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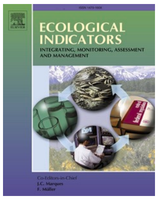

Original Articles

Black alder may enhance riparian buffer mitigation of pine-plantation effects on macroinvertebrate food webs in headwater streams

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ABSTRACT

Over the past century, drylands have undergone significant landscape transformations. Abandonment of traditional crops and pastures led to development of extensive afforestation programs with conifers, which often lacked an ecologically sound orientation, raising concerns on their potential consequences on recipient ecosystems. Forest streams heavily rely on inputs of terrestrial organic carbon and thus are particularly vulnerable to human-driven changes in catchment and riparian forests. One point of uncertainty is whether existing stands of deciduous trees in the riparian zone may buffer headwater stream food webs from the impacts of afforestation on the surrounding landscape. We used stable isotopes of carbon and nitrogen to investigate whether the presence of the nitrogen-fixing black alder in the riparian zone alters the impacts of pine plantations on macroinvertebrate food webs of headwater streams. We observed a consistent consumption of leaf litter by shredders, but a higher importance of autochthonous support to all macroinvertebrate functional feeding groups than initially expected, especially in absence of alder. In addition, we discerned a potential trend toward a food chain lengthening at streams holding riparian alder in winter. Overall, our results indicate that riparian alder can enhance the buffer effect exerted by other broadleaf species through a reduction of the usual wide nutritional imbalance existing between benthic consumers and resources, which may translate into longer food chains. These findings highlight the critical role of riparian vegetation, particularly deciduous species like black alder, in maintaining headwater stream ecosystem integrity within afforested landscapes. Incorporating riparian vegetation management into afforestation planning can enhance stream food-web stability and support more balanced aquatic ecosystems.

1. Introduction

Globally, natural forest area is decreasing in favor of planted forests, which already represent 7 % of all the forests around the world (FAO & UNEP, 2020). From 1990 to 2020 natural forests lost 301 million hectares, while planted forests increased their surface by 123 million hectares, with no continent or climatic domain free from this trend (FAO, 2020). The Mediterranean region is not an exception, with millions of hectares currently covered by plantations. These plantations consist mainly of native pine species, but also include exotic conifers and eucalyptus, and were planned in an effort to replace the natural forest lost over decades of agricultural and timber exploitation (Pausas et al., 2004). These restoration works considered forest cover fundamental to mitigate erosion and floods (García-Rodríguez, 2010). However, the lack of an ecologically sound design—such as inadequate species selection, absence of ecological corridors, establishment of monocultures, limited selection of native vegetation, poor snag management or no consideration of local environmental conditions (Hartley, 2002)—impeded preventable drawbacks of plantations on biodiversity and functioning of recipient ecosystems (e.g. Andrés & Ojeda, 2002; Larrañaga et al., 2021; Rubio-Ríos et al., 2023).

Forest streams may be especially susceptible to the establishment of plantations on their surroundings due to their fundamental reliance on terrestrial organic detritus (Wallace et al., 1997; Kominoski et al., 2011). In these streams, although increased light may enhance the assimilation of higher-quality autochthonous resources (Brett et al., 2017; Estévez et al., 2019), macroinvertebrate secondary production is largely supported by coarse particulate organic matter (e.g. leaf litter, twigs, trunks;

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Wallace et al., 1997). Therefore, stream functioning can be directly affected if these allochthonous inputs undergo nutritional changes (e.g. Alonso et al., 2022; Rubio-Ríos et al., 2021, 2023) or if the quantity of high-quality inputs decreases (Arias-Real et al., 2018). Nevertheless, the general relationship between pine plantations and streams ecosystem functioning remains largely unknown because contradictory effects of plantations on stream processes and biodiversity are reported. On the one hand, establishment of plantations around stream ecosystems have been shown to alter aquatic hyphomycetes communities (Ferreira et al., 2017), lower shredder biomass (Whiles & Wallace, 1997) and decelerate leaf litter decomposition (Kominoski et al., 2011; Martínez et al., 2013) or nutrient cycling rates (Rubio-Ríos et al., 2023) in streams. Conversely, other studies have reported no difference in fungal or invertebrate communities (Martínez et al., 2013, 2016) or in leaf litter decomposition rates (Ferreira et al., 2017; Rubio-Ríos et al., 2023) among natural and plantation streams. Geographical variations in climate, topography, soil characteristics and hydrology among different regions may significantly influence the response of stream ecosystems processes and biodiversity to pine plantations, contributing to this lack of consensus. Additionally, differences in riparian vegetation and its putative effects on invertebrates can play a key role in shaping regional streams dynamics (González-Bergonzoni et al., 2018; Oester et al., 2023), further promoting contrasting effects across regions.

The presence of deciduous species interspersed between plantations and streams could act buffering plantations-derived effects on these ecosystems through different mechanisms (Rubio-Ríos et al., 2023). For example, reducing the arrival of sediment and nutrients to the stream (Lowrance et al., 1997; Broadmeadow & Nisbet, 2004), or promoting macroinvertebrate detritivore and decomposer activity through the supply of palatable organic matter (Wallace et al., 1997). The latter presumably further boosted if plant key-species (*sensu* Folke et al., 1996), as the N-fixing black alder (*Alnus glutinosa* (L.) Gaertn), are present in the riparian area (Rubio-Ríos et al., 2021, 2023). Black alder is a dominant riparian species in Europe and is widely considered to play a key role in stream ecosystem functioning at instream (Alonso et al., 2021, 2022), riparian (Rubio-Ríos et al., 2023), and catchment scales (Shaftel et al., 2012). Its nutrient-rich leaf litter constitutes an allochthonous resource of key importance in aquatic ecosystems (Hladyz et al., 2009), which usually drives essential instream processes such as litter decomposition, nutrient cycling and macroinvertebrate secondary production, and biodiversity-ecosystem function (B-EF) relationships (Pérez et al., 2021).

Such effects of riparian vegetation on streams ecosystems can cascade through trophic levels, altering the energy transfer efficiency (Rudolf & Lafferty, 2011) and influencing the abundance and distribution of herbivorous and predatory taxa (Polis, Anderson & Holt, 1997). These alterations may be exacerbated considering the low-quality resource that pine needles represent for aquatic macroinvertebrates (Márquez et al., 2017). The productivity hypothesis predicts longer food-chains with increasing basal productivity (Pimm, 1982), while the subsidy-quality hypothesis suggests that ecosystems receiving high-quality allochthonous inputs can increase their functioning and strengthen trophic cascades (Osakpolor et al., 2023), potentially supporting longer food-chains. Therefore, the combination of reduced primary production typical of forested streams and the low-quality organic matter inputs from pines, is expected to result in a reduction of the food chain lenght (Friberg & Winterbourn, 1997; Wallace et al., 1997).

Here, we aim to assess whether presence of black alder in the riparian area may modulate consumer–resource interactions in headwater streams draining pine plantations. To this effect, we selected 6 headwater streams flowing through pine plantations and with similar riparian plant communities, the main difference being the presence or absence of riparian alder. In each stream we analyzed individuals of all macroinvertebrates feeding functional groups (i.e., collectors, scrapers, shredders and predators) and their potential resources (i.e., epilithic biofilm (hereafter epilithon), benthic fine particulate organic matter and leaf litter) at two different seasons (before and after leaves fall; hereafter fall and winter, respectively) for their carbon and nitrogen stable isotope composition (i.e., $\delta^{13}C$ and $\delta^{15}N$). We used this data to estimate trophic position of functional feeding groups, total food chain length (FCL), as well as the importance of each resource to the diet of each feeding group. We tested the following hypotheses: (1) both basal resources and benthic macroinvertebrates will exhibit lower C:N values in streams with riparian alder (+ *alder*), due to the presence of alder litter and the consequent alder-induced N enrichment of streamwater; (2) + *alder* streams will mostly rely on allochthonous resources (leaf litter), whereas the importance of autochthonous resources (instream primary production) will increase in those lacking alder (− *alder*), despite their scarcity; (3) based on Pimm's productivity and subsidy-quality hypotheses, the presence of riparian alder will lead to longer food chains, through increased nutrient availability and high-quality organic matter inputs; and (4) these patterns will be more pronounced after senescence, when all leaves are available for instream consumers.

