LIMNOLOGY and OCEANOGRAPHY

Strategies of shredders when feeding on low-quality leaf-litter: Local population adaptations or fixed species traits?

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Abstract

The linkage between leaf-litter and macroinvertebrate shredders is pivotal for stream food webs. Global change is predicted to decrease the nutritional quality of litter inputs to streams. However, little is known about shredder's ability to develop local interpopulation adaptations to face nutrient-depleted leaf-litter. We hypothesized that this adaptation could be present in populations receiving low-quality leaf-litter. We performed feeding tests on three abundant shredders species from lowland (a snail) and mountain (two insects) streams. Two populations of each species were derived from two subregions contrasting in average quality of litter inputs. Individuals were fed on four diets of contrasting quality: two leaf-litter species with two qualities each, and their feeding rates, survivorship, growth, and energetic storage were evaluated. Results suggest that local population adaptation to low-quality litters is not common, being essentially a fixed species trait that varies across species, in particular among snails and insects. The ability of the snail to cope with low-quality litters suggests that ecosystem processes in lowland streams may resist reductions in litter quality. Conversely, potential alterations of riparian vegetation linked to global changes might disrupt mountain stream ecosystem functioning.

Studies on resource–consumer interactions point to major impacts of global changes on the functioning of green and brown food webs (e.g., Hoekman 2010; West and Post 2016). However, the inherent complexity of species interactions and the diversity of species-specific responses hinder forecasting ecosystem alterations triggered by global changes (Winder and Schindler 2004; O'Connor et al. 2012). In headwater forest streams, food webs rely greatly on terrestrial subsidies of organic matter, i.e., leaf-litter (Collins et al. 2016). For these ecosystems, changes in resource–consumer interaction can modify the flux of energy and matter to higher trophic levels (Covich et al. 1999; Piscart et al. 2011). Two primary intrinsic factors drive this interaction, (1) the quality of leaf-litter as a food, and (2) feeding behavior and digestive performance of shredder species (Graça 2001; Graça et al. 2015).

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Leaf traits of the riparian vegetation could change significantly in global warming scenarios, mostly in subtropical and mid-latitude regions where aridity, risk of heat waves and drought frequency increase (Giorgi and Lionello 2008; Spinoni et al. 2018). There, increasing frequency of stream segments with intermittent flow is expected, giving rise to canopy openings and changes in the composition of riparian vegetation (Salinas and Casas 2007; Stromberg et al. 2013). Climate change might also trigger significant shifts in leaf traits—e.g., increasing toughness, silica (Si), concentration and carbon (C) : nutrient ratio—due to changes in plant functional types of the riparian vegetation, even if the threshold between permanent and intermittent discharge is not crossed (Salinas et al. 2018). Moreover, land-use changes, e.g., native forest replacement by plantations and invasions by exotics tree species, often result in substantial declines in leaf-litter quality (high toughness and C:nutrients ratios) entering streams (Richardson et al. 2007). This is particularly true in northern temperate regions where native riparian species are of notably higher nutritional quality than non-native counterparts (Ferreira et al. 2016; 2019). High toughness and C : nutrients ratios are often reported to negatively affect palatability and digestibility of leaves (Graça and Cressa 2010; Cooke et al. 2016). In addition, climate change could prompt to important intraspecific leaf trait changes. The high phenotypic

plasticity and elevated responsiveness of plants to climate variations and CO_2 concentration at leaf-level (Sultan 2000; Stiling and Cornelissen 2007) often lead to a high intraspecific variability of leaf traits, reaching even the level of interspecific variation (Lecerf and Chauvet 2008; Albert et al. 2010). A growing body of evidence points to major consequences of intraspecific leaf-trait plasticity on resource–consumer interactions, with ripple effects on ecosystem functioning (e.g., Tuchman et al. 2002; Kominoski et al. 2007; Graça and Poquet 2014).

Climate and land-use driven changes in litter-quality might exacerbate the already large nutritional imbalance of detritivores in headwater streams (Cross et al. 2005; Lauridsen et al. 2012). The theory of ecological stoichiometry proposes that organisms must develop strategies to maintain elemental homeostasis when feeding on nutrient-poor resources: i.e., preferential selection of nutrient-rich resources, increased consumption of the nutrient-poor resource to compensate deficiencies, and/or some mechanisms of post-ingestive regulation (Sterner and Elser 2002; Frost et al. 2005). Few studies have comprehensively tested these capabilities on stream shredders fed on low-quality litters, and data available point to different limitations, conflicting results, or species-specific idiosyncrasies (Fuller et al. 2015; Santonja et al. 2018). For example, it seems that successful search and finding of sparse food with a high nutritive value is a highly random process (Motyka et al. 1985) that requires a great investment of energy, this being reserved only to highly mobile species (Cruz-Rivera and Hay 2000). Yet, higher feeding rates on high-quality resources appears to be the norm for shredders belonging to different phylogenetic groups when using single leaf-litter species treatments in laboratory experiments (e.g., Santonja et al. 2018). Moreover, several studies have reported either that compensatory feeding on low-quality leaf-litter may be sufficient to balance, or even overcompensate, the growth obtained when fed on high-quality resources (e.g., Swan and Palmer 2006; Fuller et al. 2015), or not (Flores et al. 2014). These conflicting results have been described for the same shredder species; as an example, both preferential (Tuchman et al. 2002; Halvorson et al. 2015) and compensatory feeding (Anderson and Cummins 1979; Fuller et al. 2015) have been reported in *Tipula abdominalis*. Therefore, some shredder species can show plasticity in the way they cope with low-quality food sources. This trait variation may be important in heterogeneous regions, such as the Mediterranean Basin (Bonada et al. 2007), enabling shredders to use efficiently the leaf-litter that is locally abundant (Jackrel and Wootton 2014). However, to our knowledge this intra-species adaptation has been poorly studied in riverine shredders.

Here, we investigate whether three species of shredders present either fixed-species traits or local adaptations to cope with variations in the nutritional value of leaf-litter, related to toughness, Si, phosphorus (P) (interspecific changes in leaf-litter) and nitrogen (N) (interspecific and intraspecific changes in leaf-litter) concentrations. To this end, we performed feeding trials to evaluate the effect of variability in leaf-litter quality on feeding rates, survivorship, growth and energetic storage of three shredder species, each one from two regions with contrasting climate. We hypothesized that if adaptation to poorer diets exists, this should be perceptible in shredder populations from streams in warmer or warmer/arid zones, where leaf-litter inputs are expected to be of lower nutritional quality compared to relatively mesic/cold regions. We also hypothesize that interspecific changes in the nutritional quality of leaf-litter would exert greater influence on feeding performance than intraspecific ones, due to high interspecific variation in other leaf traits influencing palatability/digestibility.

