



Resource preference of two stream detritivores in the laboratory largely differs from the supply of detritus below eucalypt plantations

Ana Basaguren · Aitor Larrañaga · Ainhoa Otermin · Jon Molinero · Santiago Larrañaga · Jesús Pozo

Received: 5 July 2021 / Revised: 26 April 2022 / Accepted: 12 May 2022 / Published online: 13 June 2022
© The Author(s) 2022

Abstract Detritivores are pivotal in forest streams as they process detritus and promote secondary production. Many studies have addressed the preference of freshwater detritivores towards materials of differing quality. Nevertheless, few studies compare the resource preferences in the laboratory with the availability in the field. In the present study, feeding preferences of two stream detritivores (the caddisfly *Sericostoma pyrenaicum* and the amphipod *Echinogammarus tarragonensis*), over three native leaf species (alder, chestnut and oak) and an exotic species (eucalypt) were quantified in the laboratory. Preference for eucalypt leaves conditioned for 1, 2

and 3 weeks was also described. We then contrasted the preference patterns in the laboratory feeding experiments with a 15-month-long benthic standing stock time series of a stream below a native deciduous forest and another below a eucalypt plantation. Both detritivores preferred consuming alder leaves and more conditioned eucalypt leaves, although the amphipod was more selective than the caddisfly. The consumption preference in the laboratory was unmatched by the availability in the field, especially under eucalypt plantations and for the amphipod. Our results show that the strength of the preference for high-quality resources can differ among different taxa, which can modulate their response to land use changes.

Handling editor: Marcelo S. Moretti

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10750-022-04908-7>.

A. Basaguren · A. Larrañaga (✉) · A. Otermin · J. Pozo
Department of Plant Biology and Ecology, University of the Basque Country UPV/EHU, P.O. Box 644,
48080 Bilbao, Spain
e-mail: aitor.larranagaa@ehu.eus

J. Molinero
Escuela de Gestión Ambiental, Pontificia Universidad Católica del Ecuador Sede Esmeraldas, Espejo y Subida a Santa Cruz, Esmeraldas, Ecuador

S. Larrañaga
Escuela Universitaria de Magisterio Begoñako Andra Mari—BAM. Larrauri 1A, 48160 Derio, Spain

Keywords Leaf litter quality · Invertebrate detritivores · Resource selection · Consumption rates · Microcosms

Introduction

Allochthonous inputs of leaf litter is a major energetic source for benthic communities in forested headwater streams (Vannote et al., 1980; Wallace et al., 1999; Tank et al., 2010). Once in the stream leaves are fragmented by shredder macroinvertebrates making other forms of organic matter as fine particulate organic matter available for other consumers of organic matter in the community (Wallace & Webster, 1996;

Constantini & Rossi, 2010; Graça & Cressa, 2010). Previous studies have demonstrated that shredding activity depends on traits of leaf litter, basically measured in terms of nutrient content, microbial conditioning, toughness and the amount of toxic compounds (e.g. Kochi & Kagaya, 2005; Campos & González, 2009; Jabiol & Chauvet, 2012; López-Rojo et al., 2018). Materials of higher quality increase growth rates and survival of detritivores (Canhoto & Graça, 1995; Carvalho & Graça, 2007), although some species are able to compensate for the low quality of the materials with a higher consumption rate of those resources (see Flores et al., 2014). Responses of any kind to the organic matter quality that enters freshwater systems by detritivores reveals that the land use changes might have a profound effect on macroinvertebrate communities, and indirectly, on the processes they are involved in (Graça et al., 2002; Lecerf et al., 2005; Ferreira et al., 2016). In the Iberian Peninsula monospecific forestry plantations of *Eucalyptus* spp. have spread out covering over 2% of the total land (Iglesias-Trabado & Wilstermann, 2009). Changes in the seasonality of the inputs to streams and the low quality of its leaf litter, due to the thick cuticle and toxic compounds (Boulton, 1991; Canhoto & Graça, 1999; Canhoto & Laranjeira, 2007), have been related to negative effects on biota (Basaguren & Pozo, 1994; Larrañaga et al., 2006; Canhoto & Laranjeira, 2007; Ferreira et al., 2019; Kiffer et al., 2018). Nevertheless, some studies have also reported a higher consumption of eucalypt leaf litter in field budgets, that are explained by the higher residence time of the eucalypt leaf litter in the benthos due to the synchrony of the peak fall of leaves and low discharges in summer (Bañuelos et al., 2004), although it is not clear if this consumption is created by detritivores or by microbial decomposition. Higher residence times increase the conditioning of eucalypt leaves, by which it gets softer, richer in nutrients and can become more palatable for detritivores (see Graça et al., 2001). The effects of poor resources seem to be also consumer taxon specific. While at one end of the spectrum we find gammarids and plecopterans that have been demonstrated to be very sensitive to eucalypt plantations (Basaguren et al., 2002; Larrañaga et al., 2009a, 2014), on the other end, we find shredders like the trichopterans that are able to consume and grow with very poor materials (Friberg & Jacobsen, 1999; Campos & González, 2009; Flores et al., 2014). In

contrast to field studies that are sometimes challenging to interpret as other confounding factors can also play a relevant role, laboratory experiments, such as food choice experiments, can offer a key understanding of the relevance of leaf traits to consumers. These experiments, although they offer a series of methodological challenges (see Canhoto et al., 2020), have been widely used to understand the reasons behind resource selection by the consumers. Nevertheless, resources that are preferred in these laboratory experiments might show a very limited availability in the field, making the contextualisation of laboratory trials in light of the availability of the different food items in the field an interesting integration of both kinds of experiments.

Thus, in this study, we aimed to see the selective behaviour of two detritivores in relation to the quality of the detritus (intrinsic characteristics as well as the degree of conditioning) and to relate them to the offer of detritus in two headwater streams with different riparian forests (native deciduous forest vs eucalypt plantations). With this objective, we studied the feeding preferences in laboratory trials of two common detritivores in headwater streams in the area (*Echinogammarus tarragonensis* Pinkster, 1973, Amphipoda: Gammaridae and *Sericostoma pyrenaicum* Pictet, 1865, Trichoptera: Sericostomatidae) and that differ in their requirements in terms of resource quality (amphipod more selective than the caddisfly). The resources offered were three of the most common leaf litter species under native deciduous forests of the area (*Alnus glutinosa* (L.) Gaertner, 1790, *Castanea sativa* Miller, 1768, and *Quercus robur* L., 1753; Pozo et al., 1997) together with leaves of the exotic *Eucalyptus globulus* Labill, 1800, tree, used intensively in plantations worldwide (Iglesias-Trabado & Wilstermann, 2009). Consumption in the laboratory was compared with standing stocks of benthic organic matter in streams flowing through a native deciduous forest and an eucalypt plantation. We hypothesise that (1) high-quality leaves (high levels of nutrients and low in toxic compounds) would be consumed more than the low-quality ones (Solagaistua et al., 2019), (2) consumers would be able to select leaves of low basal quality that have been conditioned for a longer time (Inkley et al., 2008), (3) the level of selectivity of resources of high quality would be consumer taxa specific, with gammarids expected to be more selective than caddisflies (Arsuffi & Suberkropp, 1989)

and (4) the mismatch between the feeding preference in the laboratory and the availability in the field below native forests or eucalypt plantations would be related to the sensitivity of these detritivores to land uses that reduce high-quality inputs to streams, such as eucalypt plantations.