2. Methods

2.1. Study sites

We studied trophic interactions of the invertebrate communities in six low-order streams located within the protected area of the Sierra Nevada National Park (southeastern Spain). Streams were relatively close to each other (<11 km distance in straight line) and located at altitudes between 1500–1700 m a.s.l. (Table 1; Fig. 1). Stream bottom is composed of mostly sand and gravel along with large boulders. Climate is Mediterranean, with cold-wet winters and warm-dry summers (Esteban-Parra et al., 2022).

In Sierra Nevada, especially since the 1950s, abandoned traditional agricultural areas have been replaced by dense pine forests (Padilla et al., 2010), resulting in the nearly monospecific stands of pine plantations observable today (~80 % of the forested area of the natural-national park; Pérez-Raya et al., 2001). At the altitudinal range studied here, forests are mainly composed of maritime pine (*Pinus pinaster* Ait.) mixed with small spots of holm oaks (*Quercus ilex* L.) at a basin scale, with black poplars (*Populus nigra* L.) and grey willows (*Salix atrocinerea* Brot.) in the riparian areas (Table S1; Padilla et al., 2010). In each stream, we assessed the taxonomic composition of riparian vegetation and instream leaf litter assemblages (see Supplementary methods). The six selected streams had a similar riparian plant community (but see Tables 1 and S1 for detailed compositional differences), with comparable broadleaf to pine trees ratios (− *alder*: 9.5 ± 3.8 %, + *alder*: 13.8 ± 3.7 %) and levels of canopy cover (− *alder*: 34.0 ± 2.9 %, + *alder*: 22.0 ± 1.3 %; Table 1). Streams mainly differed in the presence (3 streams) or absence (3 streams) of black alder (Table S1). In streams where alder was present, its litter ranged from 9.5 to 35.6 g of dry mass per square meter, accounting for ~30 % of the instream leaf litter, whereas streams without alder showed increased relative abundances of pine and willow litter (Table 1). The amount of instream litter is not necessarily proportional to riparian abundances, as upstream trees contribute litter inputs to the study reach, and litter from streamside slopes may also enter the stream through lateral movements.

The invertebrate communities of the six streams were similar (70 % of shared taxa among riparian types) and have been described previously as heterotrophic, dependent on allochtonous organic matter inputs and with normal predator to prey balance according to the ecosystem attributes described by Merrit et al. (2017) (Rubio-Ríos et al., 2023).

2.2. Sample collection and stable isotopes analyses

Samples were collected at two different seasons: just before natural leaf abscission (October 2021, hereafter fall), and approximately three months later, when leaves had been colonized by stream microorganisms and were fully available for benthic macroinvertebrates (February

Table 1

Location, geographic characteristics, riparian canopy cover (%), and taxonomic composition of instream leaf litter in the six streams studied. Values are means (±SE). Instream leaf litter values are presented as dry mass per surface area (g/m^2) and as the percentage relative to the total amount of leaf litter (%). Streams with or without riparian alder (*Alnus glutinosa*) are stated using + *alder* or −*alder*, respectively.

Riverbank type	− *alder*				+ *alder*			
Stream	Barranco de los Ciruelillos	Barranco de Alcázar	Barranco de Alhorí		Barranco de los Pasillos	Barranco de los Recodos	Río del Pueblo	
Municipality	Jérez del Marquesado	Jérez del Marquesado	Jérez del Marquesado		Aldeire	Aldeire	Lanteira	
Basin	Guadalquivir	Guadalquivir	Guadalquivir		Guadalquivir	Guadalquivir	Guadalquivir	
Altitude (m a.s.l.)	1519	1522	1507		1730	1643	1597	
Geographic coordinates	37.14 N 3.18 W	37.14 N 3.19 W	37.15 N 3.19 W	Mean	37.12 N 3.07 W	37.12 N 3.08 W	37.14 N 3.16 W	Mean
Canopy cover (%)	54.38 ± 4.49	31.33 ± 5.16	16.21 ± 1.08	33.97 ± 2.94	23.71 ± 3.45	25.04 ± 1.52	17.38 ± 0.88	22.04 ± 1.33
Broadleaf:Pine trees ratio	17.00	7.00	4.60	9.53 ± 3.80	21.00	8.50	12.00	13.83 ± 3.72
Alnus glutinosa (g/m^2)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	15.23 ± 5.06	35.64 ± 22.54	9.54 ± 4.99	20.14 ± 7.92
Populus nigra (g/m^2)	4.75 ± 1.60	16.42 ± 11.10	8.07 ± 2.63	9.75 ± 3.47	28.33 ± 10.63	31.11 ± 9.30	13.49 ± 9.66	24.31 ± 5.47
Pinus pinaster (g/m^2)	2.01 ± 0.88	10.96 ± 3.58	7.74 ± 3.48	6.90 ± 2.62	1.12 ± 0.33	19.57 ± 9.98	1.00 ± 0.43	7.23 ± 6.17
Castanea sativa (g/m^2)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	5.68 ± 2.68	0.00 ± 0.00	0.00 ± 0.00	1.89 ± 1.89
Salix atrocinerea (g/m^2)	4.25 ± 1.25	2.86 ± 0.55	8.86 ± 3.42	5.32 ± 1.82	0.20 ± 0.10	0.00 ± 0.00	0.20 ± 0.09	0.14 ± 0.07
Rubus ulmifolius (g/m^2)	0.00 ± 0.00	0.00 ± 0.00	0.78 ± 0.30	0.26 ± 0.26	0.22 ± 0.10	0.00 ± 0.00	0.00 ± 0.00	0.07 ± 0.07
Non identified (g/m^2)	13.19 ± 3.88	7.35 ± 1.41	8.17 ± 3.15	9.57 ± 1.83	12.08 ± 5.70	2.22 ± 0.75	6.27 ± 2.85	6.86 ± 2.86
Alnus glutinosa (%)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	24.11 ± 6.20	27.97 ± 5.75	37.25 ± 5.97	29.77 ± 3.90
Populus nigra (%)	24.15 ± 5.67	30.64 ± 5.94	20.97 ± 4.63	25.25 ± 2.85	42.41 ± 7.80	46.07 ± 7.73	29.43 ± 5.15	39.30 ± 5.05
Pinus pinaster (%	27.00 ± 7.63	31.45 ± 7.00	7.19 ± 2.87	21.88 ± 7.46	6.72 ± 4.17	22.13 ± 6.10	7.32 ± 3.76	12.06 ± 5.04
Castanea sativa (%)	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	8.36 ± 1.55	0.00 ± 0.00	0.00 ± 0.00	2.79 ± 2.79
Salix atrocinerea (%)	24.31 ± 5.14	10.61 ± 1.44	17.49 ± 1.06	17.47 ± 3.95	0.30 ± 0.06	0.00 ± 0.00	0.81 ± 0.20	0.37 ± 0.23
Rubus ulmifolius (%)	2.14 ± 0.45	0.00 ± 0.00	0.00 ± 0.00	0.71 ± 0.71	0.32 ± 0.06	0.00 ± 0.00	0.00 ± 0.00	0.11 ± 0.11
Non identified (%)	22.40 ± 4.74	27.29 ± 3.70	54.34 ± 3.29	34.68 ± 9.93	17.79 ± 3.30	3.83 ± 1.33	25.19 ± 6.35	15.60 ± 6.26