Materials and methods

Regions of origin of shredders

We selected macroinvertebrate shredders from four subregions located in Andalusia (southern Spain). This Mediterranean region has remarkable lithological and climatic diversity (Casas et al. 2006), which favors finding a given species within contrasting climatic conditions. Taxonomic composition of the shredder guild often varies depending on lithology of the drainage basin (Casas et al. 2011). Thus, for intra-species comparison of feeding performance we selected two subregions, widely differing in climate within each of the main lithological settings: siliceous vs. calcareous (Table 1). Within the siliceous setting, we chose the cold and subhumid Sierra Nevada (henceforth "S-cold/subhumid") and the warm and perhumid Alcornocales (henceforth "S-warm/perhumid") subregions (Table 1). In the calcareous setting, we selected the two climatic extremes in the region: the warm and semiarid lowlands of Almería (henceforth "C-warm/semiarid") and the warm and perhumid Grazalema (henceforth "C-warm/perhumid") (Table 1). In the siliceous subregions, we chose two of the most frequent and abundant shredders in mountain headwater streams in Andalusia: the caddisfly *Allogamus mortoni* (Navàs 1907) and the cranefly *Tipula leo* (Dufour 1991). In groundwater-fed low-order streams from the two calcareous subregions, we selected the snail *Melanopsis praemorsa* (Linnaeus 1758), which is an abundant generalist feeder but also behaves as an important leaf-litter shredder (Casas et al. 2011).

Quality of leaves from riparian plants in each subregion, and of leaf-litter used in feeding tests

We characterized leaf quality of the main riparian species in three permanent low-order streams within each of the four subregions. In each stream, percent coverage of all woody species and giant graminoids were recorded between June–July 2013 in six plots (36 m^2 each) randomly distributed in two strata (both stream sides) along a 100 m stream reach. For the four most abundant species in each stream, 102 leaves from

Table 1. Environmental characteristics (mean±SE or range between parentheses; $n = 3$ streams) of the four subregions of origin of shredders.

Subregion name	Lithology	Subregion code	Altitude (m a. s.l.)	Climate			Stream water		
				Annual rainfall (mm)	Annual temperature (°C)	*Q_2	Annual temperature (°C)	pH	EC (µS cm⁻¹)
Sierra Nevada	Siliceous	S-cold/subhumid	1438 (1419–1465)	554 (548–561)	10.7 (−1.1–27.7)	69±4	9.5 (1.2–17.2)	7.25±0.20	169±66
Alcornocales	Siliceous	S-warm/perhumid	448 (388–532)	1240 (1116–1303)	15.2 (6.4–27.5)	215±18	13.3 (8.2–20.1)	6.56±0.14	71±3
Semiarid lowland	Calcareous	C-warm/semiarid	377 (164–576)	348 (297–387)	17.2 (4.6–31.3)	45±3	18.0 (10.4–28.6)	7.98±0.30	2269±710
Grazalema	Calcareous	C-warm/perhumid	460 (305–688)	1189 (1140–1414)	15.0 (4.5–31.3)	160±12	14.8 (13.5–15.0)	7.68±0.21	677±160

*$Q_2 = 2000 \, P/(M^2 - m^2)$, where P, mean annual precipitation; M, mean maximum temperature in the hottest month; m, mean minimum temperature in the coldest month. Annual temperature range: Mean minimum temperature of the coldest month and mean maximum temperature of the warmest month; EC, electric conductivity; m a.s.l., meters above sea level; Q_2, Emberger's bioclimatic coefficient.

six individuals (17 leaves per individual) were collected. We measured specific leaf area (SLA) and toughness for all leaves and %C, %N, %P, %lignin, and %Si for pooled leaves from each individual tree, as proxies of food value for detritivores (Graça and Cressa 2010). We determined specific leaf area (SLA, mm² g⁻¹) by measuring area (WinDIAS 3, Delta-T devices) and dry mass (DM, 60°C, 78 h), and toughness using a calibrated texturometer (TA.XT2 Plus, Stable Micro Systems). Concentrations of C and N were determined using IR mass spectrometry (DELTA V Advantage, Thermo Fisher Scientific®), and those of P and Si using ICP mass spectrometry (iCAP 6500—ICP-OES, Thermo Scientific®). Percent lignin was measured using the acid-detergent method of Goering and van Soest (1970).

For leaf-litter used in feeding tests, we collected two species and two quality classes per species just after abscission (see below). We measured the same parameters (see above) in five randomly selected portions per species and quality class, as well as hemicellulose and cellulose as described in Fenoy et al. (2016). The nutrient concentration (C, N, and P) of leaf-litter was measured in pre-conditioned and post-conditioned material, as well as in fecal pellets produced by the experimental animals (see below).

Leaf-litter species for experimentation and microbial conditioning

To evaluate the effects of inter- and intraspecific variability of leaf-litter quality on shredders performance, we selected two riparian deciduous species: *Alnus glutinosa* (L.) Gaertn. (henceforth *Alnus*) and *Populus alba* L. (henceforth *Populus*), with contrasting leaf traits. The N fixer *Alnus*, common in temperate riparian corridors, is one of the species with highest leaf-N concentration and it has high lignin concentration (Table S1). *Populus* is common in warm temperate and Mediterranean zones. This species has relatively low leaf lignin and N concentrations, but high toughness and Si concentration (Table S1). These traits seem to be favored by climate warming, and the last three are often associated to low nutritional value for invertebrate shredders (Salinas et al. 2018). Senescent leaves of each species were collected in the two subregions from Andalusia, where they showed the highest intraspecific differences in quality (primarily in N concentration), based on results of a previous extensive study at regional scale (Salinas et al. 2018). Thus, the high- and low-quality classes of *Alnus* were collected in the siliceous subregions (S-cold/subhumid and S-warm/perhumid, respectively), where this species is common and abundant (Table S1). The high- and low-quality classes of *Populus* were collected in the calcareous subregions (C-warm/perhumid and C-warm/semiarid, respectively), where, although not abundant, this was the only tree species in common.

To standardize in-stream microbial conditioning of leaf litter offered to detritivores, litterbags (1 mm mesh-size, five bags per species and quality class) were incubated during winter in

the permanent Bacares stream (37°18′17.9″N, 2°26′40.9″W, 944 m above sea level), of intermediate chemical and thermal characteristics to those in which the shredders were sampled (Table 1). Based on previous studies, 3 weeks of in-stream incubation was estimated sufficient for optimal microbial conditioning (Casas et al. 2011). After retrieval, litterbags were transported to the lab in zip lock bags filled with stream water, in an icebox. Upon arrival, leaf-litter was immediately rinsed with filtered stream water to remove sediment slurry and leaf discs (1 cm Ø) were cut, freeze-dried, weighted, and preserved at − 20°C until required.

Experimental set-up for feeding tests

Shredders were collected from three streams per subregion and acclimated during 7 d to experimental conditions at the mean winter temperature of the streams of origin (14°C for *Melanopsis*, and 8°C for *Allogamus* and *Tipula*) under a 12 h light : 12 h dark photoperiod, in aquaria with forced aeration. During acclimation, shredders were fed ad libitum on leaf-litter from their origin streams. After this period, only active individuals of similar mass were selected for experiments. Mean mass of *Melanopsis* from C-warm/perhumid and C-warm/semiarid subregions were 34 ± 0.9 and 35 ± 1.1 mg DM respectively, without significant differences between regions ($t = −3.4$, $p = 0.73$). Mean mass of individuals of *Allogamus* ($19 ± 0.9$ and $28 ± 1.1$ mg DM) and *Tipula* ($45 ± 2.3$ and $82 ± 10.3$ mg DM) were significantly smaller in the S-cold/subhumid compared to the S-warm/perhumid subregion ($t = 6.65$, $p < 0.001$; $t = 4.67$, $p < 0.001$, respectively), probably due to lower temperature in the former subregion.