Methods

Leaf species selection experiment ('Leaves' experiment hereafter)

In June 2001, undamaged and nearly abscised leaves of alder, chestnut and oak trees were collected from site D (see below) and leaves of eucalypt from site E. Leaves were leached for 2 days in the laboratory in filtered water (Whatman GF/C, 1.2 μm , from site D) to simulate natural leaching in the field, which abiotically removes soluble substances (Bärlocher, 2020). Leached leaves give a more accurate description of the quality of the material that detritivores consume in the field. Two discs of 2.5 cm in diameter were cut from the leaves from each side of the midvein: one for chemical characterisation and the other for the feeding experiment. After air-drying (24 h, 20°C), the discs were weighed and pools consisting of 10 discs of the same species were connected by a fine thread of nylon. Four sets of 10 discs of each species were oven dried to calculate air-dried-to-oven-dried coefficients to estimate initial dry mass in the incubation chambers (coefficients for alder, chestnut, oak and eucalypt were 0.91, 0.83, 0.90 and 0.83, respectively). Incubation chambers consisted of eight flat plastic containers (14×8×8 cm) with ashed gravel bottom, aerated water (18.5°C and filtered, GF/C, 1.2 μm , from site D) and a 12:12 h light:dark photoperiod. A 10-leaf disc string of each of the four leaf species was placed in each container making 1.43 ± 0.03 (SE) g of total leaf dry mass per container on average, of which the percentages in mass of the various leaf species were 20.6% of alder, 18.8% of chestnut, 18.6% of oak and 42.0% of eucalypt on average. In 4 of the containers 10 individuals of the last instar of *S. pyrenaicum* were also included (mean dry mass \pm SE—dried at 60°C for 72 h—at the end of the experiment, DM_{end} : 8.99 ± 0.30 mg without the cases); the other 4 containers (control) had no animals and were used to estimate microbial decomposition. The experiment

lasted 5 days and the water was renewed on day 3. In August the experiment was repeated with the amphipod *E. tarragonensis*. In this case, 6-disc strings were used and 24 well-developed individuals ($\text{DM}_{\text{end}} \pm \text{SE}$ at the end of the experiment: 2.3 ± 0.16 mg) were placed in 4 containers making a total of 0.90 ± 0.03 (SE) g of total leaf dry mass per container, with 17.3, 16.5, 21.7 and 44.5% of alder, chestnut, oak and eucalypt in mass on average, respectively. Different numbers of individuals and leaf disc strings were used for *S. pyrenaicum* and *E. tarragonensis* in order to have a similar amount of material per gram of consumer in each container. This time the experiment lasted 8 days. Both *S. pyrenaicum* and *E. tarragonensis* were collected from site D with hand nets, carefully placed in individual holed containers and submerged in constantly aerated stream water within a cool box. They were kept with aeration and in the dark until the beginning of the trials.

Conditioned eucalypt selection experiment ('Eucalypt conditioning' experiment hereafter)

In July 2001, leaves of *E. globulus* were collected from trees at site E. Leaf collection was repeated one and 2 weeks later. All these leaves were conditioned in the laboratory in stream water after being collected, and thus, when we ended conditioning we had leaves that had been incubated for 1, 2 and 3 weeks. As we aimed to search for differences in consumption due to conditioning by hyphomycetes, water collected from a middle stream reach (just below E site) and filtered through a 125 μm mesh was used this time. The larger filter used here allows hyphomycete spores to go through, and thus, colonise the leaves (Cornejo et al., 2020). As for the 'leaves experiment', 8 containers were used and 10-disc strings of each of the three conditioning stages of eucalypt leaves were placed in each container (1.60 ± 0.06 (SE) of total dry mass with a contribution of 36.4, 33.7 and 29.9% of materials conditioned for 1, 2 and 3 weeks, respectively); in four of them 10 individuals of *S. pyrenaicum* were present ($\text{DM}_{\text{end}} \pm \text{SE}$ at the end: 8.64 ± 0.65 mg). The duration of the experiment was 5 days and aeration and photoperiod were the same as for the 'leaves experiment'. In October the experiment was repeated with 6-leaf strings (total mass of 0.82 ± 0.02 (SE) g and 38.7, 32.9 and 28.4% of contribution) and 24 individuals of *E. tarragonensis* in each container this

time ($DM_{\text{end}} \pm SE$: 1.27 ± 0.07 mg); the experiment lasted 8 days. Another set of discs were punched out from the materials to characterise them in a similar way as in the ‘leaves experiment’.

After each experiment, the remaining dry mass (70°C , 72 h) of each string of discs was measured. This material was ground with a Culatti mill to pass through a 0.5 mm mesh. Aliquots of leaf mass were analysed for carbon and nitrogen with CHNS/O Series II PerkinElmer elemental analyser. Phosphorus content was quantified by digestion in a mixture of nitric (5 ml), perchloric (1 ml) and sulfuric acid (0.5 ml) and spectrophotometry by the molybdenum blue method (Allen et al., 1974). Phenolic content was estimated by spectrophotometry with the Folin–Ciocalteu reactive using a methanol–water (1:1) mixture as a dissolvent and gallic acid as a standard for calibration. Lignin was measured by digestion in 72% of sulfuric acid and gravimetry in a Tecator Fiberted system (after Goering & Van Soest, 1970). Nutrient contents are expressed as molar ratios throughout this work.

Benthic organic matter standing stock

To compare laboratory consumption patterns with field benthic stocks of organic matter, we reanalysed data on these variables gathered in Molinero (2000). In that work, two reaches in two first-order streams of the Agüera basin (Northern Spain) were studied: site D ($43^{\circ}12'37''\text{N}$, $3^{\circ}15'46''\text{W}$) and site E ($43^{\circ}19'37''\text{N}$, $3^{\circ}15'46''\text{W}$). Site D runs through a native deciduous forest dominated by *Q. robur*, *C. sativa* and *A. glutinosa*, whereas site E is covered by a monoculture of *E. globulus* plantation with a minimal presence of native deciduous species. In both sites, water showed low mineralisation and nutrient levels due to the underlying geology and the absence of human settlements in the basins (Molinero et al., 1996). Pozo et al. (1997) and Molinero & Pozo (2004) describe the catchment in a more detailed way. In those two streams, benthic organic matter standing stock was collected fortnightly to monthly during the period of October 1993–December 1994 (five 30×30 cm Surber samples, 1-mm mesh size from randomly selected locations). All organic matter was dried (70°C , 72 h), combusted (500°C , 12 h) and mass values expressed as ash free dry mass per m^2 . Only leaves are considered in the present work.

Data analysis

Differences in chemical characteristics among the different food types were tested with two-way parametric MANOVA and individual ANOVA (fixed factors: leaf or conditioning, and trial) with Tukey tests for post hoc pairwise comparisons (Zar, 2010). Consumption rates were calculated as the difference between initial and final leaf dry mass in experimental containers. Mean weight losses of food items in control containers were utilised as correction factors for natural (autogenic) losses occurring in the absence of consumers (see Canhoto et al., 2020). Food consumption rate was expressed as mg of leaf dry mass per mg of animal dry mass per day ($\text{mgLeaf mgInd}^{-1} \text{d}^{-1}$). As different food items were offered simultaneously to the animals in the same container consumption rates of the different food types were not independent. To solve statistical issues, we compared the consumption rates using permutation tests: after performing an ordinary 2-way ANOVA (factors: invertebrate species and resource type) we compared the F values obtained with the real disposition of the data against the F -values distribution obtained after reshuffling the measured consumption values 10^6 times to estimate a P value (Anderson & Ter Braak, 2003). Total consumption of leaves by the two detritivores was also compared by permutation tests. Spearman rank correlation coefficients were computed for consumption rates and the chemical characteristics of the different resources to look for variables controlling food selection.

