meet their requirements for biomass and exoenzyme production (Cheever, Kratzer, & Webster, 2012; Gulis et al., 2017). Dissolved nutrients also benefit to invertebrate detritivores as nutrient immobilisation in microbial biomass increases litter palatability through lessening stoichiometric imbalance between invertebrate detritivore needs and their resources (Frainer et al., 2016; Manning et al., 2015). Nutrient availability could thus mediate the response of litter consumers and overall decomposition rate to temperature. Results from laboratory microcosm experiments suggest that temperature enhances nutrient use efficiency of microbial decomposers and that temperature and nutrient availability act synergistically to determine microbial decomposition rate (Fernandes, Seena, Pascoal, & Cássio, 2014; Ferreira & Chauvet, 2011). Invertebrate detritivores may better cope with energetic challenge posed by increased temperature through feeding on nutrient-enriched resources. However, such synergistic effect may not be apparent if high nutrient loading negatively affects invertebrate performance as suggested in a previous study hinting at reduced invertebrate-mediated decomposition of plant litter in highly eutrophic streams (Woodward et al., 2012). An integrated understanding of how different consumer types (e.g. microbes versus invertebrates) respond to joint effect of temperature rising and nutrient input (e.g. for inorganic nitrogen [N], caused by agricultural practices or atmospheric deposition) is essential if we are to understand the impact of global changes on litter decomposition.

In this study, we sought to gain a better mechanistic understanding of how water temperature influences litter decomposition rate by examining the metabolic response of microbial decomposers and invertebrate detritivores to rising temperature, and the consequences for their contribution to litter decomposition (hereafter microbial decomposition and invertebrate litter consumption, respectively). In a controlled laboratory experiment we manipulated temperature along with nutrient availability in a fully factorial fashion so as to test for the role of resource availability and quality to litter consumers in mediating temperature effect on litter decomposition. We focused on inorganic N as nutrient since it is among the main drivers of stream eutrophication across Europe (Galloway et al., 2008) and is an important element potentially mediating temperature effects on decomposition (Fernandes et al., 2014). Mixed-species assemblages were used to assess temperature effect on microbial decomposers whereas it was possible for invertebrate detritivores to obtain both species-specific and assemblage-level responses. Our main expectation deriving from the metabolic theory of ecology (Brown et al., 2004) was that the Arrhenius model with an activation energy of 0.65 eV describes well the pattern of respiration and litter decomposition rates along the temperature gradient. However, different activation energies were expected between response variables (respiration versus litter decomposition) due to possible mismatch between energy demand and resource intake, between osmotrophs (microbial decomposers) and phagotrophs (invertebrate detritivores), between levels of biological organisation (population versus assemblage of invertebrate species), and across N gradient, for instance through releasing consumers from exacerbated resource limitation at high temperature.

2 | METHODS

2.1 | Litter inoculation and microbial activity

Hazelnut (*Corylus avellana* L.) leaf litter was collected just after abscission in the Montagne Noire (southwest of France) during fall 2016, and air dried at room temperature. Leaf disks (12 mm, each including a single secondary vein) were then cut using a cork borer and allocated to the different nutrient-by-temperature treatment combinations. Batches of 240 leaf disks were placed in 16 500-ml Erlenmeyer flasks and autoclaved at 121°C during 20 min in 300 ml of deionised water.

After autoclaving, 300 ml of a microbial spore suspension was added to each Erlenmeyer flask. To obtain the spore suspension, approximately 400 g (dry mass) of alder and oak litter—which are representative of the natural range of litter quality in the Peyreblanque (a stream located in the Montagne Noire)—were used to maximise the fungal diversity in the inoculum. Litter had been distributed in four fine mesh bags placed in this stream for 21 days prior to the experiment. Litter bags were then retrieved from the stream and transported to the laboratory in cooler boxes. Leaves were carefully rinsed with tap water before being placed in 10-L buckets filled

with deionised water, under constant agitation and aeration at 12°C. Inoculation of the Erlenmeyer flasks with the resulting suspension was performed after 48 hr. The density and identity of aquatic hyphomycete conidia in this inoculum were controlled based on microscopic examination of 200 conidia on three replicates of 10 ml of conidial suspension, filtered on a 5-µm membrane and fixed with 0.5% Trypan blue in 60% lactic acid. Each 10-ml aliquot contained *c*. 11,000 conidia (10,926 ± 1,721 *SD*) belonging to 8–11 species. Conidial assemblages were dominated by *Flagellospora curvula*, *Articulospora tetracladia*, *Alatospora acuminata*, and *Tetrachaetum elegans* (40.2, 33.7, 10.0, and 7.0% of total conidia, respectively). After 48 hr, conidial suspension was replaced by 300 ml of filtered (Whatman International; 0.45 µm pore size) stream water with or without addition of KNO_3 depending on N treatment. Water originated from the Corbières stream (43°27′11″N, 2°16′49″E, 880 m above sea level), a circumneutral oligotrophic stream of the Montagne Noire ([P-PO_4^{2-}] < 8.0 µg/L, [N-NO_3^-] = 0.71 mg/L), was used for this purpose. The stream water with or without KNO_3 was renewed 3 times a week during the subsequent 2 weeks.