2022, hereafter winter; Fig. 1). In each stream, a 50-meter stream reach was selected to represent typical habitat conditions. Submerged leaf litter was collected from at least three naturally occurring leaf packs randomly distributed along the stream reach. Epilithon was obtained by scraping the surface of randomly selected rocks. Fine-particulate organic matter (FPOM) was collected from different points randomly distributed along the stream reach using a suction device. Benthic macroinvertebrates (BMI) were sampled (as many genera as possible) using a combination of repetitive kick sampling and hand collection from the bedrock surface, under stones and in leaf accumulations. All samples were preserved in an icebox and transported to the laboratory where they were oven-dried (48 h, 70 °C). Before drying, BMI were identified to the lowest possible taxonomic resolution (mostly genus) and sorted into feeding functional groups (FFGs: collectors [including collector-filterers and gatherer-collectors], scrapers, shredders and predators). BMI were assigned to specific guilds based on two biological traits defined in Tachet et al. (2010) directly related to the use of food sources: food type and feeding habit (see Table S3). Thereupon, BMI were starved for 24 h to allow gut content evacuation. After drying (48 h, 70 °C), BMI samples were immersed in a 2:1 chloroform:methanol solution (3 × 30 min immersions) to remove lipids (Blight & Dyer, 1959) and subsequently oven-dried (24 h, 60 °C). All BMI samples were treated uniformly to standardize possible effects of lipid removal on δ^{15}N values. Within each taxon, stream and season BMI individuals ($n = 1$–36) were pooled into up to 3 samples (depending on abundances and estimated dry weight). All samples (invertebrates and resources) were ground to a fine powder and submitted to the Stable Isotopes in Nature Laboratory at the University of New Brunswick (Fredericton, NB; Canada) for carbon and nitrogen stable isotope analyses (see Supplementary methods).

2.3. Data analysis

To assess whether a categorical design, grouping streams based on the presence or absence of alder on their riverbanks, was appropriate, we performed a principal components analysis (PCA) using community-weighted means (CWM) of leaf trait values based on the relative abundance of each litter species within instream leaf litter assemblages (*dbFD* function of the ‘FD’ package). The PCA explained 93.8 % of the total variation within the first 2 components, with the first dimension (60.4 % of the variation) clearly separating − *alder* from + *alder* streams (Fig. S1). Therefore, subsequent analyses followed a categorical design.

Streamwater characteristics were compared between riparian areas (− *alder vs.* + *alder*, n = 3) using t-tests. *Log* or *logit* transformations of variables were used for decimal and proportion values, respectively. Isotopic and stoichiometric differences among resources were examined using linear mixed effects regression (LMER) including resource type as a fixed factor and stream as random factor (*lmer* function of the ‘lme4′ R package). *Log* or *logit* transformations were used when needed to meet model’s assumptions. Differences within each resource and consumer FFG across riparian types (− *alder vs.* + *alder*) and seasons (fall and winter) were evaluated using generalized linear mixed models (GLMM) including the interaction between riparian type and season as fixed

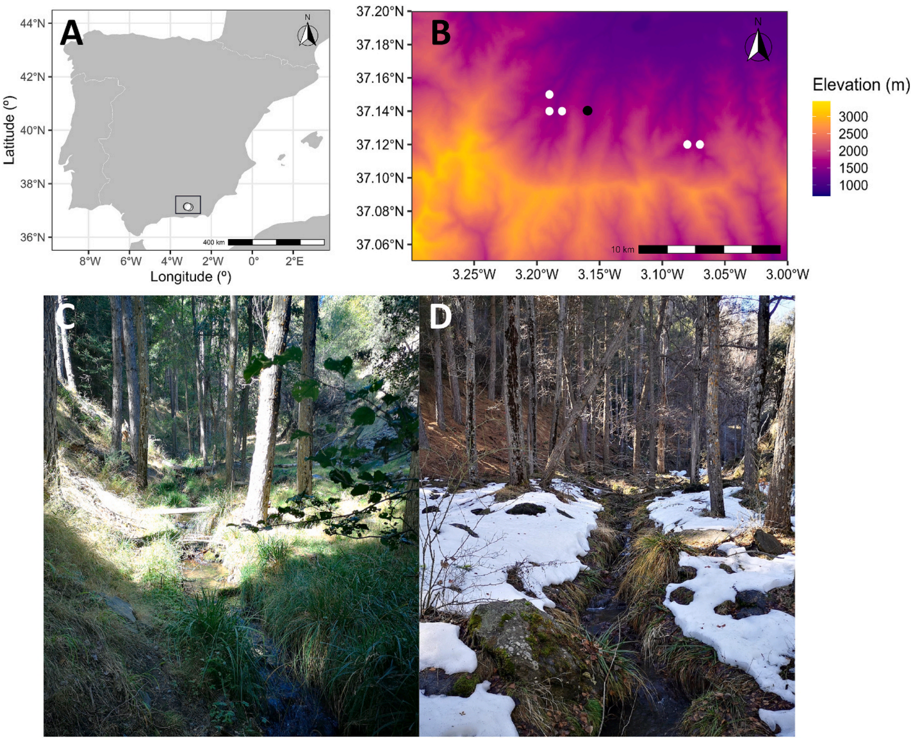

Fig. 1. Sampling locations. Map of the Iberian Peninsula showing locations of the six streams (A). Zoom of the studied region showing the selected streams over an elevation gradient in Sierra Nevada (B). One of the streams studied (Río del Pueblo; black point in B) in both seasons: (C) Fall, (D) Winter.

factor and stream as a random factor followed by Tukey's HSD post-hoc tests using the *glmer* and the *emmeans* functions of the 'lme4' and 'emmeans' R packages, respectively (Bates et al., 2015; Lenth, 2025). All analyses were adjusted to a gaussian distribution using a logit link for C and N concentrations, log link for C:N ratios and an identity link for δ^{13}C an δ^{15}N values.

We used the stable isotope mixing model MixSIAR (Stock et al., 2018) to estimate the relative contribution of the different resources to each FFG of macroinvertebrates based on their C and N isotope ratios. In favor of model accuracy, we only included the two extreme resources (i.e. epilithon and leaf litter) in the mixing models (Brett, 2014), as inclusion of benthic FPOM would introduce more uncertainty due to its mixed nature (on average 40 % epilithon + 60 % leaf litter). In each model, season and riparian type were included as fixed factors. FFG-specific trophic discrimination factor (TDF) values were calculated from our data following Caut et al. (2009), which calculations have been previously used successfully in the analysis of aquatic food webs (e.g. Burdon et al., 2019; but see Auerswald et al., 2010). For collectors mixing models we used mean TDF values of 0.86 ± 0.12 ‰ (δ^{13}C) and 2.82 ± 0.33 ‰ (δ^{15}N); for scrapers: 0.72 ± 0.25 ‰ (δ^{13}C) and 2.84 ± 0.18 ‰ (δ^{15}N); for shredders: 1.07 ± 0.14 ‰ (δ^{13}C) and 3.36 ± 0.29 ‰ (δ^{15}N); and for predators: 0.76 ± 0.17 ‰ (δ^{13}C) and 2.31 ± 0.18 ‰ (δ^{15}N). Mixing models for collectors, shredders and predators converged with three 100,000 iteration chains and a 50,000 iteration burn in ("normal" run), whereas this for scrapers converged with three 300,000 iteration chains and 200,000 iteration burn in ("long" run). Models' convergence was assessed using the Gelman-Rubin (Gelman & Rubin, 1992) and the Geweke diagnostic (Geweke, 1992). Mixing models may produce erroneous results if the isotope ratios of putative prey or sources overlap or if consumer values fall outside the range of sources (Fry 2013, Brett 2014). To minimize this bias, we included elemental concentrations (%C and %N) of each source in the models (Parnell et al. 2010). The resource use for predators represents the resource use of their prey. Effects of riparian type and season on resource use of each FFG were examined by the estimation of exact probabilities. Comparisons were considered meaningful when probability of occurrence exceeded 90 %.