Feeding tests were performed simultaneously for each shredder species using 120 individuals per taxon (60 per subregion). The initial body dry mass (DM_initial) of *Melanopsis* and *Allogamus* was estimated from measures on digital images of maximum shell length (SL) and head capsule width (HW), respectively, using the *SigmaScan® Pro v 5.0* image analyzer. Size-body dry mass (DM: 60°C, 72 h; weighting to the nearest 0.1 mg) regression was developed for *Melanopsis* (without shell) ($DM (g) = 5.9804 \times 10^{-5} \times SL(cm)^{2.6191}$, $R^2 = 0.90$, $n = 78$) measuring different sets of individuals than those used for the experiment. For *Allogamus* (without case) we used the model ($DM (g) = 2.3391 \times 10^{-4} \ e^{3.1437 \times HW(cm)}$, $R^2 = 0.90$, $n = 138$) developed in Fenoy et al. (2020). Wet mass of *Tipula* was determined by transferring larvae to filter paper (10 s) and weighting to the nearest 0.1 mg. A different set of *Tipula* individuals was used to obtain wet mass (WM)–dry mass (DM) regression (DM (g) $= 0.1311 \times WM(g)^{1.1788}$, $R^2 = 0.96$, $n = 66$).

Experimental individuals were starved during 24 h before the experiment started to allow evacuation of their guts. Shredders were placed individually in cylindrical containers of 5 cm Ø, 7 cm height, with a 0.5 mm mesh screen at the bottom to allow fecal pellets to pass through. Each container was inserted in a slightly bigger container to collect fecal pellets, filled with filtered stream water, which was renewed every 5 d,

and maintained with forced aeration (for more details see Rubio-Ríos et al. 2017). Fifteen individuals were randomly assigned to each one of the four dietary treatments (2 leaf-litter species × 2 intra-species qualities). Two pairs of pre-weighed leaf-litter discs were either exposed to the feeding action of each shredder or immersed in the container in a 250 μm mesh bag to act as control to account for leaf-litter mass losses other than consumption. During the 30-d of experiment, both sets of discs were renewed when approximately 50% of discs exposed to the shredder were consumed. After retrieval, exposed and control discs were dried (60°C, 72 h) and weighed to estimate final dry mass. At the end of the experiment, individuals were photographed (*Melanopsis* and *Allogamus*) or weighted (*Tipula*) to estimate final dry mass (DM_final) as above indicated, and frozen (− 20°C) until used for measurement of body composition (see below). Feces were collected every day and preserved frozen (−20°C) until analyzed for C, N, and P concentrations (five pools from three individuals per shredder species, diet, and subregion). Differences in stoichiometry between food and feces were used as an indicator of apparent assimilation efficiency.

Consumption, growth, and energetic reserves

Relative feeding rate (RFR, mg g^{-1} d^{-1}) was estimated as RFR $= (DM_i − DM_t)/(DM_{shredder} \times t)$: where DM_i and DM_t are initial and final dry mass (mg) of leaf discs, respectively, t is the exposure time (days) to consumption, and $DM_{shredder}$ is dry mass (g) of the shredder. Before relative feeding rate calculation, DM_t of exposed discs were corrected with mass loss of control discs. Daily instantaneous growth rate (DIGR, d^{-1}) of individual shredders was calculated as the difference between ln DM_{final} and ln $DM_{initial}$, divided by the elapsed time (days).

Energetic reserves of shredders, lipids and glycogen, were measured using the sulfo-phospho-vanillin and the anthrone reactions, respectively, following the methods described in Charron et al. (2014) with minor modifications. After removal of shells and cases, each individual was homogenized in 1 mL methanol using vortex and stainless steel balls. Each sample was aliquoted to measure total lipids and glycogen content. Optical density was measured at 525 nm for lipids and at 630 nm for glycogen. Calibration solutions were prepared using a commercial olive oil solution (5 g L^{-1}) solubilized in chloroform (for lipids) and glycogen (2.5 g L^{-1}) in distilled water.

Statistical analyses

For each leaf trait, we calculated the mean per subregion (using values from the four dominant riparian species and weighting them by the % cover of each species), as an integrative indicator of dietetic quality of riparian leaf inputs to streams. Then, we performed comparisons of weighted means for each leaf trait within lithological pairs of subregions differing in climate (S-cold/subhumid vs. S-warm/perhumid; C-warm/semiarid vs. C-warm/perhumid) using weighted

Table 2. Mean values±SE of leaf-litter traits for the two species, and the two quality classes within each species, used in feeding tests. Nutrients were measured before and after in-stream incubation for microbial conditioning. Different letters indicate significant differences following two-way ANOVA and post hoc Tukey tests. n.s.: not significant ($p > 0.05$).

Leaf-litter traits	*Alnus glutinosa*		*Populus alba*		F-value and significance level		
	High quality	Low quality	High quality	Low quality	Species	Quality	Interaction
Pre-in stream incubation							
%C	47.76±0.10[b]	51.88±0.17[a]	45.02±0.25[c]	42.98±0.22[d]	918.9 ***	257.5 ***	29.9 ***
%N	2.45±0.04[a]	2.36±0.07[a]	1.14±0.07[b]	0.86±0.01[c]	652.3 ***	6.6 *	15.5 **
%P	0.044±0.003[b]	0.028±0.004[c]	0.056±0.003[ab]	0.061±0.004[a]	46.1 ***	11.1 **	4.5 *
C : N	22.8±0.4[c]	25.8±0.7[c]	46.6±2.9[b]	58.5±0.9[a]	366.3 ***	1.0 n.s.	22.5 ***
C : P	2835±181[b]	5043±604[a]	2085±112[b]	1842±103[b]	62.6 ***	17.4 ***	6.9 *
N : P	124±7[b]	194±19[a]	45±1[c]	32±2[c]	478.7 ***	37.8 ***	0.3 n.s.
% Si	0.014±0.002[b]	0.014±0.002[b]	0.155±0.05[a]	0.215±0.22[a]	702.1 ***	2.9 n.s.	2.2 n.s.
% Hemicellulose	25.8±2.1[a]	13.1±1.5[b]	13.2±1.9[b]	20.2±3.0[ab]	1.4 n.s.	18.2 **	1.5 n.s.
% Cellulose	18.9±0.4[b]	26.1±0.6[a]	16.7±1.1[b]	18.6±1.0[b]	30.6 ***	7.9 *	26.5***
% Lignin	13.0±1.2[b]	20.6±0.6[a]	6.3±1.5[c]	7.3±0.5[c]	77.8 ***	4.7 *	12.7 **
Toughness (g)	50.5±1.7[c]	60.5±3.8[b]	71.8±1.5[a]	68.0±1.8[ab]	38.1 ***	8.9 **	2.4 n.s.
SLA (cm² g⁻¹)	170.6±4.9[a]	131.9±6.3[b]	85.9±1.3[c]	142.5±1.5[b]	101.2 ***	163.2 ***	16.9 ***
Post-in stream incubation							
%C	49.156±0.103[ab]	50.504±0.168[a]	48.473±0.247[b]	48.200±0.217[b]	14.3 **	4.2 n.s.	1.9 n.s.
%N	3.168±0.063[a]	2.800±0.037[b]	1.835±0.083[c]	1.459±0.062[d]	384.1 ***	0.7 n.s.	30.7 ***
%P	0.032±0.002[b]	0.034±0.002[b]	0.047±0.001[a]	0.050±0.001[a]	69.4 ***	0.1 n.s.	1.7 n.s.
C : N	18.129±0.341[c]	21.065±0.376[c]	31.193±2.055[b]	38.802±1.545[a]	218.6 ***	0.9 n.s.	23.2 ***
C : P	4075.317±286.240[a]	3894.384±279.519[a]	2655.184±63.389[b]	2512.817±82.701[b]	62.2 ***	0.1 n.s.	0.9 n.s.
N : P	224.767±15.013[a]	184.233±10.276[a]	86.093±4.150[b]	65.206±3.680[c]	313.8 ***	0.5 n.s.	17.8 ***