None of the offered resources in the laboratory trials displayed any shortages, so we assumed that the consumption of the different food items was following the preferences of the consumers. We wanted to estimate the contrast between resource selection in the laboratory with the benthic standing stock of leaves at sites D and E. To do that we calculated the divergence between the supply and the demand for resources by consumers. Considering alder as the preferred resource and a foundation species we took the percentage of alder ($\text{alder/leaves} \cdot 100$, alder%) as the critical variable for a simple resource quality approach. We computed the Chi-square goodness of fit (using the Yates correction, Yates, 1934) between alder percentage in the field from Molinero (2000) and alder percentage consumption in laboratory feeding experiments. To denote alder shortage (% of alder

in the benthos < % of alder consumed), we converted the final value into negative and the surplus of alder (% of alder in the benthos > % of alder consumed) was expressed with positive values. Even if leaf consumption in laboratory experiments are expressed in dry mass and those in the field in ash free dry mass we consider the bias to be negligible. Leaves and alder standing stock, and the χ^2 values between supply and demand, were compared by means of permutation tests following the ordinary 2-way ANOVAs (factors: site and date for leaves and alder standing stock) and 3-way (species, site and date; for χ^2 values). We estimated the significance of the final F values by comparing them with the F -distribution obtained with the shuffled values 10^6 times (Anderson & Ter Braak, 2003). To understand the relevance of alder quantity in the field, we integrated both quantity and quality measures in a single variable by means of an index based on the preferences in the laboratory for each detritivore (quality) and the amount of leaves in the field (quantity). Taking into consideration the four leaf species used in the laboratory, we multiplied the amount of each leaf species at each of the samplings carried out at D and E sites by its preference in the laboratory (% consumed per total leaf consumption). The sum of preference-weighted amounts of the four leaf species were summed to compute the leaf quantity index. We related this index to the quantity of alder with a linear model using all the samples of the two sites and taxa, site and their interaction as sources of variation. For this, we first \log_{10} -transformed the quantity of alder to reduce the leverage of the largest data points in the analysis. Moreover, to solve issues

with heteroscedasticity, we applied a Box–Cox transformation to the leaf quality index ($\lambda=0.424$; Box & Cox, 1964). The four leaf species considered in the laboratory experiment study accounted for over 95% of the standing stock in sites D and E.

Results

Chemical properties of the material

There were differences in the chemical properties of the material offered between trials but mainly among the different leaf species (Table 1 and 2). For the ‘Leaves’ experiment most of the variation of the models accounted for the differences among leaves rather than the differences between trials. We observed a phosphorus impoverishment with the consequent increase in the values of C:P and N:P from the June to the August experiment (Tables 1 and 2). Among leaf species, alder and eucalypt leaves showed the lowest or the highest values for most of the variables. Alder displayed the minimum values of C:N and C:P ratios, which were similar in oak, but smaller than in the other two species. Eucalypt showed the highest values for C:N and C:P and the lowest values for N:P (Tables 1 and 2). Chestnut showed the lowest levels of lignin, with the other three materials showing similar values. On the other hand, chestnut and oak showed a higher content of phenols than alder and eucalypt. In the ‘Eucalypt experiment’ differences appeared between trials and conditioning time increased the

Table 1 Chemical characteristics of the material offered to *S. pyrenaicum* and *E. tarragonensis* in the food preference experiments (mean \pm SE, $n=4$)

	Trial	‘Leaves’ experiment				Trial	‘Eucalypt conditioning’ experiment		
		Alder	Chestnut	Oak	Eucalypt		1 week	2 week	3 week
C:N	June	16.9 \pm 0.3	20.9 \pm 0.3	20.7 \pm 0.5	33.0 \pm 2.3	July	47.4 \pm 11.8	39.8 \pm 2.4	32.5 \pm 1.4
	August	16.3 \pm 0.5	25.0 \pm 1.4	19.5 \pm 0.8	31.7 \pm 3.8	October	39.0 \pm 0.7	35.7 \pm 1.7	33.7 \pm 0.6
C:P	June	1136.0 \pm 42.0	1080.9 \pm 27.9	1173.8 \pm 17.6	1415.5 \pm 65.9	July	2175.9 \pm 104.0	2317.3 \pm 11.2	2992.4 \pm 40.0
	August	1087.0 \pm 32.6	1517.5 \pm 36.4	1206.6 \pm 42.2	1436.4 \pm 62.8	October	1481.0 \pm 14.0	1922.4 \pm 94.9	1750.3 \pm 56.2
N:P	June	62.6 \pm 2.5	48.2 \pm 1.5	53.1 \pm 1.2	40.4 \pm 2.0	July	49.8 \pm 9.7	54.9 \pm 3.4	86.3 \pm 3.4
	August	62.4 \pm 0.2	55.4 \pm 3.1	57.9 \pm 1.3	44.3 \pm 5.7	October	35.4 \pm 0.4	50.2 \pm 0.5	48.4 \pm 1.4
Lignin, %	June	21.1 \pm 1.0	13.2 \pm 0.7	22.0 \pm 1.0	22.3 \pm 0.4	July	20.1 \pm 0.1	23.1 \pm 0.3	28.7 \pm 0.2
	August	19.6 \pm 1.7	14.7 \pm 0.2	24.7 \pm 0.4	22.6 \pm 0.3	October	25.3 \pm 1.7	29.4 \pm 0.7	30.9 \pm 0.4
Phenol, %	June	9.6 \pm 0.2	13.1 \pm 0.3	11.4 \pm 0.1	8.1 \pm 0.2	July	8.53 \pm 0.14	6.40 \pm 0.06	2.59 \pm 0.03
	August	8.5 \pm 1.3	13.2 \pm 0.1	13.4 \pm 0.2	8.5 \pm 0.1	October	9.75 \pm 0.19	6.20 \pm 0.13	4.53 \pm 0.10

Table 2 MANOVA and individual ANOVAs for the chemical characteristics of the material offered to *S. pyrenaicum* and *E. tarragonensis* in the food preference experiments

'Leaves'	Trial			Leaf			Trial x Leaf				
	λ	$F_{5,19}$	P	Contrast	λ	$F_{15,52,8}$	P	Contrast	λ	$F_{15,52,8}$	P
MANOVA	0.452	4.598	0.006		0.001	34.139	<0.001		0.080	5.274	<0.001
ANOVA	SS	$F_{7,23}$		SS	SS	$F_{3,23}$			SS	$F_{3,23}$	
C:N	0.017	0.001	0.970		1096.9	30.98	<0.001	Euc > Che _a Oak _{ab} Ald _b	14.63	1.24	0.318
C:P	83,000.9	10.86	0.003	Aug > Jun	455,351.3	19.85	<0.001	Euc > Che _a Oak _{ab} Ald _b	99,248.4	12.98	<0.001
N:P	129.5	4.32	0.049	Aug > Jun	1695.9	18.86	<0.001	Ald _a Oak _{ab} Che _b > Euc	19.56	0.65	0.589
Lignin, %	4.279	1.42	0.245		417.7	46.24	<0.001	Oak _a Euc _{ab} Ald _b > Che	5.879	1.95	0.149
Phenol, %	1.398	1.49	0.235		137.5	48.70	<0.001	Che = Oak > Ald = Euc	3.115	3.31	0.038
'Eucalypt conditioning'	Conditioning										
MANOVA	0.031	88.871	<0.001		0.005	38.907	<0.001		0.061	8.542	<0.001
ANOVA	SS	$F_{7,18}$		SS	SS	$F_{2,18}$			SS	$F_{2,18}$	
C:N	84.95	0.85	0.160		204.3	2.03	0.370		46.61	0.46	0.636
C:P	3.625,167.8	218.26	<0.001	Jul > Oct	590,620.3	35.56	<0.001	3w > 2w > 1w	369,060.3	22.22	<0.001
N:P	2160.0	26.99	<0.001	Jul > Oct	1239.3	15.49	<0.001	3w > 2w = 1w	586.2	7.33	0.005
Lignin, %	126.4	52.25	<0.001	Oct > Jul	100.8	41.68	<0.001	3w > 2w > 1w	9.311	3.85	0.041
Phenol, %	5.876	102.53	<0.001	Oct > Jul	62.28	1086.68	<0.001	1w > 2w > 3w	2.359	41.17	<0.001

Different subscripts separate materials by statistical significance (highest on the left)

content of lignin, C:P and N:P, and reduced that of phenols (Tables 1 and 2).