To estimate the trophic position (TP) of each FFG we used the *multiSpeciesTP* function of the 'tRophicPosition' R package (version 0.8.0, Quezada-Romegialli et al., 2018), which estimates TP through a Bayesian approach, with two isotope tracers (δ^{13}C and δ^{15}N) and two baselines (i.e. epilithon and leaf litter). TDF values used were those mentioned above, and trophic position of baselines was set to a value of 1 ($\lambda = 1$). We used 5 parallel chains with 20,000 iterations in the adaptive phase, a burn-in period of 20,000 iterations, 20,000 iterations in the sampling phase and a thinning interval of 10. Separate models were run for each FFG and, season and riparian type were used as grouping variables. Model solutions were presented using Bayesian credibility intervals. Additionally, resource use and TP were also estimated at order level within each FFG, to further deepen into the subjacent mechanisms behind the shifts observed for FFGs (*Supplementary material*).

Maximum trophic position (TP_{max}) was used as a surrogate of food chain length (FCL). It was determined using only the predatory taxa with the highest δ^{15}N values across riparian types and seasons in the previous function and package (Table S5). Differences in TP of each FFG or TPmax between riparian types and seasons were evaluated using Bayesian credibility intervals and exact probabilities (*credibilityIntervals* and *pairwiseComparisons* functions of the 'tRophicPosition' R package). These comparisons were considered meaningful when probability of occurrence exceeded 90 %.

All analyses were performed using R software version 4.4.2 (R Core Team, 2022).

3. Results

3.1. Water physicochemical characteristics

Streamwater of both riparian types is circumneutral (pH: 7.4 ± 0.1, mean ± SE), soft (specific conductivity range 25–48 µS cm^{-1}; alkalinity range 0.1–0.4 mEq L^{-1}) and oligotrophic (Table S2; average values for fall *vs*. winter, respectively): nitrate-N (+ *alder*: 109 ± 32 *vs*. 219 ± 71 μg L^{-1}; − *alder*: 9 ± 5 *vs*. 53 ± 18 μg L^{-1}), soluble reactive phosphorus (+ *alder*: 5.3 ± 0.3 *vs*. 5.7 ± 0.6 μg L^{-1}; − *alder*: 10.0 ± 4.6 *vs*. 6.3 ± 0.8 μg L^{-1}), total N (+ *alder*: 1489 ± 109 *vs*. 1459 ± 91 μg L^{-1}; − *alder*: 1232 ± 74 *vs*. 1189 ± 99 μg L^{-1}), N-NH$_4$ (+ *alder*: 8.4 ± 1.0 *vs*. 3.8 ± 3.8 ppb; − *alder*: 6.8 ± 2.6 *vs*. 14.0 ± 2.6 ppb). Streams with alder had significantly higher nitrate-N concentrations, averaging 12 and 4 times more nitrate-N concentrations than those without alder in fall and winter, respectively (Table S2).

3.2. Stoichiometry and isotopic composition of basal resources and consumers

Leaf litter presented twice more N (~2%) and, consequently, lower C:N ratios in streams with alder in both seasons (Fig. 2; Table S4). Epilithon stoichiometry remained mostly steady across riparian types and seasons, despite marginally lower %N in streams with alder in winter, which led to higher C:N ratios (Fig. 2; Table S4). FPOM exhibited higher %C, %N and C:N ratios at streams with alder in fall (Fig. 2; Table S4). Overall, C:N ratios of leaf litter were 3 and 6 times higher than those of FPOM and epilithon in streams lacking alder, respectively; whereas presence of N-rich alder leaf litter halved these differences

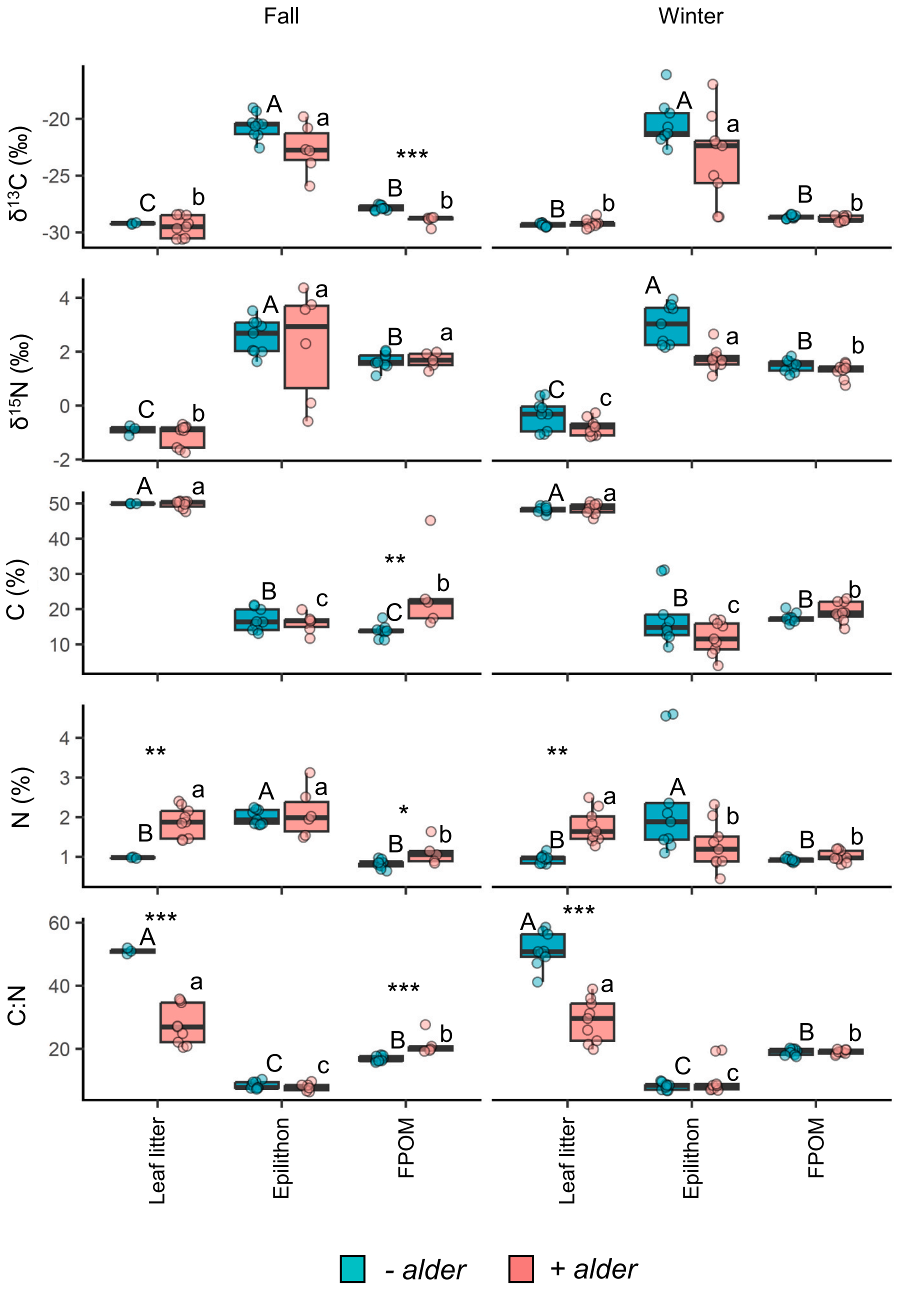

Fig. 2. Box-and-whisker plots for the stoichiometric values of the three resources studied (leaf litter, epilithon and FPOM): delta-C-13 (δ^{13}C), delta-N-15 (δ^{15}N), carbon (C) and nitrogen (N) concentrations (% of dry mass) and C:N elemental ratios (C:N) of each resource. Box represents median and the interquartile range (25–75 %), whiskers are the range and dots are replicates. Capital and lowercase letters represent comparisons among resources in fall and winter, respectively. Symbols stand for comparisons between riparian types within each resource and season. Different letters ($p < 0.05$) and symbols (*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$) indicate significant differences on the basis of linear models. See Table S4 for further information. Streams with or without riparian alder (*Alnus glutinosa*) are stated using + *alder* or −*alder*, respectively.