Four different N levels were used, with one *ambient* treatment, corresponding to the stream N concentration (0.71 mg/L ± 0.01 *SD*, *n* = 3), and three enriched treatments with KNO_3 addition of 0.7, 1.4, and 2.1 mg N/L (final concentrations 0.71, 1.41, 2.11, and 2.81 mg N/L). This range reflects the *natural* variations of N concentrations among streams in the Montagne Noire. One Erlenmeyer flask from each nutrient treatment was allocated to one temperature among four (8, 10, 12, or 14°C), leading to a total of 16 (i.e. 4 × 4) N × temperature combinations. Temperature levels correspond to a natural range of variations that occurs during spring—the season at which the experiment was carried out—in the Montagne Noire streams. Temperature treatments were achieved by regulating the temperature in large containers (30 × 52 × 16 cm) filled with 8 L of tap water and used as water baths set in an 8°C air-conditioned room. All the Erlenmeyer flasks belonging to the same temperature treatment were placed in the same water bath, in which temperature was regulated using heating cables and constantly monitored using data loggers (HOBO Temperature DataLogger; Onset Computer Corporation). During microbial inoculation, oxygen supply and leaf disk agitation were carried out by a homogenous aeration using a Pasteur pipette.

2.2 | Feeding experiment and leaf decomposition

After 14 days of inoculation, batches of 10 leaf disks from the different N × temperature combinations were distributed to feeding microcosms. All remaining leaf disks were frozen for later elemental analyses (see below). Feeding microcosms consisted in plastic containers (11 × 8 × 3 cm) supplied with homogenous substratum (*c*. 40 g of sand, grain size < 2 mm). They were filled with 100 ml of filtered stream water with or without added KNO_3 depending on N treatment and placed in the water bath at the corresponding temperature. Each feeding microcosm contained either no invertebrate (control), three individuals belonging to the same species (single-species treatments), or three individuals belonging to three different species (mixed-species treatment). These species included a freshwater crustacean *Gammarus fossarum* Koch and two caddisfly larvae, namely *Sericostoma personatum* Kirby & Spence and *Potamophylax cingulatus* Stephens. *Potamophylax* larvae were collected in the Peyreblanque stream, while *Sericostoma* and *Gammarus* originated from nearby streams (Alzeau and Corbières, respectively). All invertebrates were acclimated to laboratory conditions for 7 days and starved for 3 days prior to the experiment, at the temperature corresponding to the treatment they were attributed to. All N × temperature combinations were fully crossed with the five invertebrate conditions (control, three single-species treatments, one mixed-species treatment), and all combinations were replicated three times, which led to a total of 16 × 5 × 3, i.e. 240, microcosms.

The feeding experiment ended at different times according to the rate at which leaf disks were consumed in each invertebrate detritivore treatment. It lasted *c*. 6, 24, 30, and 52 hr for *Potamophylax*, mixed-species treatment, *Gammarus*, and *Sericostoma*, respectively. At the end of the experiment, seven leaf disks from the control microcosms (without invertebrate detritivores) were collected and freeze-dried for later ergosterol analysis. The three other leaf disks were used to measure microbial respiration. Disks from other invertebrate detritivore treatments as well as invertebrate detritivore individuals were frozen, freeze-dried and weighed to the nearest 0.01 mg to determine invertebrate consumption rates. Leaf microbial decomposition rate was expressed as the difference between initial and final litter C mass divided by time. Invertebrate consumption rate was calculated as the difference between C mass of consumed and control (i.e. from the corresponding treatment without invertebrates) leaf disks and was expressed per invertebrate dry mass and time. For these calculations, a constant proportion of 47% of C in the litter was assumed (as determined by C analysis, see below).

2.3 | Respiration measurements

Respiration was measured after the end of the feeding experiment on batches of three control leaf disks (from treatments without invertebrates), as well as on additional (i.e. not used in the feeding experiment) individuals of the three invertebrate detritivore species (× 12 replicates). Analyses were performed in climatic chambers using 24-well microplates with one oxygen sensor spot at the bottom of each well (SDR SensorDish ®; PreSens Precision Sensing). Microbial respiration was measured in all temperature × N combinations, while invertebrate respiration was assessed in stream water only (no KNO_3 addition). Each invertebrate individual was tested at a single temperature at which it was acclimated and starved for 48 hr prior to the assay. After the assay, invertebrates and leaf disks were frozen, freeze-dried, and weighed to the nearest 0.01 mg. At each assay, wells containing water only were used as blanks.

Each assay ran for up to 1 hr, with the first 10 min being excluded from the analysis. For invertebrates, assays were stopped when O_2

concentration fell below 80 µmol O_2/L, a threshold below which O_2 concentration decrease became non-linear. Oxygen consumption rates were then calculated as the O_2 concentration decrease per unit of time, and respiration rates as the mass of C emitted per unit of time and litter or invertebrate dry mass, while assuming a respiratory quotient equal to 1 (i.e. 1 mole of CO_2 emitted for each mole of O_2 consumed). The microbial respiration associated with the caddisfly cases was considered negligible due to their mostly mineral nature. The three leaf disks were pooled with the seven remaining leaf disks and used for ergosterol analysis. Temperature inside the chambers was constantly monitored during the respiration assays using the HOBO data loggers.