Leaf selection

No container showed a shortage of any of the materials by the end of the experiment and all the species displayed over 21% alder of the initial dry mass. Total leaf consumption in the ‘Leaves’ experiment was higher for *S. pyrenaicum* ($0.55 \pm 0.04SE$ mgLeaf mgInd⁻¹ d⁻¹) than for *E. tarragonensis* ($0.23 \pm 0.01SE$ mgLeaf mgInd⁻¹ d⁻¹) (permutation test p-value: 0.027) (Fig. 1, Table 3). Considering

leaf species separately also yielded a higher consumption by *S. pyrenaicum* (Fig. 1). Both detritivores consumed more alder than any other leaf species (Fig. 1, Table 3), but the selectivity was different as the preference for alder was clearer for *E. tarragonensis* (86.2% of the consumption) than for *S. pyrenaicum* (61.1% of the consumption). The least consumed resource for *S. pyrenaicum* was eucalypt (3.1%) and for *E. tarragonensis* oak (0.1%) (Fig. 1).

In the ‘Eucalypt conditioning’ experiments consumption rate was similar for both detritivores and the lowest recorded amount of any resource type by the end of the experiment was 56% for materials

Fig. 1 Consumption rates of *S. pyrenaicum* and *E. tarragonensis* in the food preference experiments (mean ± SE)

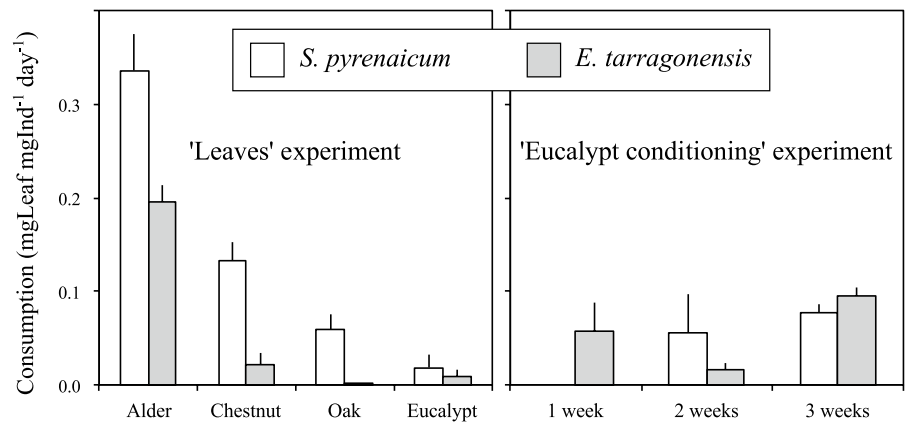


Table 3 Two-way ANOVA analyses for the consumption rates of *S. pyrenaicum* and *E. tarragonensis* in the food preference experiments. P values were obtained by permutation (see ‘‘Methods’’)

	DF	MS	F value	P value	Contrast
'Leaves' experiment Source of variation					
Total	31				
Species	1	0.0516	35.8366	<0.001	<i>S. pyrenaicum</i> > <i>E. tarragonensis</i>
Leaf	3	0.1075	74.7231	<0.001	Alder > Chestnut = Oak = Eucalypt
Interaction	3	0.0067	4.6720	0.021	
Error	24	0.0014			
Eucalypt conditioning' experiment Source of variation					
Total	23				
Species	1	0.0008	0.4268	0.515	
Conditioning	2	0.0077	4.0629	0.030	3 > 2 = 1
Interaction	2	0.0048	2.5264	0.116	
Error	18	0.0019			

Different subscripts separate consumptions by statistical significance (highest on the left)

incubated for 3 weeks. Total leaf consumption was considerably lower than in the ‘Leaves’ experiment for *S. pyrenaicum*, $0.13 \pm 0.05\text{SE mgLeaf mgInd}^{-1} \text{d}^{-1}$ (4.1-fold reduction, permutation *P* value: 0.029), but not for *E. tarragonensis*, $0.17 \pm 0.04\text{SE mgLeaf mgInd}^{-1} \text{d}^{-1}$ (1.4-fold reduction, permutation *P* value: 0.257), with no difference between the detritivores (permutation test *P* value: 0.574). No detectable consumption was detected for *S. pyrenaicum* after only 1 week of conditioning (Fig. 1). A longer conditioning time increased consumption rate (Fig. 1, Table 3), with 58% of the consumption of *S. pyrenaicum* and 57% of *E. tarragonensis* being eucalypt leaves conditioned for 3 weeks, although *E. tarragonensis* consumed more the materials incubated for just 1 week than for 2 weeks (Fig. 1).

Consumption vs leaves chemical properties

Spearman correlation coefficients showed that some chemical properties might have driven the resource selection observed (Table 4). In the ‘Leaves’ experiment, nutrient content seemed to be a decisive factor for *S. pyrenaicum* as C:N and C:P ratios were negatively correlated with consumption rates (Table 4). This species also showed a positive relationship to N:P ratios of the resource (Table 4). For *E. tarragonensis* phenol content was negatively correlated with leaf consumption in the ‘Leaves’ experiment. In the ‘Eucalypt conditioning’ experiment, chemical properties correlated with consumption rates completely changed. For *S. pyrenaicum* lignin content and C:P ratio were positively correlated to consumption, whereas phenol content was negatively (Table 4). For *E. tarragonensis* none of the parameters correlated significantly with consumption rates (Table 4).

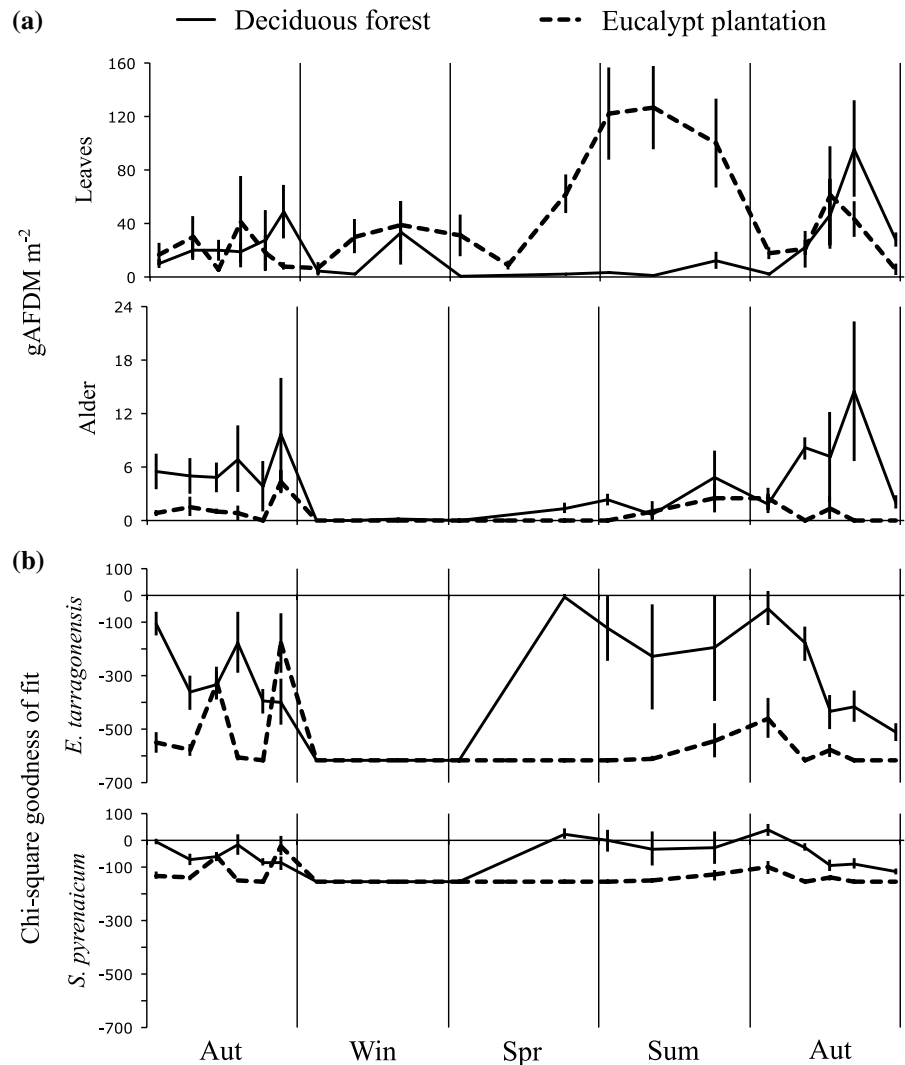
Field benthic standing stock vs consumption preference in laboratory microcosmos