(Fig. 2; Table S4). The isotopic composition of resources was very similar among riparian types and seasons (Figs. 2, 3; Table S4). In general, epilithon had more positive δ^{13}C (range: –23.5 to –20.5 ‰) and δ^{15}N (range: 1.7 to 3.0 ‰) values than FPOM (δ^{13}C range: –28.9 to –27.9 ‰; δ^{15}N range: 1.3 to 1.7 ‰) and leaf litter (δ^{13}C range: –29.5 to –29.2 ‰; δ^{15}N range: –1.1 to –0.3 ‰), which was typically depleted by ~2–3 ‰ in ^{15}N (Figs. 2, 3; Table S4), particularly in streams with alder.

Consumers' stoichiometry remained mostly consistent across riparian types and seasons (Table 2, S5). All FFGs presented lower δ^{13}C values in streams with alder (Table 2, S5), with rather stable values across seasons. δ^{15}N values of collectors and shredders slightly increased from fall to winter (up to 1 ‰), but with no significant differences between riparian types or seasons (Table 2, S5). Scrapers showed an enrichment of 0.7 ‰ in ^{15}N from fall to winter at streams without alder, achieving higher values than those from streams with alder (+ *alder*: 3.6 ‰ ±0.3; – *alder:* 4.4 ‰ ±0.3). Predators presented the highest δ^{15}N value in winter at streams with alder (6.3 ‰ ±0.3), with quite stable values (range: 5.4–5.7 ‰) for the other riparian types and seasons (Table 2, S5). A clear differentiation among FFGs appears along the δ^{15}N axis of the isotopes biplot (Fig. 3), with predators at the top, shredders at the bottom and collectors and scrapers at intermediate positions.

3.3. Resource use

During fall, both collectors (– *alder*: 78 %, 72–83; + *alder*: 70 %, 59–81; mean, 95 %CI) and scrapers (– *alder*: 88 %, 82–93; + *alder*: 66 %, 48–82) assimilated more epilithon than leaf litter (Fig. 4A, B, E, F, S2; Table S6), with probabilities exceeding 90 % (Table S7). Although both FFGs exhibited a slight increase in the use of leaf litter at streams with alder, this shift was only meaningful (>90 % probabilities, Table S7) for scrapers (– *alder*: 12 %, 7–18; + *alder*: 34 %, 18–52). Predators followed a similar trend, exhibiting a clear preference (>90 % probabilities) for epilithon feeders at both riparian types (– *alder*: 90 %, 86–94; + *alder*: 80 %, 71–90), but twice more predation of leaf litter feeders in presence of alder (– *alder*: 10 %, 6–14; + *alder*: 20 %, 10–29; Fig. 4D, H, S2; Table S6, S7). Shredders exhibited a mixed diet at streams without alder (epilithon: 54 % 1–70; leaf litter: 46 %, 30–99), but a predominant use of leaf litter (>90 % probabilities) when alder was present (73 %, 49–99; Fig. 4C, G, S2; Table S6, S7).

In winter, collectors maintained high assimilation of epilithon (>90 % probabilities, Table S7) at both riparian types (– *alder*: 75 %, 68–82; + *alder*: 82 %, 63–97; Fig. 4I, M, S2), which was mirrored by predators (Fig. 4L, P, S2; Table S6). Scrapers presented more pronounced differences between riparian types than in fall, with epilithon being the preferred resource in streams without alder (82 %, 70–91; Fig. 4J), but with the consumption of litter becoming significant when alder was present (45 %, 32–57; Fig. 4N, S2; Table S6). Shredders always assimilated leaf litter the most (>99 % probabilities, Table S7), but specially in streams with alder where leaf litter represented the 90 % (78–100) of shredder's diet (Fig. 4K, O, S2; Table S6). In general, specific orders followed the patterns observed for the FFGs to which they belong, except for plecopteran shredders who exhibited a higher assimilation of epilithon at both riparian types during fall (Fig. S3).

3.4. Trophic position and food chain length

Trophic position (TP) ranged from 1.4 for shredders to 3.7 for predators (Fig. 5; Table S8). TP of collectors and scrapers generally increased when riparian alder was present during both seasons, but this trend exhibited probabilities exceeding 90 % only in winter (Fig. 5, S4; Table S8). For collectors, this pattern was likely driven by the presence of dipteran and oligochaete collectors in streams without alder, which exhibited lower TP than trichopteran collectors (i.e. *Hydropsyche* individuals; Fig. S5). TP of shredders slightly decreased with alder presence in fall, but exhibited a meaningful (>90 % probability) increase in winter (Fig. 5, S4; Table S8). These shifts being primarily controlled by dipteran and trichopteran shredders, respectively (Fig. S5). TP of predators also exhibited an increase at streams with alder, especially in winter (Fig. 5, S4; Table S8), due to the consistently higher TP of plecopteran and trichopteran predators when alder was present (Fig. S5). Across seasons, collectors (86 % probabilities), shredders (87 % probabilities) and predators (>90 % probabilities) showed a TP increase from fall to winter, but only when alder was present (Fig. 5; Table S8).

At both seasons, TPmax (i.e. FCL) was slightly higher in streams with alder, but a meaningful change (>90 % probabilities) was only observed when comparing –*alder* streams in fall and + *alder* streams in winter (Fig. 5, Table S8). In fall, TP_{max} was exhibited by individuals of the order Odonata in streams without alder (TP_{max} = 3.1, 2.5–3.7; Median, 95 % CI) and caddisflies of the family *Rhyacophilidae* in streams with alder (TP_{max} = 3.3, 2.1–3.9). In winter, the TP_{max} was associated with individuals of the family *Rhyacophilidae* in both riparian types (– *alder*:

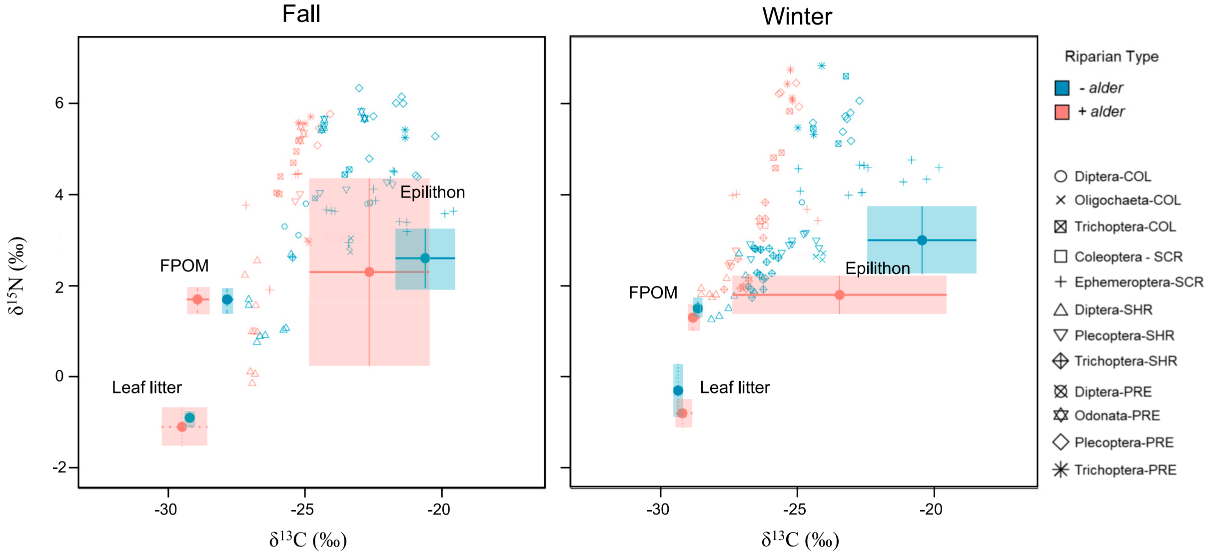

Fig. 3. δ^{15}N and δ^{13}C biplot showing the basal sources (mean ± SD; filled dots) and individual values of consumers (open symbols) grouped by riparian type (with (+) or without (–) alder; *Alnus glutinosa*) in fall and winter. The suffixes –COL, –SCR,-SHR, and –PRE denote collector, scraper, shredder and predator feeding functional groups, respectively, indicating the functional group to which the taxa within each order belong.

Table 2

Mean (± SD) δ^{13}C and δ^{15}N (‰), C and N concentrations (%), and C:N ratio of the consumers (sorted by Feeding Functional Group, FFG) at riparian type and season studied. Capital letters represent vertical comparisons (among riparian types and seasons) on the basis of generalized linear mixed models followed by pairwise multiple comparisons (Tukey test). Streams with or without riparian alder (*Alnus glutinosa*) are stated using + *alder* or −*alder*, respectively.

Variable	Season	Riparian Type	Collector	Scraper	Shredder	Predator
δ13C	Fall	− *alder*	−23.7 ± 1.1 ^{A}	−22.1 ± 1.4 ^{A}	−25.2 ± 1.8 ^{A}	−22.4 ± 1.3 ^{A}
		+ *alder*	−25.4 ± 0.5 ^{A}	−25.9 ± 0.8 ^{A}	−26.6 ± 0.7 ^{AB}	−24.8 ± 0.4 ^{BC}
	Winter	− *alder*	−24.1 ± 0.5 ^{A}	−22.3 ± 1.6 ^{A}	−26.2 ± 0.9 ^{B}	−23.7 ± 0.8 ^{B}
		+ *alder*	−25.6 ± 0.3 ^{A}	−26.0 ± 1.3 ^{A}	−27.2 ± 0.7 ^{B}	−25.3 ± 0.3 ^{C}
δ15N	Fall	− *alder*	3.6 ± 0.6 ^{A}	3.7 ± 0.5 ^{B}	2.3 ± 1.4 ^{A}	5.4 ± 0.7 ^{B}
		+ *alder*	4.0 ± 0.9 ^{A}	3.8 ± 1.1 ^{AB}	1.6 ± 1.4 ^{A}	5.5 ± 0.2 ^{B}
	Winter	− *alder*	4.1 ± 1.6 ^{A}	4.4 ± 0.3 ^{A}	2.4 ± 0.5 ^{A}	5.7 ± 0.5 ^{B}
		+ *alder*	5.0 ± 0.5 ^{A}	3.6 ± 0.3 ^{AB}	2.4 ± 0.6 ^{A}	6.3 ± 0.3 ^{A}
C	Fall	− *alder*	43.1 ± 4.1 ^{A}	42.9 ± 2.2 ^{AB}	44.0 ± 0.9 ^{A}	44.8 ± 2.6 ^{BC}
		+ *alder*	42.4 ± 5.0 ^{A}	44.9 ± 0.4 ^{A}	44.1 ± 0.7 ^{A}	45.4 ± 1.6 ^{AC}
	Winter	− *alder*	40.3 ± 2.8 ^{A}	41.7 ± 0.8 ^{B}	42.3 ± 1.3 ^{B}	42.4 ± 0.9 ^{AD}
		+ *alder*	41.5 ± 0.7 ^{A}	43.0 ± 2.4 ^{B}	43.3 ± 1.6 ^{AB}	42.3 ± 1.0 ^{BD}
N	Fall	− *alder*	11.1 ± 0.9 ^{A}	12.3 ± 1.0 ^{A}	11.1 ± 0.8 ^{A}	11.3 ± 0.8 ^{A}
		+ *alder*	11.0 ± 0.9 ^{A}	12.4 ± 0.5 ^{A}	10.8 ± 0.8 ^{AB}	11.8 ± 0.8 ^{A}
	Winter	− *alder*	10.8 ± 0.6 ^{A}	12.0 ± 0.4 ^{A}	9.8 ± 1.0 ^{B}	11.1 ± 0.4 ^{A}
		+ *alder*	10.9 ± 0.5 ^{A}	11.6 ± 0.9 ^{A}	9.9 ± 1.4 ^{B}	11.6 ± 0.4 ^{A}
C:N	Fall	− *alder*	3.9 ± 0.6 ^{A}	3.5 ± 0.2 ^{AB}	4.0 ± 0.3 ^{A}	4.0 ± 0.3 ^{A}
		+ *alder*	3.9 ± 0.2 ^{A}	3.6 ± 0.2 ^{AB}	4.1 ± 0.2 ^{A}	3.9 ± 0.4 ^{A}
	Winter	− *alder*	3.7 ± 0.2 ^{A}	3.5 ± 0.1 ^{B}	4.4 ± 0.5 ^{A}	3.8 ± 0.2 ^{A}
		+ *alder*	3.8 ± 0.1 ^{A}	3.7 ± 0.5 ^{A}	4.5 ± 0.7 ^{A}	3.7 ± 0.1 ^{A}

3.2, 1.7–5.3; + *alder*: 3.7, 3.0–4.2).

4. Discussion

We assessed whether alder presence may enhance the buffering role of riparian communities against potential negative effects exerted by pine plantations on stream food webs. Streams with riparian alder presented significantly increased streamwater nitrate-N in both seasons (12 × in fall, 4 × in winter), in alignment with previous studies reporting higher nitrate-N in streamwater when N-fixing species are present along riverbanks (Pereira et al., 2021). While the interseasonal increase in nitrate-N—likely resulted from the rapid leaching of soluble N of recently shed leaves upon submersion (Davis et al., 2006; Robbins et al., 2023)—reduced the relative differences between riparian types, the total increase in streamwater nitrate-N remained substantially higher when alder was present (∼100 μg L^{-1}) compared to streams lacking alder (∼40 μg L^{-1}), supporting the role of alder litter as N supplier to streams (Compton et al., 2003; Shaftel et al., 2012). Despite such nutrient enrichment, epilithon and FPOM exhibited limited stoichiometric plasticity and their C:N ratios remained stable across riparian types or seasons (Sabater et al., 2011; Tant et al., 2013; Sanpera-Calbet et al., 2017). This could be partially explained if both resources were colonized by a dominant heterotrophic microbial community, since bacteria lack internal nutrient storage and are thus more stoichiometrically homeostatic than algae (Makino et al., 2003). The influence of alder on streamwater N concentration and consequently on N:P ratios may also explain the stable C:N ratios of epilithon and FPOM, as it could reduce nutrient-driven stoichiometric changes through and inhibition of biological N immobilization due to P limitation (Stewart et al., 2019; Devotta et al., 2021).