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.
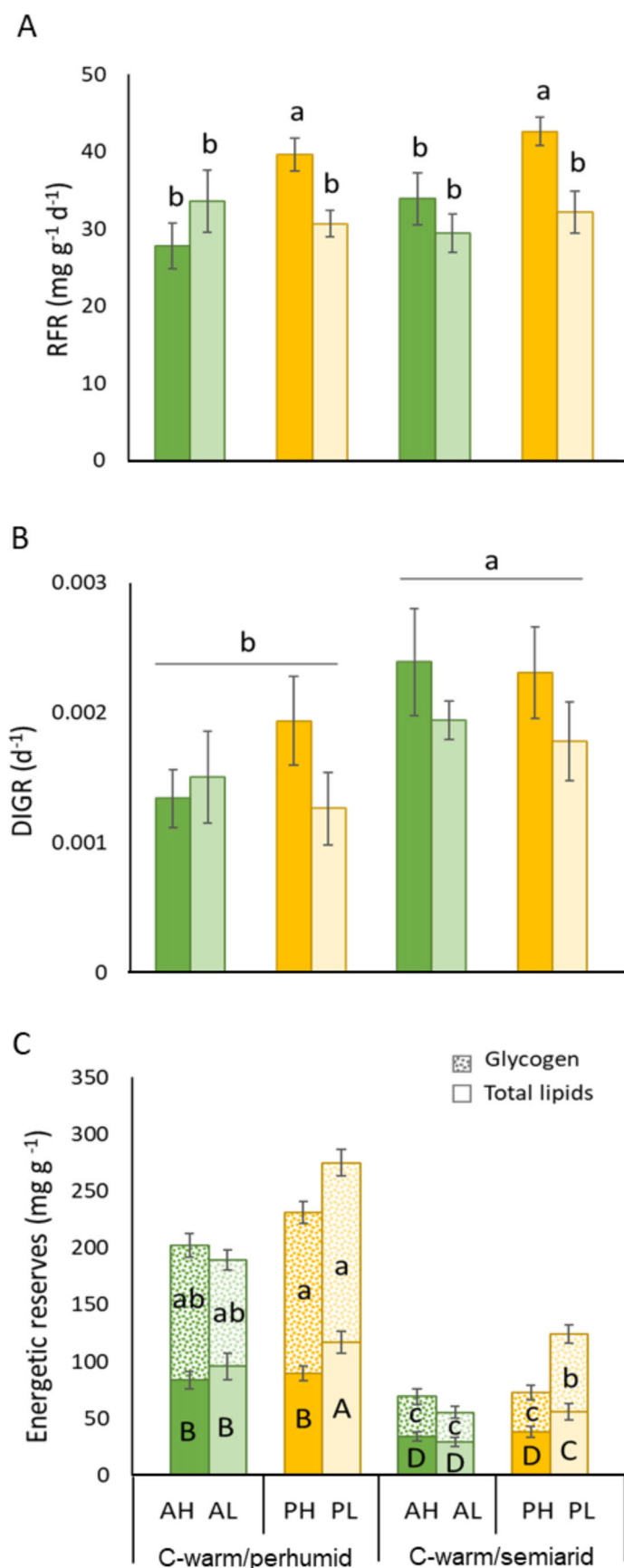
t-tests (package *weights*, R Development Core Team 2018), that replace the sample means by the corresponding weighted versions in the relevant formula. We used factorial ANOVA and post hoc Tukey's test to compare leaf-litter traits of species and quality classes. We used t-test to compare nutrient ratios (C : N, C : P, and N : P) between fecal pellets egested by a shredder species and the corresponding post-incubated (instream) leaf-litter used to feed them. Factorial ANOVAs (subregion × leaf-litter species × quality class) were performed to assess effects of shredder origin and changes in diet quality, on relative feeding rate, growth rate and energy reserves. Mantel-Cox Log-Rank tests were performed to determine whether independent factors significantly affected shredders survival. Log- or arcsin-transformed data were performed to achieve normality assumptions. When these transformations were not possible due to negative values, $1/x$ transformation was used. All analysis, except *t*-tests (see above), were carried out in Statistica v7 (StatSoft, OK, USA).

Results

Leaf traits of major riparian species in the four subregions and experimental diets

Overall, a higher average foliar nutrient concentration (N and P) was detected for the main riparian plant species in the S-cold/subhumid (Sierra Nevada) and in the C-warm/perhumid (Grazalema) subregions, compared with their respective counterparts (Table S1). Moreover, leaves from the S-cold/subhumid subregion showed lower C concentration and a higher Si concentration compared to those from the S-warm/perhumid subregion, but no significant differences in leaf toughness appeared between the two subregions. In the C-warm/semiarid subregion, Si concentration and toughness were significantly higher than in the C-warm/perhumid subregion (Table S1).

Leaf litter species used as experimental diets differed significantly in all traits measured (Table 2). *Alnus* showed significantly higher N concentration and lower molar C : N ratio compared to *Populus*. However, the opposite pattern was detected for P concentration and molar C : P and N : P ratios (Table 2). After in-stream incubation, a general increase in N and decrease in P concentrations were measured, although interspecific differences in nutrient concentrations remained. *Populus* showed much higher toughness and Si concentration compared to *Alnus*, which in turn showed higher lignin concentration than the former (Table 2).

Fig 1. Mean ± SE of (**a**) relative feeding rate (RFR, mg$_{leaf-litter}$ g^{-1}$_{shredder}$ d^{-1}), (**b**) daily instantaneous growth rate (DIGR, d^{-1}), and (**c**) energy reserves, i.e., total lipid and glycogen content (mg g^{-1}) for *M. praemorsa* fed on two qualities of *Alnus* (AH and AL: High and low, respectively) and *Populus* (PH and PL: High and low, respectively). Subregions of origin of shredders are also indicated. Different letters indicate significant differences ($p < 0.05$).