Leaf composition and standing stock at deciduous (D) and eucalypt (E) sites differed markedly (Fig. 2a, Table 5). Total leaf amount was higher at E, but alder amount was higher at D (Fig. 2a, Table 5). Both total leaf and alder leaf showed a marked seasonality at both sites, but while for alder this seasonality was similar at both sites (but with noticeable larger fluctuations in site D), for total leaves there was a clear between-site difference (Fig. 2a, Table 5). The difference appeared as a result of eucalypt leaf inputs at E in summer (Fig. 2a). Chi-square goodness of fit between supply in the field and preference observed in the ‘Leaves’ experiment was nearly always negative at both sites (Fig. 2b), i.e. rarely was observed a higher relative amount of alder than the relative alder amount consumed in the laboratory. As *E. tarragonensis* showed itself to be more selective in the laboratory, the supply-preference disparity was higher with lower χ^2 values. E site showed a higher disparity than site D (Fig. 2b). Winter showed the highest disparities between supply and preference, whereas summer was the season showing the lowest disparities (Fig. 2b). In autumn, the disparity gradually became higher because the stock of other leaf species in the benthos became higher too (Fig. 2a,b). The standing stock of alder and the leaf quantity index were positively related (Fig. 3, Table 6). Nevertheless, covariation was different, with leaf quality index increasing faster with alder, and to larger values, in site D (Fig. 3, Table 6). With low alder quantities other leaf resources contributed more to the leaf quality index in site E than in site D (Fig. 3). The annual cycle of the leaf quantity index was very similar to that for alder standing stock, and higher values for the index than

Table 4 Significant Spearman rank correlation coefficients between the chemical characteristics of the material offered to *S. pyrenaicum* and *E. tarragonensis* in the food preference experiments and consumption rates

Experiment	Invert. species	Parameter	Rho	<i>P</i> value
‘Leaves’	<i>S. pyrenaicum</i>	C:N	−0.811	<0.001
		N:P	0.737	0.001
		C:P	−0.681	0.004
‘Eucalypt conditioning’	<i>E. tarragonensis</i>	Phenol, %	−0.552	0.027
		<i>S. pyrenaicum</i>	Lignin, %	0.690
	C:P		0.676	0.016
	Phenol, %		−0.620	0.032
	<i>E. tarragonensis</i>	No significant relationship		

Fig. 2 **a** Benthic alder and leaf standing stock (AFDM), and **b** chi-square goodness of fit between the relative alder offer in the field and the food preferences shown by *S. pyrenaicum* and *E. tarragonensis* in the ‘leaves’ experiment (surplus of alder is denoted by positive values and shortage by negative ones) (mean \pm SE)



for the alder standing stock were only visible from January to August (Fig. S1, Table S1). As for alder standing stock, leaf quantity index values were higher in the stream under native deciduous forest and there was a marked seasonality (Fig. S1, Table S1).

Discussion

General patterns of preference

Our results support that detritivores are selective consumers, which can choose among resources of different quality entering the stream (Leberfinger & Bohman, 2010; Jabiol & Chauvet, 2012; Reis et al.,

2019). As it is common in other previous feeding experiments (e.g. Friberg & Jacobsen, 1994; González & Graça, 2003; Graça & Cressa, 2010; Dray et al., 2014; Balibrea et al., 2017) food selection was related to its quality, as both *S. pyrenaicum* and *E. tarragonensis* preferred alder leaves over the rest of the native (chestnut and oak) and non-native (eucalypt) leaf species. In line with our results, Canhoto & Graça (1995) observed that the dipteran *Tipula lateralis* Meigen, 1804, also preferred alder leaves over chestnut, oak (*Quercus faginea* Lam., 1785) and eucalypt leaves. Similarly, the caddisfly *Limnephilus atlanticus* Nybom, 1948, preferred alder over other common resources in Azorean streams (Balibrea et al., 2017). Our study has revealed that

Table 5 ANOVA analyses for the leaf and alder standing stock and the chi-square goodness of fit of the relative alder offer in the deciduous and the eucalypt site. *p*-values were obtained by permutation (see “Methods”)

	DF	MS	<i>F</i> value	<i>P</i> value	Contrast
Leaf standing stock					
Source of variation					
Site	1	19,499.7	13.67	<0.001	Eucalypt > deciduous
Date	19	4219.2	2.96	<0.001	
Site × Date	19	5482.3	3.84	<0.001	
Error	160	1426.3			
Alder standing stock					
Source of variation					
Site	1	463.0	20.20	<0.001	Deciduous > eucalypt
Date	19	51.3	2.24	0.009	
Site × Date	19	35.0	1.53	0.086	
Error	160	22.9			
Chi-square goodness of fit					
Source of variation					
Species	1	8,254,717.9	354.21	<0.001	<i>S. pyrenaicum</i> > <i>E. tarragonensis</i>
Site	1	1,836,601.0	78.81	<0.001	Deciduous > eucalypt
Date	19	67,649.6	2.90	<0.001	
Species × Site	1	530,718.2	22.77	<0.001	
Species × Date	19	20,956.4	0.90	0.589	
Site × Date	19	133,764.2	5.74	<0.001	
Species × Site × Date	19	44,080.8	1.89	0.015	
Error	320	23,304.4			

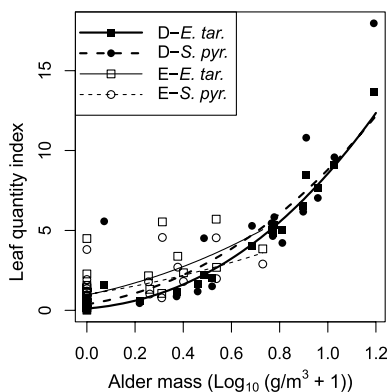


Fig. 3 Alder mass and leaf quantity index (see “Methods”) relationship for the stream under deciduous forest (D) and eucalypt plantation (E). The quantity indexes have been computed using laboratory leaf preferences of the two detritivores. Leaf quality index was Box–Cox transformed for the analysis, but untransformed values are shown in the plot together with the backtransformed regression lines obtained in the linear model

the amount of nitrogen or phosphorus (C:N and C:P ratios) was positively related to the consumption rates by *S. pyrenaicum*, whereas the amount of phenol showed a negative relationship with consumption for both species, which indicates that each consumer might be responding to a different set of variables that define the quality of the resource. Irons et al. (1988) also stated that resource preferences by detritivores were ruled by its nutrient amount when they found a positive correlation between the amount of nitrogen in detritus and the consumption by the caddisfly *Hydatophylax variabilis* Martynov, 1910. Similarly, Arias-Real et al. (2018) observed a positive effect of the quality of the resource on the consumption and growth of the caddisfly *Potamophylax latipennis* Curtis, 1834. This preference towards nutrient-rich materials is observed even in field experiments for processing rates of leaf species of different amount of nutrients (López et al., 2001; Martínez et al., 2013). On the other hand, phenolics have been credited as inhibitors of the consumption elsewhere (Canhoto & Graça, 1995). In the second experiment, conditioning of a poor resource like eucalypt litter proved

Table 6 ANOVA analysis for the variability of the leaf quality index (see “Methods”) by the amount of alder, the site and the taxa considered for the computation of the index

Source of variation	DF	MS	F value	P value	Contrast
Alder mass [Log10(x + 1)]	1	140.671	194.19	<0.001	Positive covariation
Site	1	4.093	5.65	0.093	
Species	1	0.137	0.19	0.801	
Alder mass × Site	1	5.233	7.22	0.009	Covariation differs with site
Alder mass × Species	1	0.051	0.07	0.296	
Site × Species	1	1.718	2.37	0.126	
Alder mass × Site × Species	1	0.044	0.06	0.806	
Error	70	0.724			