2.4 | Ergosterol and elemental analyses

Carbon and N litter analyses were performed on extra batches of 10 leaf disks after microbial inoculation for each combination of N × temperature. Nitrogen litter concentration was determined using a CHN analyser (Flash 200, ThermoFisher Scientific) on ground material (mixer mill Retsch MM200; Retsch, Haan, Germany). Ergosterol content of the leaf disks, as a biomarker for fungal biomass, was determined by high-performance liquid chromatography after extraction in alkaline methanol and purification of the extract by means of solid-phase extraction (Gessner, 2005). Fungal biomass was determined from a standard conversion factor between ergosterol content and fungal biomass (5.5 mg ergosterol per g of mycelium; Gessner & Chauvet, 1993).

2.5 | Statistical analyses

To investigate the temperature effect on processes, we used the linearised Arrhenius relationship between log-transformed process rates and temperature (Gillooly et al., 2001). This allowed us to determine the activation energy of the process, which can be used for comparison of temperature effects across processes and studies. To standardise temperature, values were centred around 10°C (see Perkins et al., 2012).

$$\ln(I) = \ln\left[I\left(T_c\right)\right] - Ea \times \left(1/kT - 1/kT_c\right)$$

where I is the process rate, $I(T_c)$ the value of I at 10°C, Ea the activation energy (eV), k the Boltzmann constant (8.672×10^{-5} eV/K), T the temperature (K), and T_c the standard temperature (i.e. 10°C = 283.15 K).

One ANCOVA model was performed for each process (respiration and leaf decomposition) and organism separately (i.e. microbes, invertebrate single-species, and mixed-species) to test for the combined effects of temperature and N concentration. Because we did not expect a linear response of processes to N availability, N was included as a factor in the models. For microbial processes, litter N content and fungal biomass, the statistical analyses were performed on the average values of samples originating from the same Erlenmeyer flask to avoid pseudo-replication. For invertebrates, because processes followed hump-shaped relationships, ANCOVAs (using the Arrhenius model) were fitted on the rising part of the curves (i.e. excluding the highest temperature level), while gross N effects were tested separately using ANOVAs (with Tukey HSD post hoc comparisons) including the entire temperature gradient.

The ratio between respiration and decomposition rate (i.e. microbial decomposition and invertebrate consumption), which scales with the proportion of detrital C converted into decomposer biomass, was compared between organisms and along the temperature gradient using an ANCOVA with species identity and temperature as explanatory variables. ANCOVAs were also used to compare fungal biomass and litter N content among temperature (continuous) and N availability (factor, 4 levels) treatments. For each ANCOVA model, the comparison between N availability levels was performed using Tukey HSD test when N availability had a significant effect.

Finally, the effect of invertebrate species mixing on leaf consumption rates was addressed using the comparison between observed and expected values of this process (Chapman, Whittaker, & Heal, 1988):

$$\text{Mixing effect} = \left(\text{Observed} - \text{Expected}\right) / \text{Expected}$$

where Observed values are the feeding rates in three-species assemblages and Expected values are based on the sum of the average feeding rate of each taxa in single-species treatments. Mixing effects were considered significant when the 95% confidence interval did not overlap 0.

All statistics were performed using R 3.3.1 (R Core team, 2016).

3 | RESULTS

3.1 | General trends

A two-fold range (*c*. 8–16°C) was achieved for water temperature when assessing respiration rate of microbial communities on leaf litter and individual invertebrate detritivores. Due to practical limitations, a lower upper temperature level (*c*. 14°C) was achieved during experiment assessing litter decomposition rate. Response variables tended to be greater at high versus low temperature. Temperature effects were stronger on respiration than on litter decomposition rates for all organisms (microbial communities and the three invertebrate species). This pattern resulted in a decrease of the decomposition/respiration ratio along the temperature gradient, though with contrasting severity across organisms (Figure 1). Nitrogen addition had less consistent and most often weaker effects on response variables than temperature. The lack of significant interaction indicates that N addition did not alter temperature effects (Table 1).