At streams with riparian alder, litter assemblages presented reduced C:N ratios, halving the typical imbalance between detrital resources and shredders (6x *vs.* 12x in streams with and without alder, respectively, supporting our 1st hypothesis; Cross et al., 2003; Frainer et al., 2016). Given the marked preference of shredders for leaf litter, this reduction can support higher shredder biomass and activity, potentially influencing energy flow within stream ecosystems (Demi et al., 2019). Despite this improvement, shredders may still face nutritional challenges (Sterner & Elser, 2002) when high-quality leaf litter inputs are limited. In response, shredders supplemented their diet with epilithon, whose C:N ratio was only twice that of shredder bodies (Torres-Ruiz et al., 2007; Guo et al., 2016, 2018). This dietary plasticity may have allowed them to maintain stoichiometric homeostasis across riparian types and seasons (Cross et al., 2003; Van Der Lee et al., 2021), contrary to our first hypothesis predicting lower shredder C:N ratios in streams with riparian alder (Oester et al., 2024). Epilithon likely plays a greater role in streams lacking alder inputs (Gee, 1988; Leberfinger et al., 2011; Guo et al., 2018), and particularly before leaf abscission, when it represented 54 % of shredders' diet (supporting our 2nd hypothesis). This resource appears to be especially important for shredder stoneflies (Plecoptera), which may rely more heavily on it in the absence of fresh litter (Fig. S3). In addition, interspecific competition (Bastian et al., 2008; Firmino et al., 2022), may also compel some shredders to exploit resources other than leaf litter.

Overall, both collectors and scrapers assimilated more epilithon than leaf litter, in agreement with previous findings (e.g. Finlay, 2001; Lau et al., 2009). Epilithon is typically considered a key resource for scrapers, but it has also been reported as an important resource for other FFGs (e.g. Labed-Veydert et al., 2022). Here, collectors consistently showed a higher consumption of epilithon—ranging from 70 to 82 %—across riparian types and seasons. Scrapers, however, significantly reduced the consumption of epilithon in favor of leaf litter when alder was present, especially in winter (Junker & Cross, 2014; partially supporting our 2nd and 4th hypotheses). This shift may result from the high availability of high-quality alder leaf litter (e.g. Bogatov et al., 2024), or from the incorporation of fine particles or dissolved organic carbon from leaf litter into the epilithon matrix (Lovatt et al., 2014), which could lead some scrapers to ingest it along with epilithic algae. According to our 2nd hypothesis, we expected a higher assimilation of allochthonous resources that would cascade to predators (subsidy-quality hypothesis, Osakpolor et al., 2023; Estévez et al., 2019). However, the generally higher assimilation of autochthonous resources by collectors and scrapers was mirrored by predators in both seasons. This suggest a potentially more efficient transfer of autochthonous rather than

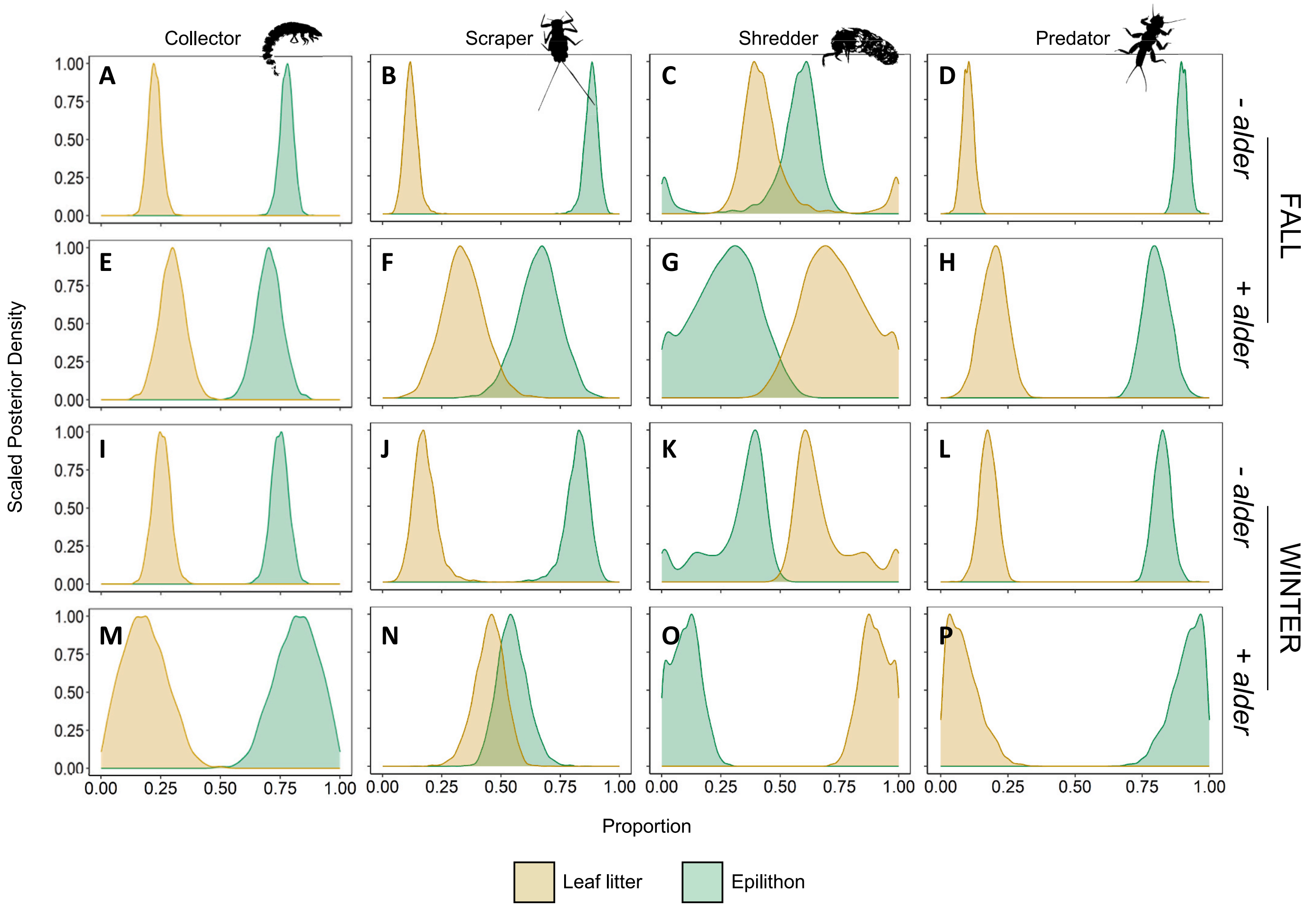

Fig. 4. Relative contribution (proportion) of main food resources consumed by the different FFGs of benthic macroinvertebrates at streams without (− *alder*) and with *(+ alder)* riparian alder (*Alnus glutinosa*) in fall and winter. Resource use was estimated using MixSIAR Bayesian mixing models. Note that the resource use for predators represents the resource use of their prey.