A

B

C
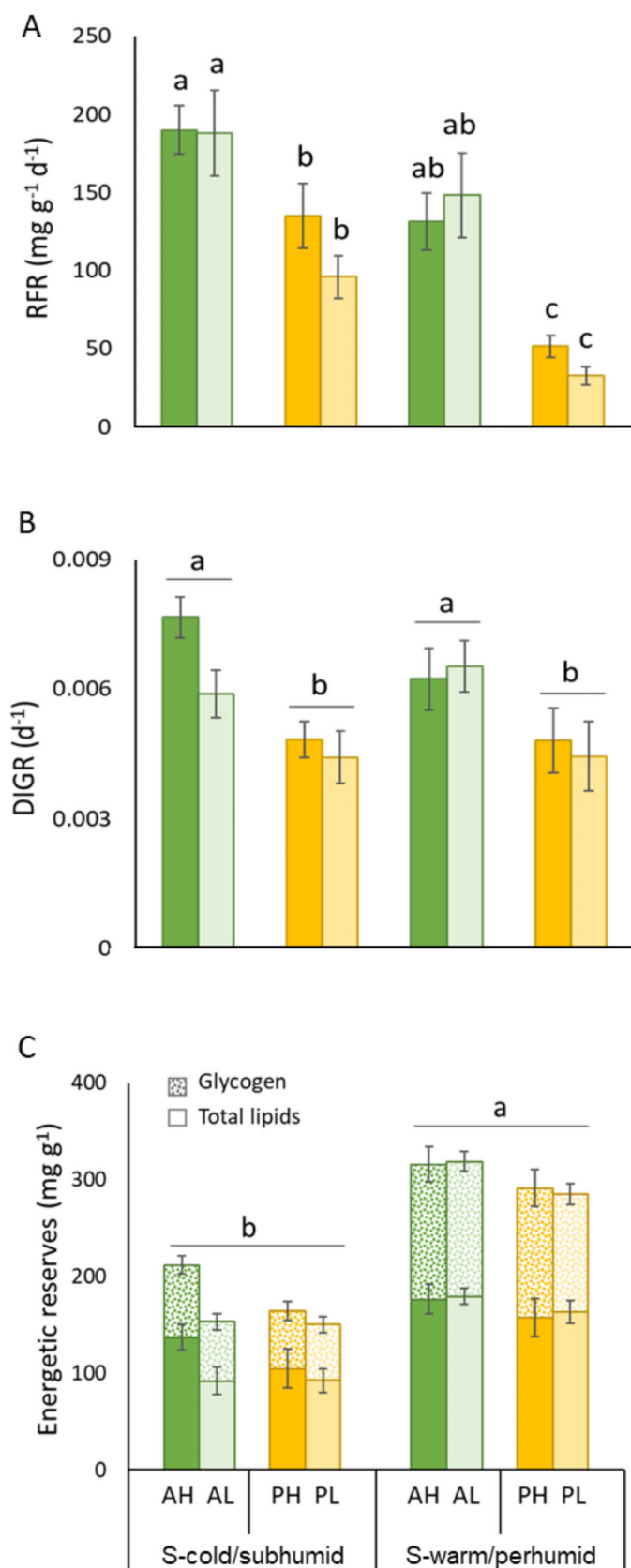
Alnus showed significant intraspecific differences in a greater number of leaf-litter traits than *Populus* (Table 2). The "high quality" category of *Alnus* showed significantly higher N concentration (notably after in-stream incubation), hemicellulose and SLA, but lower cellulose and lignin concentrations and toughness compared to the "low quality" category. The "high quality" category of *Populus* showed significantly higher C and N concentrations, but lower molar C : N ratio and SLA, than the "low quality" category within this species (Table 2). Moreover, intraspecific differences in % P and C : P ratio disappeared for both litter species after in-stream microbial colonization (Table 2).

Relative feeding rate

Leaf-litter species significantly affected relative feeding rate (RFR) in the three shredder species (Figs. 1a, 2a, 3a, Table S2). Whereas *Melanopsis* consumed higher quantities of *Populus* than *Alnus*, the reverse was true for *Allogamus* and *Tipula*. Subregion only influenced the relative feeding rate for *Allogamus* ($p = 0.01$ for the interaction between "subregion" and "litter species", Table S2), which seems due to animals from the S-cold/subhumid subregion feeding on *Populus* at a higher rate than the animals from the S-warm/perhumid subregion (Fig. 2a). An interaction effect between "litter species" and "litter quality" was found in *Melanopsis* and *Tipula* (Table S2), with greater consumption of the high-quality *Populus* and the reverse for *Alnus*, respectively (Figs. 1a, 3a), and no influence on *Allogamus* relative feeding rate (Table S2).

Survival and growth

All individuals of *Melanopsis* survived throughout the course of the experiment in the four diets. Survival was slightly lower in *Allogamus* (97%) and notably lower in *Tipula* (71%). However, neither subregion of origin (log rank Mantel-Cox: $\chi^2_{Allogamus} = 0.402$, $p = 0.526$; $\chi^2_{Tipula} = 0.272$, $p = 0.602$) nor diet (log rank Mantel-Cox: $\chi^2_{Allogamus} = 1.072$, $p = 0.300$; $\chi^2_{Tipula} = 3.012$, $p = 0.083$) significantly affected survival of *Allogamus* and *Tipula*.

Melanopsis from the C-warm/semiarid subregion showed significantly higher growth rate than those from the C-warm/perhumid subregion, without significant effects of litter species, quality class or interactions (Fig. 2b, Table S2). *Allogamus* and *Tipula* fed on *Alnus* showed higher growth rate (Figs. 2b, 3b, Table S2) than those fed on *Populus*. It is worth noting the negative growth rate obtained when *Tipula* fed on *Populus* (Fig. 3b). Moreover, growth rate of *Tipula* was higher in the

Fig 2. Mean $\pm$ SE of (**a**) relative feeding rate (RFR, mg$_{leaf-litter}$ g$^{-1}_{shredder}$ d^{-1}), (**b**) daily instantaneous growth rate (DIGR, d^{-1}), and (**c**) energy reserves, i.e., total lipid and glycogen content (mg g^{-1}) for *A. mortoni* fed on two qualities of *Alnus* (AH and AL: High and low, respectively) and *Populus* (PH and PL: High and low, respectively). Subregions of origin of shredders are also indicated. Different letters indicate significant differences ($p < 0.05$).
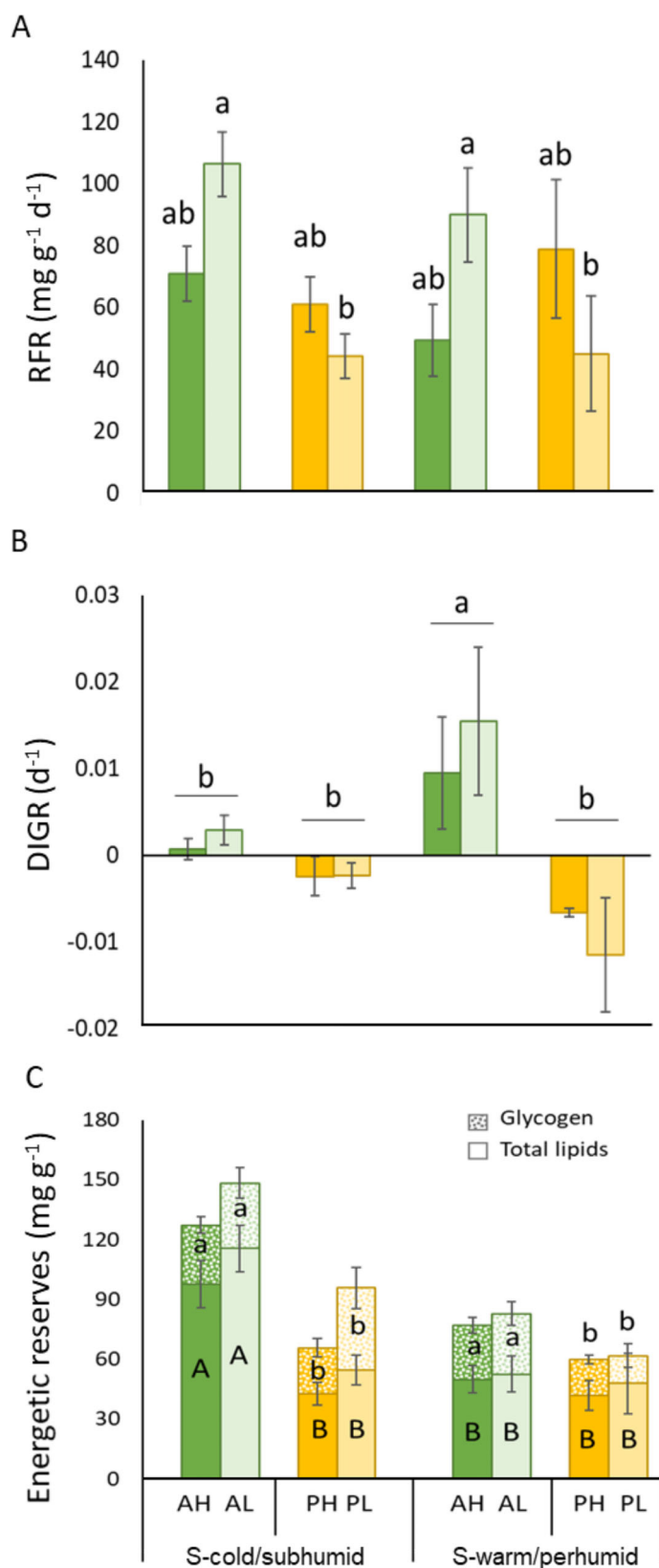
S-warm/perhumid subregion compared to the S-cold/subhumid subregion when fed with *Alnus*, but no significant differences between subregions appeared when fed *Populus* (Fig. 3b, Table S2).