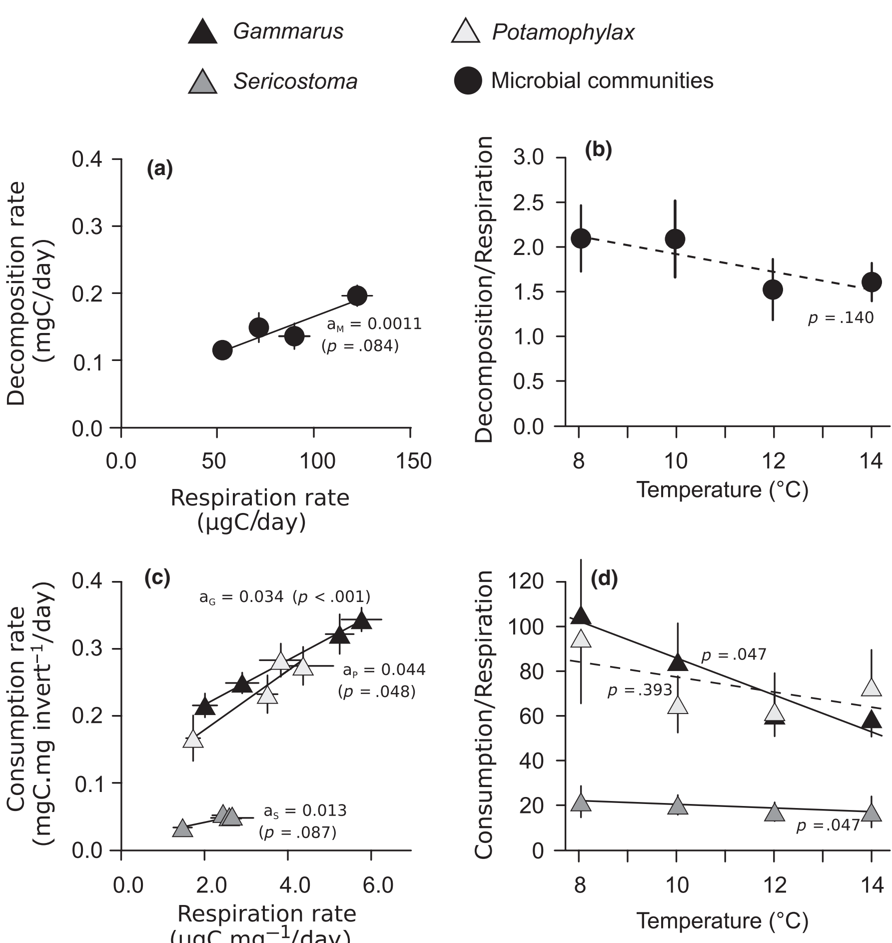


FIGURE 1 (a) Relationship between microbial decomposition and respiration; (b) variation of the microbial decomposition/respiration ratio along the temperature gradient; (c) relationship between invertebrate litter consumption and respiration; and (d) variation of the invertebrate consumption/respiration ratio along the temperature gradient. Microbial processes are expressed per batch of 10 leaf disks, while invertebrate processes are expressed per unit of invertebrate dry mass. In (a) and (c), the four symbols correspond to the different temperature treatments and the error bars are *SE*. The slopes of the regressions (plain lines when significant; dashed lines if non-significant) are given for each organism (a_G: *Gammarus*, a_P: *Potamophylax*, a_S: *Sericostoma*, a_M: micro-organisms) together with the corresponding *p*-values. All values are averaged across N treatments. To calculate errors associated with the ratio of average decomposition and respiration rates (b and d), we used a propagation of uncertainty assuming that the relative error of the ratio equals the sum of the relative errors of leaf decomposition and respiration rates

3.2 | Microbial decomposers

Microbial respiration and to a lesser extent microbial decomposition increased nearly exponentially along the temperature gradient (Figure 2a,d) and this effect was independent of N content (ANCOVA; interaction temperature × N: $p > 0.5$; Table 1). Activation energies (± 95% confidence interval) estimated over all N levels were 1.00 ± 0.23 eV and 0.56 ± 0.53 eV for litter respiration and decomposition rates, respectively (Table 1). However, when corrected for fungal biomass, the activation energy of microbial respiration fell close to that of microbial decomposition (0.55 ± 0.22 eV). Fungi achieved higher biomass and litter contained more N at high versus low temperature (Table 1) and this temperature effect seems to reach a plateau between 10–12°C for fungal biomass whereas saturation was less evident for litter N content (Figure 3).

Leaf microbial decomposition was slightly higher at intermediate than at the lowest N level (ANCOVA Table 1; Figure 4a) while respiration was not significantly influenced by N concentration (ANCOVA Table 1; Figure 4d). Nitrogen effects on microbial leaf decomposition were not reflected by changes in fungal biomass (ANCOVA Table 1) and litter N content, although the latter effect was close to significance level (ANCOVA Table 1), with slightly lower N litter content in the N-poor (1.59% litter dry matter ± 0.11 *SD*) than in the N-rich treatment (1.74% litter dry matter ± 0.14 *SD*).