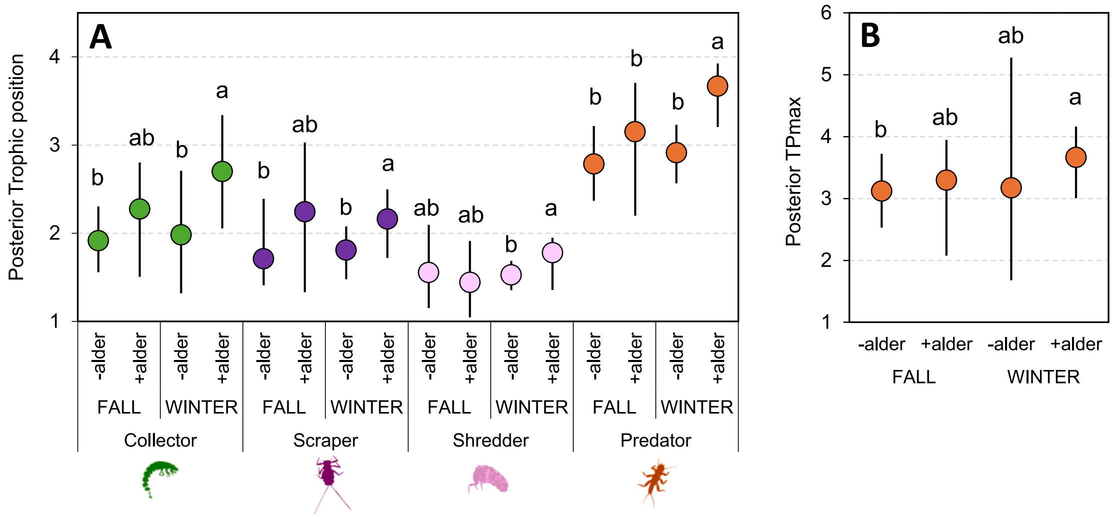

Fig. 5. (A) Trophic position of consumers grouped by functional feeding groups (FFGs) and riparian type (−*alder vs.* + *alder*) in both seasons (Fall and Winter) estimated using bayesian inference. (B) Food chain length (TPmax) across riparian types and seasons estimated using Bayesian inference. Dots represent the median of posterior trophic position estimates and whiskers indicate the 95 % Bayesian credibility intervals. Lowercase letters represent comparisons between riparian types and seasons within each FFG. Different letters indicate a > 90 % probability that two groups differ based on pairwise comparisons of posterior distributions within a Bayesian framework (see Table S8). Streams with or without riparian alder (*Alnus glutinosa*) are stated using + alder or −alder, respectively.

allochthonous energy, even in what are typically considered highly heterotrophic systems such as the streams assessed here (Brett et al., 2017; Labed-Veydert et al., 2023). Overall, these results support the Riverine Ecosystem Synthesis (RES; Thorp et al., 2006), which posits that secondary production is primarily supported by autochthonous resources, although some species may rely on allochthonous organic matter.

Trophic positions presented interesting variations among riparian types or seasons. Whilst TP of predators would probably shift following that of their prey, an increase in the TP of any a priori non-predatory FFG could be related with the ingestion of animal-derived organic matter. Here we observed a slight interseasonal increase in the TP of collectors and shredders in streams with alder (but see the trend for plecopteran shredders which presented a higher TP during fall, likely derived from its higher reliance on epilithon during this season; Fig. S3). Increased epilithon consumption by collectors during this season may have elevated their TP. For shredders, this rise is likely explained by increased availability of high-quality leaf litter in these streams during winter. However, prior studies have reported that omnivorous organisms can lower their TP when nutrient rich plant material is available (Van Der Lee et al., 2021). In addition, use of animal material by collectors (e.g. Hydropsychidae larvae; Fuller & Mackay, 1981; Hellmann et al., 2013) or shredders has been previously documented (Rubio-Ríos et al., 2021; Firmino et al., 2022). Therefore, the possibility of individuals within these FFGs utilizing animal-based resources cannot be categorically dismissed, especially in February, since some macroinvertebrates may be in later instars with high nutritional demands for metamorphosis, and predation may help to fulfill these needs. Regardless of the reason, such an increase resulted in a rise in the TP of predators, which was reflected in a slight lengthening of the FCL only in streams with riparian alder (partially supporting our 3rd hypothesis). This pattern aligns with experimental evidence showing stronger consumptive predator effects on detritivores in alder litter assemblages, likely driven by the higher resource quality and lower structural complexity of alder leaves, which may enhance predation efficiency and energy transfer to higher trophic levels (Jabiol et al., 2014).

Between riparian types, all FFGs exhibited overall higher TPs in streams with riparian alder. However, different magnitudes in TP increases from fall to winter led to more notable differences among riparian types in the later season (supporting our 4th hypothesis). Nevertheless, despite the general elevated TP of all consumers—including that of predators—in alder streams during winter, no significant differences in FCL were observed between riparian types (contrary to our 3rd hypothesis). Variations in FCL could stem from (i) the presence of different top or intermediate predators, (ii) a general increase in predator TP within the system, or (iii) reduced trophic omnivory coupled with increased dietary specialization among food chain components (see Post et al., 2000). Here, the likelihood of different predators influencing FCL is low, given the proximity of the six streams (see Table S5). Additionally, while some FFGs relied more heavily on a single resource, others exhibited a more mixed diet. Therefore, the most plausible explanation for a potential increase in FCL is the general rise observed in the TP of predators. These patterns may support previous studies highlighting the important role of leaf litter in promoting the lengthening of the food chain in forested streams (e.g. Thompson & Townsend, 2005; Majdi & Traunspurger, 2017). Nonetheless, lack of differences suggests that while predator TP tends to increase in the presence of riparian alder, this effect is insufficient to induce a notable shift in the FCL across riparian types. This may be caused by the presence of other broadleaf deciduous species within riparian areas, which already act buffering pine plantations impacts on streams. Furthermore, the proximity between the riparian types may facilitate energy transfer from one system to another through emergent species, which could reduce the expected differences based on instream productivity and further soften any potential impact on FCL.

5. Conclusion

The role of riparian vegetation is crucial for managing and restoring Mediterranean forests, particularly within the framework of current ecosystem restoration initiatives during the UN Decade of Ecosystem Restoration (United Nations, 2019). Food web metrics based on stable isotope analysis provide a comprehensive approach for assessing the ecological effects of pine plantations on stream ecosystems. These metrics have the ability to detect subtle ecological changes (Alp & Cucherousset, 2022) and thus, could serve as valuable tools for monitoring the effects of afforestation on stream ecosystems and guiding the design and implementation of riparian buffer corridors, helping to mitigate adverse effects on stream ecosystems.

Our results indicate that riparian alder can influence resource availability and use through a reduction of the usual wide nutritional imbalance existing between benthic consumers and resources. This reduction may enhance the buffering effect exerted by other deciduous species interspersed between plantations and streams, mitigating plantation-derived effects on food webs of Mediterranean streams. Overall, our study offers insights into current conditions, but emphasizes the need for further research on mechanisms behind resource subsidies in streams and their potential effects at the ecosystems level, particularly as global warming may reduce the nutritional quality of leaf litter entering streams under deciduous forests (Salinas et al., 2018; Rubio-Ríos et al., 2022).

Our findings also support the generalist behavior assumed for many stream invertebrates (e.g. Anderson & Cabana, 2007; Carvalho & Graça, 2007). Such feeding-plasticity likely contributes to the lack of significant differences between riparian types, as invertebrates can alternate among basal resources to thrive and fulfill their nutritional requirements. This ability underlines the need to work with specific taxa, given that responses to shifts in resources stoichiometry or nutrient enrichment may depend on specific life-history traits and thus, can be different for taxa belonging to the same functional group. Therefore, functional feeding groups may not always provide a reliable prediction of resource use by instream invertebrates (see Labed-Veydert et al., 2021) and species-specific traits may determine different sensitivities to nutrient enrichment (Demi et al., 2019).

CRediT authorship contribution statement

Juan Rubio-Ríos: Writing – review & editing, Writing – original draft, Visualization, Resources, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Brian Hayden:** Writing – review & editing, Resources. **Bobby J. Nakamoto:** Writing – review & editing, Resources, Data curation. **J. Jesús Casas:** Writing – review & editing, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2025.113637.

Data availability

Data supporting the findings of this study are available online: https://osf.io/eqs4b/.

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