Energy reserves

Unlike growth rates, energetic reserves (lipids and glycogen) of *Melanopsis* were significantly higher in individuals from the C-warm/perhumid subregion, these presenting a significantly higher accumulation when fed *Populus* litter (Fig. 1c, Table S2). In *Allogamus*, significantly higher reserves were measured in individuals from the S-warm/perhumid compared to those from the S-cold/subhumid subregion (Fig. 2c, Table S2). In the case of *Tipula*, lipid reserves were significantly higher in individuals from the S-cold/subhumid subregion when fed *Alnus* (significant interaction between "subregion" and "litter-species"), but glycogen was significantly higher in individuals from both regions when fed *Alnus* (Fig. 3c, Table S2).

Comparison of nutrient ratios between feces and diets

We found significant differences between feces and diet in individuals of the two or at least one of the two subregions compared (Fig. 4, Table S3). For *Melanopsis* fed on high quality *Alnus* and *Populus*, there was a subtle but statistically significant trend toward lower fecal C:N ratio relative to the corresponding diet, suggesting slight N-enrichment of feces (Fig. 4a, Table S3). In general, no differences in C : P or N : P ratios between feces and diets were detected, except in some cases, but without a clear pattern. (Fig. 4a, Table S3).

For *Allogamus*, the only statistically significant difference in fecal C : N ratio was found in individuals from the S-cold/subhumid subregion fed on the high quality class of *Alnus* and *Populus*, suggesting a lower N assimilation efficiency relative to C, when compared to that measured in individuals from the S-warm/perhumid subregion. Further, fecal N : P ratio of individuals from the S-warm/perhumid subregion fed on *Alnus* were significantly lower than those of diets, this suggesting a greater assimilation efficiency of N, relative to P, in the N-richer diets. No clear trend was detected for C : P ratios (Fig. 4b, Table S3).

Tipula from both subregions showed a high capacity for assimilating N relative to that of C and P. In general, this pattern occurred in all diets except for *Alnus* low-quality, in which no significant differences in ratios between feces and diets appeared (Fig. 4c, Table S3).

Fig 3. Mean ± SE of (**a**) relative feeding rate (RFR, mg$_{leaf-litter}$ g$^{-1}_{shredder}$ d^{-1}), (**b**) daily instantaneous growth rate (DIGR, d^{-1}), and (**c**) energy reserves, i.e., total lipid and glycogen content (mg g^{-1}) for *T. leo* fed on two qualities of *Alnus* (AH and AL: High and low, respectively) and *Populus* (PH and PL: High and low, respectively). Subregions of origin of shredders are also indicated. Different letters indicate significant differences ($p < 0.05$).
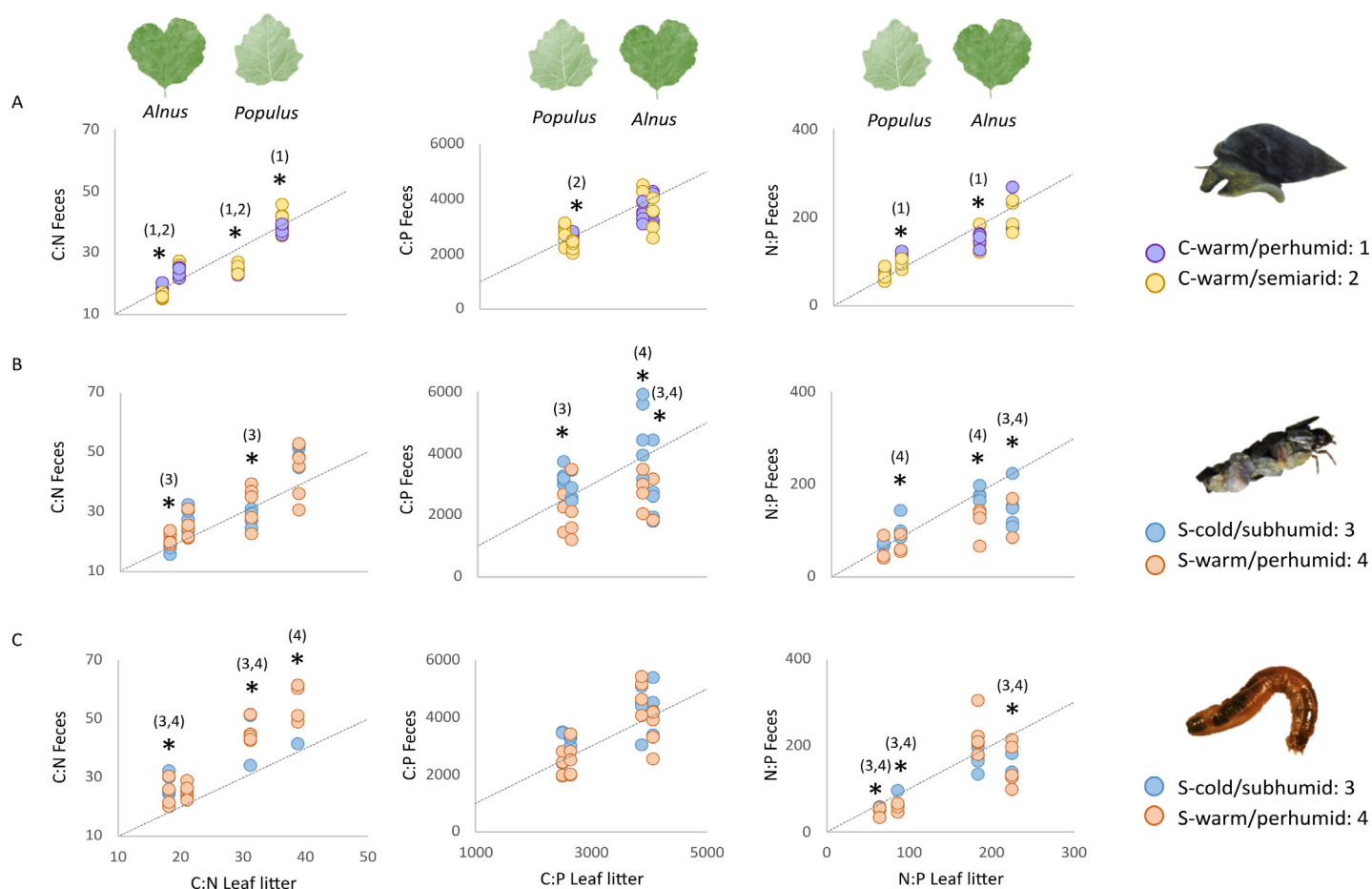
Fig 4. Relationship of molar C : N, C : P, and N : P ratios between feces (*Y*-axes) and the four leaf-litter species/quality classes offered (*X*-axes) to *M. praemorsa* (**a**), *A. mortoni* (**b**), and *T. leo* (**c**). The dotted line represents the ratio 1 : 1. The asterisks indicate a significant deviation from the 1 : 1 ratio ($p < 0.05$). The number in parentheses indicates the subregion for which significant differences were found.