3.3 | Invertebrate detritivores

Detritivore dry mass varied across species (*Gammarus*: 2.5–9.1 mg; *Potamophylax* 15.7–61.7 mg; *Sericostoma* 7.6–22.8 mg) but biomass variations were randomly distributed over N and temperature

TABLE 1 *p*-values associated with ANCOVA models testing for the effect of temperature, N treatments and their interaction on microbial and invertebrate processes as well as N and fungal biomass litter content

	Temperature (*df* = 1)	Nitrogen (*df* = 3)	Interaction (*df* = 3)
Microbial			
Decomposition			
mg C/day	**0.036**	0.058	0.539
Respiration			
mg C mg litter DM^{-1}/day	**<0.001**	0.698	0.616
Litter			
N content			
% of litter DM	**0.017**	0.067	0.116
Fungal biomass			
% of litter DM	**0.003**	0.933	0.843
Invertebrates			
Gammarus			
Consumption			
mg C mg invert. DM^{-1}/day	**0.001**	0.609	0.226
Potamophylax			
Consumption			
mg C mg invert. DM^{-1}/day	**0.021**	0.109	0.827
Sericostoma			
Consumption			
mg C mg invert. DM^{-1}/day	0.118	0.494	0.645
Mixed-species			
Consumption			
mg C mg invert. DM^{-1}/day	0.877	**0.032**	0.460

Note: For microbial and invertebrate processes, the temperature effect was fitted according to the Arrhenius linearised model (see Methods), while for litter N and fungal biomass, a linear relationship was assumed. N treatments were included as a factor. Significant *p*-values are given in bold.

treatments (ANOVA, $p > 0.897$ and $p > 0.183$ for feeding and respiration assays, respectively). Temperature stimulated invertebrate detritivore respiration and leaf litter consumption significantly (Table 1) until *c*. 11–15°C (depending on the process), temperature above which activities began levelling out or declined slightly (Figure 2b,e). An exception is leaf consumption by *Sericostoma* and by the mixed invertebrate assemblage, for which temperature effect was not significant (Tables 1 and 2). Activation energies calculated for each process (excluding the highest temperature tested) differed substantially among species, with *c*. 2-fold differences between extreme values (Table 2). When calculated across invertebrate detritivore species, activation energies (± 95% confidence interval) were 0.93 ± 0.29 eV for respiration rate and 0.56 ± 0.46 eV for litter consumption rate. When the three invertebrate detritivore species were mixed together, activation energy for litter consumption rate was close to 0 eV (0.12 ± 0.31; Table 2, Figure 2c). This result arises because invertebrate detritivore mixing led to antagonistic effect on litter mass loss at the high temperature levels (12 and 14°C) whereas additive mass loss was recorded at low temperature (Figure 5). ANCOVAs (based on three temperature levels for invertebrate consumption rate) revealed no significant N effect and no interaction between N level and temperature (Table 1), except for leaf consumption by mixed invertebrate assemblage, which slightly increased with N supply (Table 1; Figure 4c).

Even when including the high temperature level in the analysis, leaf consumption by invertebrates was not significantly affected by dissolved N availability in single invertebrate detritivore species treatments (ANOVAs: *Gammarus*: $p = 0.269$; *Sericostoma*: $p = 0.074$) except for *Potamophylax* (ANOVA: $p = 0.023$) with the consumption rates at intermediate N levels being 1.4–1.9 times higher than at the lowest and highest N concentrations (Figure 4b). Leaf consumption in mixed-species treatments increased with N availability, with a 29.5% higher consumption in the N-rich than in the N-poor treatment (Figure 4c). This result occurs together with a significant negative mixing effect on leaf consumption in the N-poor treatment only (Figure 5b).

4 | DISCUSSION

A striking pattern across our results is that temperature had most often a stronger stimulating effect on respiration rate of litter consumers (i.e. microbial communities and invertebrates) than on litter decomposition rate. Such results raise fundamental questions on how these consumers meet their energy requirements at high temperature, since apparent exploitation of energy and nutrients from leaf litter does not increase as fast as metabolic cost. If we assume rates of resource consumption to be proportional to amounts of assimilated energy and nutrients by litter consumers, temperature rise may actually decrease the efficiency of the conversion of litter material into consumer biomass and exoenzymes. Previous studies have reported negative temperature effect on C use efficiency in microbial decomposers (Allison, Wallenstein, & Bradford, 2010) and on ingestion efficiency in animals (Rall, Vucic-Pestic, Ehnes, Emmerson, & Brose, 2010). As rate of litter mass loss driven by microbial decomposers and invertebrates does not increase with temperature as fast as microbial respiration rate, we can also expect that warming will promote transformation of litter C into CO_2 and therefore accelerate the return of aquatic detrital C to the atmosphere (Boyero et al., 2011).

Here we report a strong difference in the temperature sensitivity of microbial versus invertebrate-mediated decomposition as activation energy of litter consumption rate by the three-species invertebrate assemblage is nearly five-fold lower than that estimated for the decomposition driven by microbial decomposer assemblages. Temperature invariance of litter decomposition rate in streams along latitudinal gradients has been associated with a greater diversity and