Alder mass was log-transformed to reduce the leverage of the largest values and a Box–Cox transformation was applied to Leaf quality index to deal with heteroscedasticity. *P* values were obtained by permutation (see “Methods”)

to be able to increase palatability of the material as consumption increased with conditioning time as in other studies (Friberg & Jacobsen, 1994; Graça et al., 2001; Graça & Cressa, 2010; Biasi et al., 2019). Chemical differences between the three eucalypt conditioning times were not as evident as between the different leaf species, and consequently, conditioning did not overcome the basal low quality of the eucalypt leaf litter. In this case, we cannot attribute the consumption increase with conditioning time to the lignin increase (see Schindler & Gessner, 2009) or the C:P ratio increment, as happened to appear in the Spearman correlations, but to the leaching of the chemical defences of the leaves, i.e. loss of phenolic compounds, that are responsible for an increase in consumption (Kochi & Kagaya, 2005). Nevertheless, we need to bear in mind that, together with the leaching of the chemical defences, a series of physical and chemical changes occur during the conditioning that are intercorrelated. In this sense, we did not measure some of the parameters that are highlighted to be important in the literature, such as leaf toughness (Graça & Cressa, 2010; Reis et al., 2019), the degree of microbial colonisation (Jabiol & Chauvet, 2012; Cassoti et al., 2019) or the availability of protein or lipids (Müller-Navarra et al., 2000; Assmann et al., 2011).

Taxa-specific selectivity

Although we observed a clear preference for alder leaves for both taxa the selectivity strength was different for both. While for *S. pyrenaicum* ca. 62% of the total consumption was alder, similar to the value

for *T. lateralis* (also an insect) in the study by Canhoto & Graça (1995), the amphipod *E. tarragonensis* was more selective (80% of the total consumption was alder). This result is consistent with the higher selectivity by the amphipod *Gammarus pulex* L., 1758, than by the caddisfly *Sericostoma personatum* Kirby & Spence, 1826, in the study by Friberg & Jacobsen (1994). We can think of three, undoubtedly correlated, reasons that can create these differences in the selectivity. Firstly, the lower body carbon:nutrient ratios in crustacea than in insects (Evans-White et al., 2005; Fink et al., 2006; Mehler et al., 2013) should force amphipods to be more selective and search for higher quality food than caddis to maintain internal homeostasis. Nevertheless, while the selection by the caddis *S. pyrenaicum* seemed to follow the nutritional quality of the resource in our study, as both C:N and C:P of the leaves related negatively to the consumption rates, *E. tarragonensis* appeared to mainly avoid the toxicity of the different resources as only phenol levels were negatively related to consumption rates, although differences in consumption of alder and eucalypt cannot be attributed to phenol levels only as these were comparable in these two resources. Nevertheless, this lack of relationship between consumption by the amphipod and the resource nutrient content do not match with larger homeostatic constraint that crustacea face. A second possible reason for the differences in selectivity between the two consumers might be the capacity of guts to digest resources. Insects are demonstrated to have a more complex gut system than crustacea (Rong et al., 1995) that allows *S. pyrenaicum* to digest more recalcitrant materials. Thirdly, the way the two detritivores seek food

is different and can have an effect on the selectivity of the resource. The higher mobility of the amphipod *E. tarragonensis* than of the caddis *S. pyrenaicum*, which needs to carry the case, enables the former to be constantly trying and comparing the various food items available in its environment, and ultimately it can be more selective. This constant movement is an advantage for resource seeking, but can go against the survival of the animal when the resource available is of low quality. If we compare the total leaf mass consumed from the experiment where alder was available to when it was not, the amphipod did not reduce it while for the caddis the reduction was very marked (75% less). This suggests that caddis larvae are able to regulate their energy acquisition by completely reducing feeding rates when they detect toxic resources in their environment (Canhoto & Laranjeira, 2007), or, alternatively, compensating for the low quality by incrementing feeding rates when such a toxicity is not present (Flores et al., 2014). Contrarily, gammarids might be forced to continue consuming resources even if the only available resource has toxic compounds like eucalypt leaves and will ultimately increment their death rates (Larrañaga et al., 2014).

Effect of standing stocks in the field: native deciduous forests vs eucalypt plantations

The feeding experiments in the laboratory have offered the animals the resources in overabundance and with similar accessibility to all of them. On the other hand, alternative resources, such as biofilm, are not important for the two selected consumers (Basaguren et al., 2002; Carvalho & Graça, 2007; Piscart et al., 2011) and they are rather scarce in low-order streams in the area (Izagirre & Elozegi, 2005), such as site D and E in our study. Thus, we should consider the consumption pattern we have observed as those that maximise the fitness of the consumer as has been observed elsewhere (Li & Dudgeon, 2008). On the other hand, our approach of comparing percentages of consumption in the laboratory and supply in the field could be interpreted similarly to the studies based on stoichiometry. Total leaf quantity can limit consumer performance. Nevertheless, consistent with the stoichiometrical approach, where the relative amount of nutrients in relation to carbon is important and limits growth, reproduction and therefore fitness

of macroinvertebrates (Elser et al., 2003; Flores et al., 2014; Larrañaga et al., 2014), we can expect that the low relative density of alder leaves (high-quality food) in relation to other resource types to be detrimental to consumers. The same amount of alder, but sparsely distributed in a complex matrix filled with inorganic or low-quality organic materials might have the same effect of a lower supply of high-quality material due to the difficulty that consumers have in finding it. Some works in the Northern Hemisphere trying to assess the impact exotic plantations of eucalypt have highlighted the low quality of its leaf litter (e.g. Canhoto & Graça, 1995) but have observed larger inputs of detritus in these altered systems that can be even higher than those in native deciduous forests (Pozo et al., 1997). Nevertheless, we have observed that following the preferences in the laboratory experiment the value of the leaf standing stock (i.e. leaf quantity index) is closely related to the standing stock of alder, with some minor differences when alder is very scarce and other leaf species are very abundant. Thus, it is unsurprising to see the impact of land uses that remove alder's presence in the riparian forest on benthic communities (Abelho & Graça, 1996; Larrañaga et al., 2009a), and even in the energy acquisition patterns of detritivores (Larrañaga et al., 2009b). In the present work, we observed that the gap between the supply (field offer) and the demand (laboratory consumption of high-quality food, alder) is very large and that the detritivores meet their most preferred amount of alder very few times throughout the year. The mismatch between supply in the field and preference in the laboratory is much higher for the amphipod, as it has shown to be much more food selective than the caddisfly. This wide gap between supply and preference might partially explain the large reduction in *Echinogammarus* spp. density from streams below native deciduous forests to streams below eucalypt plantations we observed previously (Larrañaga et al., 2009a). Sericostomatids, on the other hand, are usually less abundant in streams of the area, but they do not respond with such a strength to the presence of eucalypt, which might be an output, as the present study has demonstrated, to the greater similarities between their preference and the supply in the field.

In conclusion, our study suggests that the effects of land use changes on specific river detritivores can be related to their feeding preferences, which should ultimately be linked to their resource requirements.

We can anticipate that the impairment created by land use changes that reduce the quality of the detritus entering streams, such as eucalypt plantations, on the organisation of the food webs and the functioning of ecosystems will be proportional to the relevance of taxa that show a high preference for high-quality resources.

Acknowledgements This study was funded by the Spanish Dirección General de Enseñanza Superior e Investigación Científica (Project DGEIC PB98-0151) and a predoctoral Grant for A. Otermin from the Basque Government.

Funding Open Access funding provided thanks to the CRUE-CSIC agreement with Springer Nature. This study was funded by the Spanish Dirección General de Enseñanza Superior e Investigación Científica (Project DGEIC PB98-0151) and financial support in terms of a predoctoral Grant to A. Otermin from Basque Government.

Data availability Upon request to authors.

Code availability Upon request to authors.