Discussion

Our main hypothesis stated that if shredder's intra-species adaptations to cope with decreasing leaf-litter quality exist, these could be perceptible in populations already dealing with this scenario, i.e., streams located in warm or warm/arid zones presenting nutrient-depleted leaf-litter inputs. Our data revealed lower average nutritive value of the riparian foliage in warmer or in warm/semiarid zones. These results, together with other recent observations (e.g., Salinas et al. 2018), support the notion that climate change can likely exacerbate the large dietary imbalance of stream detritivores (Cross et al. 2005), either due to plant species turnover (interspecific variability) or phenotypic plasticity of species (intraspecific variability). However, results from our experiments did not support our hypothesis: the responses of feeding and growth rates, and assimilation, to changes in litter quality did not differ between populations of the three shredder species, and when exceptions did occur, these were most likely

not due to local adaptations to use low-quality litter (discussed below).

Adaptive phenotypic plasticity, or intra-species adaptations due to genetic diversity of populations, allows species to cope with environmental variability, decreasing their risk of extinction in a changing world (Gienapp et al. 2008). Nevertheless, despite the potential benefits of these microevolutionary adaptations under a warming climate, adaptive phenotypic plasticity, for instance, is far from being widespread or maximal, due to genetic and/or environmental constraints (costs and limits) (e.g., Auld et al. 2009; Merilä and Hendry 2014). This could explain why feeding and assimilation patterns of the different diets were similar between the two populations of each shredder species. Alternatively, it could be suggested that the average decrease in nutritional quality of leaf-litter inputs is not the prevailing selection pressure on shredders feeding traits. It may be thought that the relatively high diversity typical of riparian vegetation, together with microbial conditioning that

enhances the nutritive value of recalcitrant leaf-litter, could buffer the strength, as a selection pressure, of dominant low-quality litter inputs. In fact, the homogeneous microbial conditioning carried out in our experiment fundamentally buffered differences between quality classes in each litter species, at least in terms of nutrient concentration.

Notwithstanding the above, *Melanopsis* performance showed geographical differences regardless of diet quality: a higher growth but much lower (less than half) energy reserves were measured in individuals from the C-warm/semiarid subregion when compared to the C-warm/perhumid subregion. This suggests a physiological trade-off in resource allocation between these two traits, i.e., prioritization of growth in protein in the first subregion vs. accumulation of carbon reserves in the second one. The causes of such differential nutrient allocation between the two populations are difficult to disentangle. It may be that the fast growth recorded for snails from the C-warm/semiarid subregion could be simply a compensatory mechanism (Metcalfe and Monaghan 2001) produced when resource quality was improved (providing the experimental leaf-litter) after a period of retarded growth due to poor food quality (leaf-litter at home streams). However, compensatory growth is commonly driven by hyperphagia (i.e., large increases in ingestion rates) (Gurney and Nisbet 2004), and this was not observed in our experiment. Alternatively, it could be considered that under a situation of poor food-quality or scarcity, tissue protein can be the main contributor to meet N demands for gametogenesis, as it has been shown in studies of marine bivalves exhibiting high phenotypic plasticity (Bayne 2004; and references therein). Thus, as no fundamental differences in assimilation efficiencies of C and N appeared between the two populations of *Melanopsis*, it seems that the excess C acquired was mostly channeled toward energetic storage in individuals from the C-warm/perhumid subregion, while those from the C-warm/semiarid subregion perhaps eliminate excess C by increasing respiration rate (Hessen et al. 2013). This last response should be matched by reduced rates of N excretion to maintain fast growth. Extraordinary flexibility in physiological rates as an adaptation to surplus dietary C seems to be a normal feature in freshwater snails (Fink and von Elert 2006), including the capacity to grow relatively fast on high C diets by increasing its relative allocation to respiration (Rollo and Hawryluk 1988).

Significant differences in performance were also detected between populations of *Allogamus* and *Tipula* but, particularly in the first species, these are potentially related to differences in body size—smaller in the cold compared to the warm subregion of the siliceous domain—rather than to local adaptations. Higher relative feeding rates in smaller individuals and greater energy storage as metamorphosis approaches in larger individuals have been reported in other caddisfly species (e.g., Kiffer et al. 2016), and in most aquatic insects (e.g., Cavaletto and Gardner 1999). We could not avoid differences in body size because the insects were collected at the same time from

regions differing in water temperature. Such differences in individual body size, as well as the limited number of populations compared (just one per climatic setting), can be considered drawbacks to generalize the results of our experiment. Nonetheless, body size did not seem to influence the lack of compensatory feeding or differences in assimilation efficiency of nutrients among diets. Furthermore, while individuals came from only a population per subregion, they were collected in three different streams per subregion, thus presumably encompass a relatively large genetic pool with the potential to represent intraspecies adaptations to local conditions.

Overall, our findings highlight that feeding performance when facing variations in nutritional value of leaf-litter is a fixed trait for shredders, at least for the species studied here. These showed species-specific responses, but with a major distinction between the snail and the two insects. Furthermore, in line with our second hypothesis, interspecific differences in leaf-litter quality proved to have greater effects on feeding performance than intraspecific ones. Results for *Melanopsis* were in accord with our first prediction of increasing feeding rate on the poor-quality litter species, but not with the second one of increasing assimilation of the limiting nutrient relative to carbon. *Melanopsis* faced interspecific changes in litter quality by increasing feeding rate on *Populus*. This litter was poorer in N but richer in P and Si compared to *Alnus*, and silicon appears to hinder N assimilation by preventing the leaf cell walls from being broken apart and/or by causing mid-gut damage (Massey et al. 2006; Massey and Hartley 2009). Thus, compensatory feeding of *Melanopsis* on *Populus* likely offset reduced N concentration and possible difficulties for its assimilation, with respect to growth and energy reserves. In addition, the scraping feeding mode of the snail could allow individuals to perform a selective ingestion of the softer leaf matrix, leaving the vascular skeleton (Chergui and Pattee 1991; this study), overcoming adverse effects from high toughness of *Populus* as a pre-ingestive constraint. These and the above-mentioned putative post-assimilatory mechanisms to eliminate the excess C acquired, suggesting notable behavioral and physiological adjustments by freshwater snails to compensate for poor-quality food (Rollo and Hawryluk 1988; Fink and von Elert 2006). Moreover, as freshwater molluscs appear to have greater P requirements than detritivore insects (Frost et al. 2006), the higher P concentration of *Populus* might have increased palatability of this litter to *Melanopsis* compared to insect species.