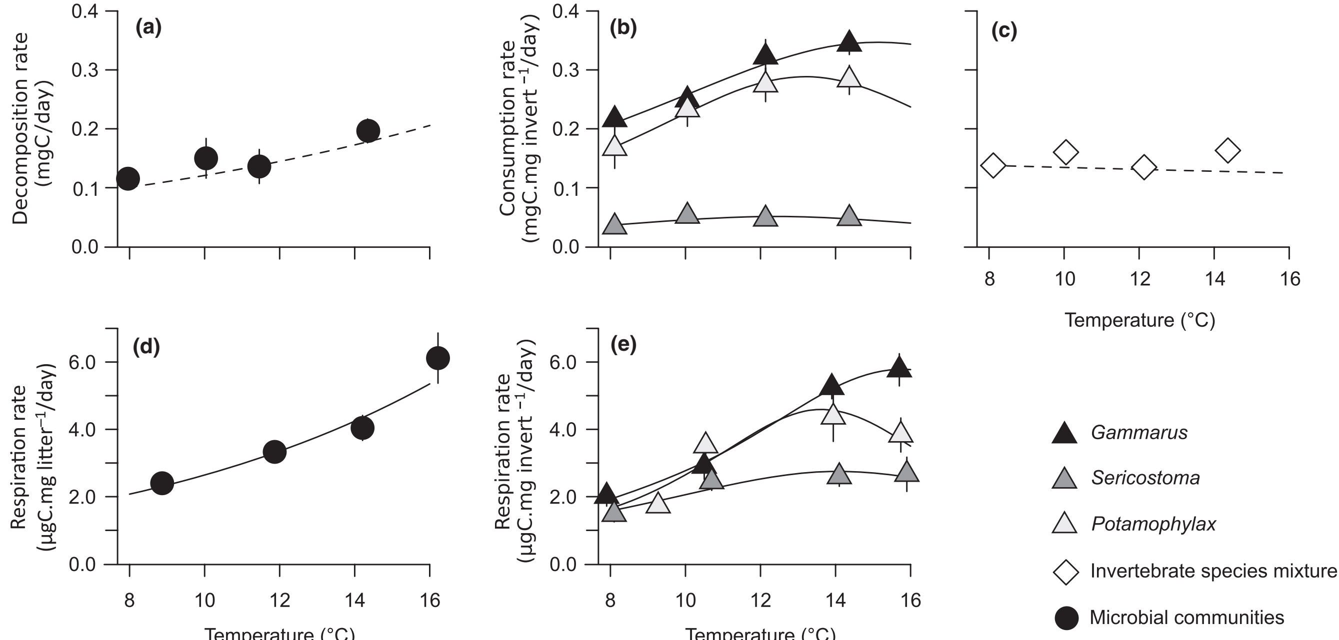


FIGURE 2 Average (± *SE*, *n* = 12) litter decomposition (a–c) and respiration rates (d, e) along the temperature gradient in microbial communities (a, d), invertebrate single-species treatments (b, e), and invertebrate species mixture (c). For microbial processes (a, d), the regression lines are the Arrhenius models. For invertebrates (d, e), we computed Lorentzian models using non-linear regressions to illustrate the decrease of the processes at the high temperature treatments. The dotted lines indicate non-significant fits. Respiration rates are calculated assuming a respiratory quotient of 1 (see Methods)

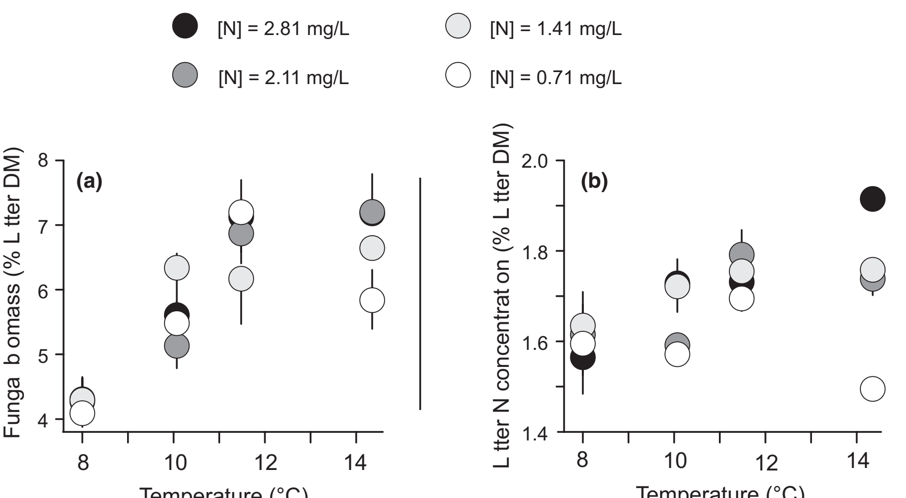


FIGURE 3 Average (± *SE*, *n* = 12) (a) fungal biomass and (b) N litter concentration along the temperature gradient in different N availability treatments

abundance of invertebrate detritivores in cold versus warm climatic zone (Dobson, Mathooko, Magana, & Ndegwa, 2002), leading to higher invertebrate-driven decomposition at high latitudes (Boyero et al., 2011, 2012; Irons et al., 1994) while microbial organic matter decomposition follows the opposite pattern (Boyero et al., 2011; Irons et al., 1994; Tiegs et al., 2019). In our study, as invertebrate detritivore density and diversity were set constant, temperature invariance of litter consumption rate in invertebrate detritivore assemblages was mediated by per capita effects. Two nonexclusive mechanisms can explain this result: (1) invertebrate detritivore species displayed variable response to temperature and therefore may complement each other along the temperature gradient (i.e. insurance hypothesis; Yachi & Loreau, 1999); (2) interspecific interaction shifts from neutral below 11°C to antagonistic above this value, probably because increased invertebrate detritivore foraging activity exacerbates competition for leaf litter consumption. These two mechanisms may be prevalent where local invertebrate detritivore diversity is high, notably in temperate regions (Boyero et al., 2012), although per capita effects might, in fact, be small compared with demographic response in mediating temperature effect on litter decomposition. For instance, the positive effect of temperature on microbial respiration in part arises from increased fungal biomass (with possible shifts in community composition), in combination with a stimulation of fungal mass-specific activity.

