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

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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.

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 tricopterans 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 ± SE—dried at 60°C for 72 h—at the end of the experiment: DMend: 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 (DMend ± 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 lead 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 sporeae 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) g 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 (DMend ± 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<sub>end</sub>± 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°12′37″N, 3°15′46″W) and site E (43°19′37″N, 3°15′46″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<sup>2</sup>. 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 (mgLeaf mgInd<sup>−1</sup> d<sup>−1</sup>). 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 <span>F</span> values obtained with the real disposition of the data against the <span>F</span>-values distribution obtained after reshuffling the measured consumption values 10<sup>6</sup> times to estimate a <span>P</span> 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 (alder/leaves · 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 $\chi^2$ 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 $\chi^2$ 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-weighed amounts of the four leaf species were summed to compute the leaf quantity index. 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

| Trial | ‘Leaves’ experiment | ‘Eucalypt conditioning’ experiment |
|-------|---------------------|-----------------------------------|
| Alder | C:N | 16.9±0.3 | 62.6±2.5 | 21.1±1.0 | 9.6±0.2 | 8.5±1.3 | 47.4±11.8 | 49.8±9.7 | 20.1±0.1 | 8.5±0.2 |
| | C:P | 20.9±0.3 | 48.2±1.5 | 13.2±0.7 | 13.1±0.3 | 13.2±0.1 | 39.8±2.4 | 54.9±3.4 | 23.1±0.3 | 6.4±0.1 |
| | N:P | 20.7±0.5 | 53.1±1.2 | 22.0±1.0 | 11.4±0.1 | 13.4±0.2 | 31.7±3.8 | 44.3±5.7 | 22.3±0.4 | 8.1±0.2 |
| | 33.0±2.3 | 40.4±2.0 | 22.3±0.4 | 8.1±0.2 | 8.5±0.1 | 47.4±11.8 | 49.8±9.7 | 20.1±0.1 | 8.5±0.2 |
| | C:N | 16.3±0.5 | 25.0±1.4 | 19.5±0.8 | 24.7±0.4 | 14.7±0.2 | 39.0±0.7 | 35.7±1.7 | 25.3±1.7 | 8.5±0.2 |
| | C:P | 1080.9±27.9 | 1173.8±17.6 | 1206.6±42.2 | 1173.8±17.6 | 1206.6±42.2 | 2317.3±11.2 | 2992.4±40.0 | 2992.4±40.0 | 8.5±0.2 |
| | N:P | 62.6±1.2 | 57.9±1.3 | 24.7±0.4 | 14.7±0.2 | 13.4±0.2 | 47.4±11.8 | 49.8±9.7 | 20.1±0.1 | 8.5±0.2 |
| | Lignin, % | 33.0±2.3 | 40.4±2.0 | 22.3±0.4 | 8.1±0.2 | 8.5±0.1 | 39.0±0.7 | 35.7±1.7 | 25.3±1.7 | 8.5±0.2 |
| | | 2175.9±104.0 | 1415.5±65.9 | 1436.4±62.8 | 1415.5±65.9 | 1436.4±62.8 | 2175.9±104.0 | 2317.3±11.2 | 2992.4±40.0 | 2992.4±40.0 |
| | | June | August | July | October | July | October | July | October | July |
| | | | | | | | | | | |
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 |
|----------|-------|------|--------------|
| MANOVA   | $\lambda$ | $F_{5,19}$ | $P$ | Contrast | $\lambda$ | $F_{15,52.8}$ | $P$ | Contrast | $\lambda$ | $F_{15,52.8}$ | $P$ |
| ANOVA    | SS | $F_{1,23}$ | | | SS | $F_{1,23}$ | | | SS | $F_{3,23}$ | |
| C:N      | 0.017 | 0.001 | 0.970 | | 1096.9 | 30.98 | <0.001 | Euc > Chea Oakab Aldb | 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 > Chea Oakab Aldb | 99,248.4 | 12.98 | <0.001 |
| N:P      | 129.5 | 4.32 | 0.049 | Aug > Jun | 1695.9 | 18.86 | <0.001 | Alda Oakab Cheb > Euc | 19.56 | 0.65 | 0.589 |
| Lignin, % | 4.279 | 1.42 | 0.245 | Aug > Jun | 417.7 | 46.24 | <0.001 | Oakab Eucab Aldb > 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' | Trial | Conditioning | Trial x Conditioning |
|------------------------|-------|--------------|---------------------|
| MANOVA     | $\lambda$ | $F_{5,14}$ | $P$ | Contrast | $\lambda$ | $F_{10,28}$ | $P$ | Contrast | $\lambda$ | $F_{16,22}$ | $P$ |
| ANOVA      | SS | $F_{1,18}$ | | | SS | $F_{1,18}$ | | | 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 ± 0.04SE mgLeaf mgInd⁻¹ d⁻¹) than for E. tarragonensis (0.23 ± 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”)