Declarations

Conflict of interest None.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication The authors agree on the publication of this manuscript in the current format.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Abelho, M. & M. A. S. Graça, 1996. Effects of eucalyptus afforestation on leaf litter dynamics and macroinvertebrate community structure of streams in Central Portugal. *Hydrobiologia* 324: 195–204.
- Allen, S. E., H. M. Grimshaw, J. A. Parkinson & C. Quarmby, 1974. *Chemical Analysis of Ecological Materials*, Blackwell Scientific Publications, Oxford, UK:
- Anderson, M. J. & C. F. K. Ter Braak, 2003. Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation* 73: 85–113.
- Arias-Real, R., M. Menéndez, M. Abril, F. Oliva & I. Muñoz, 2018. Quality and quantity of leaf litter: both are important for feeding preferences and growth of an aquatic shredder. *PLoS ONE* 13: e0208272.
- Arsuffi, T. L. & K. Suberkropp, 1989. Selective feeding by shredders on leaf-colonizing stream fungi: comparison of macroinvertebrate taxa. *Oecologia* 79: 30–37.
- Assmann, C., K. Rinke, J. Nechwatal & E. Von Elert, 2011. Consequences of the colonisation of leaves by fungi and oomycetes for leaf consumption by a gammarid shredder. *Freshwater Biology* 56: 839–852.
- Balibrea, A., V. Ferreira, V. Gonçalves & P. M. Raposeiro, 2017. Consumption, growth and survival of the endemic stream shredder *Limnephilus atlanticus* (Trichoptera, Limnephilidae) fed with distinct leaf species. *Limnologia* 64: 31–37.
- Bañuelos, R., S. Larrañaga, A. Elozegi & J. Pozo, 2004. Effects of eucalyptus plantations on CPOM dynamics in headwater streams: a manipulative approach. *Archiv Fur Hydrobiologie* 159: 211–228.
- Bärlocher, F., 2020. Leaching. Bärlocher, F., M.O. Gessner & M.A.S. Graça (eds), *Methods to Study Litter Decomposition: A Practical Guide*, 2nd ed. Springer Nature, Cham, Switzerland: 36–41.
- Basaguren, A. & J. Pozo, 1994. Leaf litter processing of alder and eucalyptus in the Agüera stream system (Northern Spain) II Macroinvertebrates Associated. *Archiv Fur Hydrobiologie* 132: 57–68.
- Basaguren, A., P. Riaño & J. Pozo, 2002. Life history patterns and dietary changes of several caddisfly (Trichoptera) species in a northern Spain stream. *Archiv Fur Hydrobiologie* 155: 23–41.
- Biasi, C., G. B. Cogo, L. U. Hepp & S. Santos, 2019. Shredders prefer soft and fungal-conditioned leaves, regardless of their initial chemical traits *Iheringia, Série. Zoologia* 109: e2019004.
- Boulton, A. J., 1991. Eucalypt leaf decomposition in an intermittent stream in south-eastern Australia. *Hydrobiologia* 211: 123–136.
- Box, G. E. & D. R. Cox, 1964. An analysis of transformations. *Journal of the Royal Statistical Society, Series B* 26: 211–252.
- Campos, J. & J. M. González, 2009. *Sericostoma vittatum* (Trichoptera) larvae are able to use pine litter as energy source. *Internationale Revue Der Gesamten Hydrobiologie Und Hydrographie* 94: 472–483.
- Canhoto, C. & M. A. S. Graça, 1995. Food value of introduced eucalypt leaves for a Mediterranean stream detritivore: *Tipula lateralis*. *Freshwater Biology* 34: 209–214.
- Canhoto, C. & M. A. S. Graça, 1999. Leaf barriers to fungal colonization and shredders (*Tipula lateralis*)

- consumption of decomposing *Eucalyptus globulus*. *Microbial Ecology* 37: 163–172.
- Canhoto, C. & C. Laranjeira, 2007. Leachates of *Eucalyptus globulus* in intermittent streams affect water parameters and invertebrates. *Internationale Revue Der Gesamten Hydrobiologie Und Hydrographie* 92: 173–182.
- Canhoto, C., M.A.S. Graça, & F. Bärlocher, 2020. Feeding preferences. In Bärlocher, F., M.O. Gessner & M.A.S. Graça (eds), *Methods to study litter decomposition: A practical guide*, 2nd ed. Springer Nature, Cham, Switzerland: 475–481.
- Carvalho, E. M. & M. A. S. Graça, 2007. A laboratory study of feeding plasticity of the shredder *Sericostoma vitatum* Rambur (Sericostomatidae). *Hydrobiologia* 575: 353–359.
- Casotti, C. G., W.P.Jr. Kiffer, L.C. Costa, P. Barbosa & M.S. Moretti, 2019. The longer the conditioning, the better the quality? The effects of leaf conditioning time on aquatic hyphomycetes and performance of shredders in a tropical stream. *Aquatic Ecology* 53: 163–178.
- Constantini, M. L. & L. Rossi, 2010. Species diversity and decomposition in laboratory aquatic systems: the role of species interactions. *Freshwater Biology* 55: 2281–2295.
- Cornejo, A., J. Pérez, A. Alonso, N. López-Rojo, S. Monroy & L. Boyero, 2020. A common fungicide impairs stream ecosystem functioning through effects on aquatic hyphomycetes and detritivorous caddisflies. *Journal of Environmental Management* 263: 110425.
- Dray, M. W., T. W. Crowther, S. M. Thomas, A. D. A'Bear, D. L. Godbold, S. J. Ormerod, S. E. Hartley & H. Jones, 2014. Effects of elevated CO₂ on litter chemistry and subsequent invertebrate detritivore feeding responses. *PLoS ONE* 9: e86246.
- Elsler, J. J., K. Acharya, M. Kyle, J. Cotner, W. Makino, T. Markow, T. Watts, S. Hobbie, W. Fagan, J. Schade, J. Hood & R. W. Sterner, 2003. Growth rate-stoichiometry couplings in diverse biota. *Ecology Letters* 6: 936–943.
- Evans-White, M., R. S. Stelzer & G. A. Lamberti, 2005. Taxonomic and regional patterns in benthic macroinvertebrate elemental composition in streams. *Freshwater Biology* 50: 1786–1799.
- Ferreira, V., J. Koricheva, J. Pozo & M. A. S. Graça, 2016. A meta-analysis on the effects of changes in the composition of native forests on litter decomposition in streams. *Forest Ecology and Management* 364: 27–38.
- Ferreira, V., L. Boyero, C. Calvo, F. Correa, R. Figueroa, J. F. Gonçalves Jr., G. Goyenola, M. A. S. Graça, L. U. Hepp, S. Kariuki, A. López-Rodríguez, N. Mazzeo, C. M'Erimba, S. Monroy, A. Peil, J. Pozo, R. Rezende & F. Teixeira-de-Mello, 2019. A global assessment of the effects of eucalyptus plantations on stream ecosystem functioning. *Ecosystems* 22: 629–642.
- Fink, P., L. Peters & E. Von Elert, 2006. Stoichiometric mismatch between littoral invertebrates and their periphyton food. *Archiv Fur Hydrobiologie* 165: 145–165.
- Flores, L., A. Larrañaga & A. Elozegi, 2014. Compensatory feeding of a stream detritivore alleviates the effects of poor food quality when enough food is supplied. *Freshwater Science* 33: 134–141.
- Friberg, N. & D. Jacobsen, 1994. Feeding plasticity of two detritivore-shredders. *Freshwater Biology* 32: 133–142.
- Friberg, N. & D. Jacobsen, 1999. Variation in growth of the detritivore-shredder *Sericostoma personatum* (Trichoptera). *Freshwater Biology* 42: 625–635.
- Goering, H.K. & P.J. Van Soest, 1970. Forage fibre analysis. *Agriculture Handbook No. 379*. Agricultural Research Service, United States Department of Agriculture, Washington DC.
- González, J. M. & M. A. S. Graça, 2003. Conversión of leaf litter to secondary production by shredding caddis-fly. *Freshwater Biology* 48: 1578–1598.
- Graça, M. A. S. & C. Cressa, 2010. Leaf quality of some tropical and temperate tree species as food resource for stream shredders. *Internationale Revue Der Gesamten Hydrobiologie Und Hydrographie* 95: 27–41.
- Graça, M. A. S., C. Cressa, M. O. Gessner, M. J. Feio, K. A. Callies & C. Barrios, 2001. Food quality, feeding preferences, survival and growth of shredders from temperate and tropical streams. *Freshwater Biology* 46: 947–957.
- Graça, M. A. S., J. Pozo, C. Canhoto & A. Elozegi, 2002. Effects of eucalyptus plantations on detritus, decomposers, and detritivores in streams. *The Scientific World Journal* 2: 1173–1185.
- Iglesias-Trabado, G. & D. Wilstermann, 2009. *Eucalyptus universalis*. Global cultivated eucalypt forests map 2009. <https://git-forestry-blog.blogspot.com/2008/09/eucalyptus-global-map-2008-cultivated.html>. Accessed: March 2019
- Inkley, M. D., S. A. Wissinger & B. L. Baros, 2008. Effects of drying regime on microbial colonization and shredder preference in seasonal woodland wetlands. *Freshwater Biology* 53: 435–445.
- Irons, J. G., M. W. Oswood & J. P. Bryant, 1988. Consumption of leaf detritus by a stream shredder: influence of tree species and nutrient status. *Hydrobiologia* 160: 53–61.
- Izagirre, O. & A. Elozegi, 2005. Environmental control of seasonal and inter-annual variations of periphytic biomass in a North Iberian stream. *Annales De Limnologie - International Journal of Limnology* 41: 35–46.
- Jabiol, J. & E. Chauvet, 2012. Fungi are involved in the effects of litter mixtures on consumption by shredders. *Freshwater Biology* 57: 1667–1677.
- Kiffer, W. P., Jr., F. Mendes, C. G. Casotti, L. C. Costa & M. Moretti, 2018. Exotic *Eucalyptus* leaves are preferred over tougher native species but affect the growth and survival of shredders in an Atlantic Forest stream (Brazil). *PLoS ONE* 13: e0190743.
- Kochi, K. & T. Kagaya, 2005. Green leaves enhance the growth and development of a stream macroinvertebrate shredder when senescent leaves are available. *Freshwater Biology* 50: 656–667.
- Larrañaga, A., S. Larrañaga, A. Basaguren, A. Elozegi & J. Pozo, 2006. Assessing impact eucalyptus plantations on benthic macroinvertebrate communities by a litter exclusion experiment. *Annales De Limnologie - International Journal of Limnology* 42: 1–8.
- Larrañaga, A., A. Basaguren, A. Elozegi & J. Pozo, 2009a. Impacts of *Eucalyptus globulus* plantations on Atlantic streams: changes in invertebrate density and shredder traits. *Fundamental and Applied Limnology* 175: 151–160.