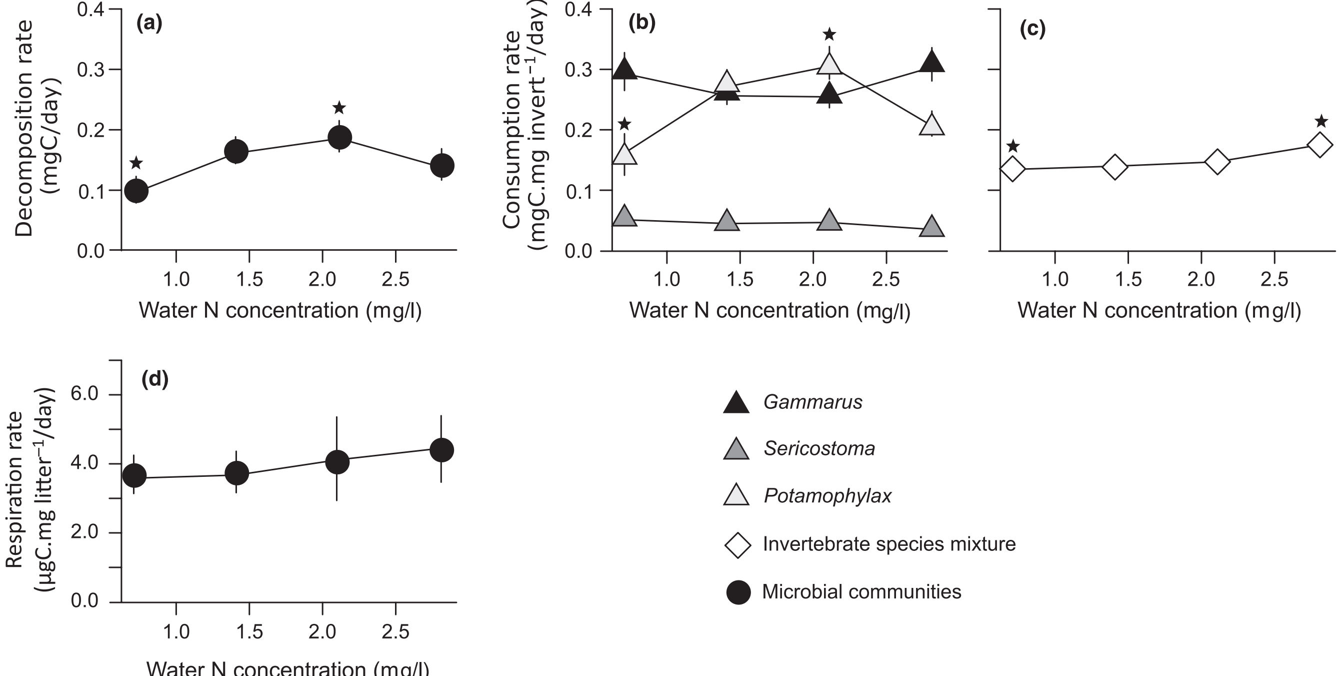


FIGURE 4 Average (± *SE*, *n* = 12) litter microbial decomposition rates (a), invertebrate consumption rates (b,c), and microbial respiration rates (d) along the N availability gradient in microbial communities (a, d), invertebrate single species treatments (b), and invertebrate species mixture (c). Stars indicate the N treatments for which the response variable significantly differs from each other for a given decomposer assemblage (Tukey HSD). Respiration rates are calculated assuming a respiratory quotient of 1 (see Methods)

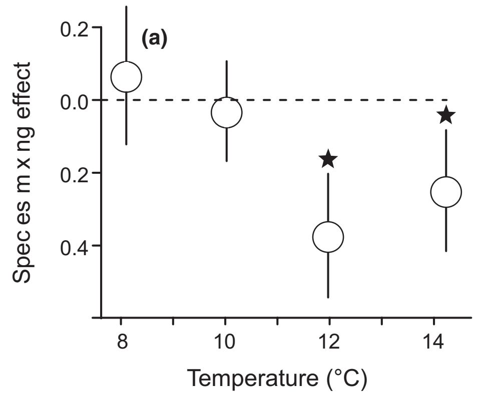
TABLE 2 Activation energy (± 95% confidence interval) of the Arrhenius models linking respiration and leaf decomposition (i.e. microbial decomposition and invertebrate consumption) rates to temperature for the different organisms and levels of biological organisation

	Respiration	Leaf decomposition
Microbial community	1.00 ± 0.23*	0.56 ± 0.53*
Mass-specific fungal processes	0.55 ± 0.22*	–
Gammarus	1.15 ± 0.36*	0.69 ± 0.39*
Potamophylax	0.99 ± 0.56*	0.86 ± 0.69*
Sericostoma	0.55 ± 0.39*	0.47 ± 0.60 n.s
Invertebrate mixed-species	–	0.12 ± 0.31 n.s

Note: Significant estimates are given with the symbol *, and non-significant estimates with n.s.