| Source of variation | DF | MS    | F value | P value | Contrast          |
|---------------------|----|-------|---------|---------|-------------------|
| ‘Leaves’ experiment |    |       |         |         |                   |
| Total               | 31 | 0.0516| 35.8366 | < 0.001 | S. pyrenaicum > E. tarragonensis |
| Species             | 1  | 0.1075| 74.7231 | < 0.001 | Alder > Chestnut = Oak = Eucalypt |
| Leaf                | 3  | 0.0067| 4.6720  | 0.021   |                   |
| Interaction         | 3  | 0.0014|         |         |                   |
| Error               | 24 |       |         |         |                   |
| ‘Eucalypt conditioning’ experiment | |       |         |         |                   |
| Total               | 23 | 0.0008| 0.4268  | 0.515   |                   |
| Species             | 1  | 0.0077| 4.0629  | 0.030   | 3 > 2 = 1         |
| Conditioning        | 2  | 0.0048| 2.5264  | 0.116   |                   |
| Interaction         | 18 | 0.0019|         |         |                   |
| Error               | 18 |       |         |         |                   |
incubated for 3 weeks. Total leaf consumption was considerably lower than in the ‘Leaves’ experiment for \textit{S. pyrenaicum}, 0.13 ± 0.05SE mgLeaf mgInd⁻¹ d⁻¹ (4.1-fold reduction, permutation \(P\) value: 0.029), but not for \textit{E. tarragonensis}, 0.17 ± 0.04SE mgLeaf mgInd⁻¹ 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 \textit{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 \textit{S. pyrenaicum} and 57% of \textit{E. tarragonensis} being eucalypt leaves conditioned for 3 weeks, although \textit{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 \textit{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 \textit{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 \textit{S. pyrenaicum} lignin content and C:P ratio were positively correlated to consumption, whereas phenol content was negatively (Table 4). For \textit{E. tarragonensis} none of the parameters correlated significantly with consumption rates (Table 4).

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

| Experiment               | Invert. species | Parameter | Rho   | \(P\) value |
|-------------------------|-----------------|-----------|-------|-------------|
| ‘Leaves’                | \textit{S. pyrenaicum} | C:N       | −0.811| <0.001      |
|                         |                 | N:P       | 0.737 | 0.001       |
|                         |                 | C:P       | −0.681| 0.004       |
|                         | \textit{E. tarragonensis} | Phenol, % | −0.552 | 0.027       |
| ‘Eucalypt conditioning’ | \textit{S. pyrenaicum} | Lignin, % | 0.690  | 0.013       |
|                         |                 | C:P       | 0.676  | 0.016       |
|                         | \textit{E. tarragonensis} | Phenol, % | −0.620 | 0.032       |

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 \textit{E. tarragonensis} showed itself to be more selective in the laboratory, the supply-preference disparity was higher with lower \(\chi^2\) 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
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
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).

### 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”).

| Source of variation | DF | MS   | F value | *p* value | Contrast                   |
|---------------------|----|------|---------|-----------|---------------------------|
| Leaf standing stock |    |      |         |           |                           |
| 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|    |      |         |           |                           |
| 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    | *S. pyrenaicum* > *E. tarragonensis* |
| 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](image) 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.
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 of the leaves, 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, 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

### 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”)

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, 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 & Elosegi, 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.

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Code availability Upon request to authors.

Declarations

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