- Larrañaga, A., A. Basaguren & J. Pozo, 2009b. Impacts of *Eucalyptus globulus* plantations on physiology and populations densities of macroinvertebrates inhabiting Iberian Atlantic streams. *Internationale Revue Der Gesamten Hydrobiologie Und Hydrographie* 94: 497–511.
- Larrañaga, A., A. Basaguren & J. Pozo, 2014. Resource quality controls detritivore consumption, growth, survival and body condition recovery of reproducing females. *Marine and Freshwater Research* 65: 1–8.
- Leberfinger, K. & I. Bohman, 2010. Grass, mosses, algae, or leaves? Food preference among shredders from open-canopy streams. *Aquatic Ecology* 44: 195–203.
- Lecerf, A., M. Dobson, C. K. Dang & E. Chauvet, 2005. Riparian plant species loss alters trophic dynamics in detritus-based stream ecosystems. *Oecologia* 146: 432–442.
- Li, A. O. Y. & D. Dudgeon, 2008. Food resources of shredders and other benthic macroinvertebrates in relation to shading conditions in tropical Hong Kong streams. *Freshwater Biology* 53: 2011–2025.
- López, E. S., I. Pardo & N. Felpeo, 2001. Seasonal differences in green leaf breakdown and nutrient content of deciduous and evergreen tree species and grass in a granitic headwater stream. *Hydrobiologia* 464: 51–61.
- López-Rojo, N., A. Martínez, J. Pérez, A. Basaguren, J. Pozo & L. Boyero, 2018. Leaf traits drive plant diversity effects on litter decomposition and FPOM production in streams. *PLoS ONE* 13: e0198243.
- Martínez, A., A. Larranaga, J. Pérez, A. Basaguren & J. Pozo, 2013. Effects of pine plantations on structural and functional attributes of forested streams. *Forest Ecology and Management* 310: 147–155.
- Mehler, K., K. Acharya, D. Sada & Z. Yu, 2013. Elemental stoichiometry of basal resources and benthic macroinvertebrates along a land use gradient in a Great Basin watershed. *Hydrobiologia* 716: 115–129.
- Molinero, J., 2000. Nitrógeno y fósforo en la materia orgánica particulada bentónica: Influencia de la vegetación riparia, de las características del cauce y de la química del agua. Ph.D. Thesis, University of the Basque Country, Bilbao, Spain.
- Molinero, J. & J. Pozo, 2004. Impact of a eucalyptus (*Eucalyptus globulus* Labill) plantation on the nutrient content and dynamics of coarse particulate organic matter (CPOM) in a small stream. *Hydrobiologia* 528: 143–165.
- Molinero, J., J. Pozo & E. González, 1996. Litter breakdown in streams of the Agüera catchment: influence of dissolved nutrients and land use. *Freshwater Biology* 36: 745–756.
- Müller-Navarra, D. C., M. T. Brett, A. M. Liston & C. R. Goldman, 2000. A highly unsaturated fatty acid predicts carbon transfer between primary producers and consumers. *Nature* 403: 74–77.
- Piscart, C., J. M. Roussel, J. T. A. Dick, G. Grosbois & P. Marmonier, 2011. Effects of coexistence on habitat use and trophic ecology of interacting native and invasive amphipods. *Freshwater Biology* 56: 325–334.
- Pozo, J., E. González, J. R. Díez, J. Molinero & A. Elosegui, 1997. Inputs of particulate organic matter to streams with different riparian vegetation. *Journal of the North American Benthological Society* 16: 603–611.
- Reis, D. F., M. M. D. Machado, N. P. Coutinho, J. V. Rangel, M. S. Moretti & P. B. Morais, 2019. Feeding preference of the shredder *Phylloicus* sp. for plant leaves of *Chrysophyllum oliviforme* or *Miconia charitacea* after conditioning in streams from different biomes. *Brazilian Journal of Biology* 79: 22–28.
- Rong, Q., K. R. Sridhar & F. Bärlocher, 1995. Food selection in three leaf-shredding stream invertebrates. *Hydrobiologia* 316: 173–181.
- Schindler, M. H. & M. O. Gessner, 2009. Functional leaf traits and biodiversity effects on litter decomposition in a stream. *Ecology* 90: 1641–1649.
- Solagaistua, L., A. Elosegui & A. Larrañaga, 2019. Consumption and performance responses of the amphipod *Echinogammarus berilloni* change during laboratory incubation. *Annales De Limnologie - International Journal of Limnology* 55: 25.
- Tank, J. L., E. J. Rosi-Marshall, N. A. Griffiths, S. A. Entrekin & M. L. Stephen, 2010. A review of allochthonous organic matter dynamics and metabolism. *Journal of the North American Benthological Society* 29: 118–146.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130–137.
- Wallace, J. B. & J. R. Webster, 1996. The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology* 41: 115–139.
- Wallace, J. B., S. L. Eggert, J. L. Meyer & J. R. Webster, 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs* 69: 409–442.
- Yates, F., 1934. Contingency tables involving small numbers and the χ^2 test. Supplement to the *Journal of the Royal Statistical Society* 1: 217–235.
- Zar, J. H., 2010. *Biostatistical Analysis*, 5th ed. Prentice-Hall, Upper Saddle River, New Jersey:

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.