These findings support the idea that the relative importance of microbial decomposers and invertebrate detritivores to litter decomposition may shift along temperature gradients, towards higher microbial contribution with increasing temperature. In contrast, Follstad Shah et al. (2017) did not report difference in the temperature sensitivity of litter decomposition assessed in the field, whether it was driven by microbial decomposers alone in fine mesh bags or together with invertebrate detritivores in coarse mesh bags. The latter study however suggests that temperature sensitivity estimated by the mean of Arrhenius model can be variable depending on the climatic region (e.g. tropical versus temperate) and litter quality (see also Gonçalves, Graça, & Canhoto, 2013), for instance. Previous studies have suggested that nutrient availability could also drive variation in temperature response of litter decomposition (Fernandes et al., 2014; Ferreira & Chauvet, 2011). Here we did not detect a significant interaction between N availability and temperature despite plausible mechanisms from which this pattern may arise (Cross, Hood, Benstead, Huryn, & Nelson, 2015). High growth or activity, as entailed by increased temperature, has to be fuelled with the necessary elements (i.e. nutrients), which can be limiting in the environment (as N is for microbial decomposers) (Ferreira et al., 2015). Relaxing this limitation may thus ensure them to achieve higher biomass per unit of detrital C and higher production of exoenzyme per biomass unit, providing condition for larger temperature effect size. We found that microbial decomposition on hazelnut litter was limited below inorganic N concentration of 1 mg N/L, which is consistent with the results of previous studies on hazelnut litter (Jabiol, Lecerf, Lamothe, Gessner, & Chauvet, 2019). This weakness of a N effect, possibly explained by limiting phosphorus concentrations in stream water (Güsewell & Gessner, 2009), reduced the scope for strong synergies with temperature effect on microbial decomposition but also on invertebrate detritivore litter consumption, since nutrient effects on invertebrate litter consumption are mediated by microbial litter conditioning (Manning et al., 2015).

Our study used short term time scales to assess temperature effects on stream organisms and decomposition rates, precluding generalisation to consequences of climate warming for *in natura* litter decomposition. Moreover, the assumption of an invariant respiratory quotient (RQ = 1) is clearly wrong (e.g. Dilly, 2003; Romero-Kutzner



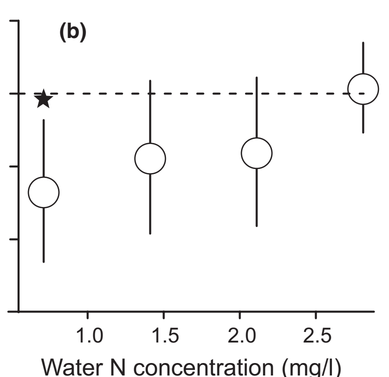


FIGURE 5 Invertebrate detritivore species mixing effect (± 95% confidence interval) on leaf consumption rates along the (a) temperature and (b) N availability gradients. Mixing effect was considered significant when 95% confidence interval did not overlap 0

et al., 2015) and often made because of a lack of comprehensive data. Another potential limitation of leaf litter respiration data is that microbial communities associated with leaf litter may include some autotrophs as well as heterotrophs that are not involved in leaf decomposition. This could explain why microbial respiration rates increased more quickly with temperature than litter decomposition did. The use of labelled C sources, for instance, could help future studies to elucidate the variations of the respiratory quotient of leaf decomposers along gradients of environmental conditions (e.g. temperature, C quality, nutrient availability). Such studies are clearly required to support the reliable C fluxes estimations needed for global C cycle modelling.

Our results remain helpful to explain reported patterns of temperature effect on litter decomposition assessed in the field and inform future research. Field studies involving respiration assessments over broad temperature gradients are now needed to test if our predictions hold true in a more realistic context. An important point to make here is to recognise the complexity of patterns and processes underlying temperature effect on litter decomposition. The metabolic theory of ecology provides a valuable framework to describe broad-scale patterns of temperature sensitivity of litter decomposition rate and eventually to quantify it (Follstad Shah et al., 2017; Tiegs et al., 2019). However, systematic deviation from, and large noise around, prediction of the heuristic metabolic theory of ecology model suggest that we must move forward toward less simplistic assumptions. Our results show that: (1) the assumption of monotonicity does not hold (at least for invertebrates); (2) species or consumer types (i.e. microbes versus invertebrates) are not equal in how their performance changes with temperature; and (3) litter consumer metabolism is not the sole constraint over temperature response of litter decomposition.

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CONFLICT OF INTEREST

No conflict of interest.

DATA AVAILABILITY STATEMENT

All data is available on demand and on the French data repository system HAL (CNRS).

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