Interspecific differences in leaf-litter quality had far reaching consequences for the two insect species, particularly *Tipula*, compared to *Melanopsis*. In contrast with our predictions, both insect species showed higher consumption and growth rates in the N-fixer *Alnus* compared to *Populus*, and similar apparent assimilation efficiency of limiting nutrients relative to carbon in both litter species. A common perception is that shredders are highly nutrient-limited (Evans-White and

Halvorson 2017), particularly by nitrogen, which seems to be a key driver of invertebrate (i.e., insects) consumption of litter (e.g., Evans-White et al. 2005; Frainer et al. 2016). Compensatory feeding in low-quality resources has been reported for caddisfly and *Tipula* species in single-leaf species experiments (Flores et al. 2014; Fuller et al. 2015), a strategy that, in the case of *Tipula*, could have countered its negative growth in *Populus*. Indeed, increased consumption of low-quality resources to maintain growth rates seems to be a more common response when offering single diets (this experiment) than in multiple-choice feeding experiments (Cruz-Rivera and Hay 2000; Swan and Palmer 2006; but see Santonja et al. 2018). However, it cannot be ruled out a selective feeding on higher quality patches of discs (Flores et al. 2014; Hood et al. 2014), which might explain the lack of differences in insects' feeding rates between qualities of the same litter species.

Factors determining compensatory feeding in detritivore shredders are poorly known, but it has been suggested that it could depend on species idiosyncrasies interacting with certain leaf-litter traits (e.g., toughness) other than limiting nutrients (Flores et al. 2014; Frainer et al. 2016). In this regard, our results obtained when the two insect species were faced to intraspecific qualities of *Alnus* litter appear particularly meaningful. Feeding rates of *Allogamus* were not affected by the quality of *Alnus*, in line with results obtained using artificial diets just differing in N and P concentrations (Fenoy et al. 2020). This suggests that the lack of compensatory feeding in this species is an idiosyncrasy independent of litter traits that might have hindered its accomplishment. However, *Tipula* showed a tendency toward compensatory feeding between *Alnus* quality classes, a common adaptation to meet nutritional requirements in slow moving species, such as tipulids, when the quality of available food is low (Canhoto and Graça 2006). Overall, our results point to the existence of a critical litter-quality threshold between *Alnus* and *Populus* from which *Tipula* could not perform this feeding strategy. These two litter species differed in several traits others than elemental nutrients, but the most prominent divergence was for Si, with between 10 and 15-fold greater Si concentration in *Populus*. It is relatively well known, particularly in grasses, that silicification can reduce leaf consumption, digestion efficiency, and growth rates of folivorous insects (Massey et al. 2006; Massey and Hartley 2009), but little is known on the magnitude of this process in tree species and the subsequent effects on leaf-litter shredding by freshwater detritivores. These effects have been firmly related to silicon' abrasiveness, which produces irreversible mandible wear and, perhaps, degradation of the mid gut of caterpillars, reducing N absorption (Massey and Hartley 2009). Our results suggest no abrasive effect of silicon on digestion and N absorption for both insects. Thus, it is more likely that feeding deterrence and/or mandible wear due to Si in *Populus* diets reduced consumption rates—by about half compared to *Alnus*—for

Allogamus. Moreover, these hindrances exerted constraints to potential compensatory feeding in *Tipula*, with detrimental post-ingestive consequences, particularly in the second species.

The ability of *Melanopsis* to perform compensatory feeding in *Populus* relative to *Alnus* is in line with the general perception that effects of accumulated silicon in plant tissues would be less intense for snails. Several studies have reported no effects of increased Si concentration on consumption rates on herbivorous and detritivores snails (Schaller 2013; Horgan et al. 2017; but see Griffin et al. 2015), which has been attributed to the renewable teeth of their radula making it less susceptible to wear caused by silicon (Horgan et al. 2017). However, despite this ability, we did not observe compensatory feeding between the quality classes of *Populus*. It may be that the nearly 40% more Si in the low—compared to the high-quality class—prevented compensatory feeding by exceeding a certain threshold in Si tolerance. Yet, this suggestion is inconsistent with studies showing that snail species do not exhibit feeding deterrence in common reed litter (Schaller 2013), which normally has much higher Si concentration than poplar (Salinas et al. 2018). Alternatively, the threshold for compensatory feeding of *Melanopsis* between high- and low-quality classes of *Populus* could be related to litter C : N ratio. Given that this snail showed no particular ability to improve N assimilation relative to C, it appears that the excess of C gained eating low-quality *Populus* imposes metabolic constrains to increase feeding rate in this litter. This argument finds some support in the fact that when feeding on this low-quality litter, *Melanopsis* accumulated significantly higher reserves compared to high-quality *Populus*, assuming this is a mechanism to eliminate excess of carbon acquired (see above). Further research is needed to clarify this issue, but it seems that compensatory feeding could be conditioned by metabolic constrains in combination with thresholds of litter quality, as it has been suggested for herbivorous insects (Kerslake and Hartley 1997; Johnson et al. 2014).

No global conclusion can be drawn from our results, given the low number of shredder species used in the experiments. However, since the species studied here are widespread and locally abundant, our results may serve to outline possible trends of trophic interactions in Mediterranean low-order streams in the context of global change. Global climate and land-use changes can result in impoverished nutritional quality of leaf-litter inputs to stream detritivores. Recently, Rota et al. (2018) have encouraged studies to advance our knowledge on phenotypic determinants of resource use in shredders. Our results suggest that interpopulation adaptations to improve feeding performance of shredders facing reduced litter quality are not common. Instead, this ability appears to be a fixed-species trait that varies among major phylogenetic groups: snails vs. insects. *Melanopsis* has a key role for the incorporation of leaf-litter into detrital food webs in spring-fed lowland streams (Casas et al. 2011). The remarkable

capacity of this snail to feed on litter with high C:N ratio and Si concentration shown here, suggests that ecosystem processes are less likely to be affected by decreasing litter quality triggered by global changes. Water extraction and contamination that cause population decline or extinction of this snail (e.g., Bartolini et al. 2017) represent a much more serious threats for the conservation of these lowland ecosystems. Conversely, headwater streams in mountainous regions are in general free of these anthropogenic impacts, for being located in unpopulated watershed and/or under some nature conservation status. However, in these streams, where most shredders are insects, decreasing litter quality as a result of climate and/or land-use changes, particularly if these alter riparian plant species composition, may cause major alterations in ecosystem processes, i.e., litter decomposition, nutrient cycling, and energy flow through stream food web.

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Conflict of Interest

The authors declare no conflict of interest.