



Alder stands promote N-cycling but not leaf litter mass loss in Mediterranean streams flowing through pine plantations

Juan Rubio-Ríos^{a,b,*}, María J. Salinas-Bonillo^{a,b}, Javier Pérez^c, Encarnación Fenoy^{a,b}, Luz Boyero^c, J. Jesús Casas^{a,b}

^a Department of Biology and Geology, University of Almeria (UAL), 04120 Almería, Spain

^b Andalusian Centre for the Evaluation and Monitoring of Global Change, CAESCG, Almería, Spain

^c Department of Plant Biology and Ecology, University of the Basque Country (UPV/EHU), 48940 Leioa, Spain

ARTICLE INFO

Keywords:

Afforestation
Alnus glutinosa
 Net diversity effect
 N-fixing species
 Poplar
 Riparian buffer

ABSTRACT

During the last century, the abandonment of traditional dryland farming and pastures in the Mediterranean basin promoted the development of ambitious afforestation programs causing a drastic transformation of the landscape. Afforestation programs were usually accomplished without considering the potential ecological impacts on the recipient ecosystems. Forest streams rely on terrestrial organic detritus, so their functioning and conservation status can be altered by changes in riparian forest biodiversity and composition. However, the influences of conifer plantations in particular on stream functioning are still unclear, possibly because the presence of multiple species in plantations or the presence of other species in the riparian zones of streams may act as buffers of such effects. Here, by means of a field experiment, we assessed whether the presence of black alder in the riparian zone and/or as leaf litter within the stream may mitigate the impacts exerted by pine plantations on stream ecosystem functioning. We found (i) that streams were functionally similar but differed in water N concentrations; (ii) no differences in litter mass loss between riparian types, but higher total litter mass loss of those mixtures containing alder leaf litter; and (iii) higher N losses (or lower N gains) for all litter types in streams without riparian alder. These results demonstrate that microbial decomposers can use either stream water N or litter N, and that detritivores can feed simultaneously on resources of contrasting quality to balance their diet. Our study underscores the effect of even low-density riparian cover of alder promoting microbial nutrient cycling by moderate increases of water N concentrations. We suggest thinning of pine plantations combined with planting of native deciduous species as alder to alleviate the effects of pine plantations on Mediterranean streams.

1. Introduction

Deforestation for wood resources, land cleaning and energy has led to profound alterations of global forests throughout history. Nowadays, ~7% of worldwide forest cover consist of planted forests established for wood production (FAO, 2015; FAO and UNEP, 2020). At present, millions of hectares of the Mediterranean Basin are covered by forest plantations, which are predominantly composed of pines and other fast-growing species. Plantations were widely used during the last century as a tool for the recovery of forests after centuries of human exploitation (Pausas et al., 2004). Afforestation programs were usually accomplished without ecologically sound design and management, which could have avoided potential negative influences on the recipient ecosystems (e.g.

Andrés and Ojeda, 2002; Martín-Peinado et al., 2016; Molina et al., 2021).

Conifer plantations, for example, present a much higher evapotranspiration than deciduous trees and may eventually cause a significant reduction of the streamflow (Swank and Douglass, 1974). Such reduction can be enough to turn perennial into intermittent streams or to shorten the length of the flow season in those already intermittent (Cornish, 1989). Likewise, pine plantations have been shown to significantly diminish the amount of light reaching the stream if they grow on riparian zones compared to broadleaved species which canopy is more variable and usually allows arrival of some pulses of light to the stream (Boothroyd et al., 2004). In small streams, that shade can suppress algal growth and alter stream nutrient retention efficiency (Sabater et al.,

* Corresponding author at: Department of Biology and Geology, University of Almeria (UAL), 04120 Almería, Spain.

E-mail address: jrr812@ual.es (J. Rubio-Ríos).

<https://doi.org/10.1016/j.foreco.2023.121072>

Received 10 January 2023; Received in revised form 23 April 2023; Accepted 1 May 2023

Available online 19 May 2023

0378-1127/© 2023 The Author(s). Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

2000). Besides, deciduous riparian forests may compensate for shading effects by greater organic matter inputs that fuel instream microbial and chemical processes (Wallace et al., 1997; Dosskey et al., 2010). In conifer plantations, although litter inputs to streams are steady throughout the year (Inoue et al., 2012), conifer needles are not easily processed by stream biota (Collen et al., 2004; Principe et al., 2015; Márquez et al., 2017). Their low nutrient concentrations and palatability, compared to those of many broadleaf deciduous species (Graça and Cressa, 2010; Casas et al., 2013; Martínez et al., 2013; Martínez et al., 2016), can hinder the performance of fluvial communities and, therefore, the rates of some key stream ecosystem processes (e.g. Wipfli and Musslewhite, 2004; Kominoski et al., 2011; Ferreira et al., 2017).

Previous studies have reported distinct structure of aquatic hyphomycetes community (Ferreira et al., 2017) or lower shredder biomass (Whiles and Wallace, 1997; Riipinen et al., 2010) in streams flowing through conifer plantations than those draining deciduous forests. Consequently, leaf litter decomposition and nutrient cycling rates have been shown to be slowed down in those streams flowing through conifer plantations (e.g. Whiles and Wallace, 1997; Kominoski et al., 2011; Martínez et al., 2013). Nevertheless, the effects of conifer plantations on stream communities and litter decomposition are still unclear, with other studies reporting no apparent differences in fungal or invertebrates communities (Martínez et al., 2013; Martínez et al., 2016) and similar decomposition rates between streams flowing through conifer plantations and broadleaf forests (Riipinen et al., 2010; Ferreira et al., 2017). Notwithstanding all the above mentioned, most studies coincide that needles decompose more slowly than deciduous broadleaf litter (e.g. Albariño and Balseiro, 2002; Collen et al., 2004; Casas et al., 2013).

These discrepancies can derive from the presence of deciduous riparian forests in streams flowing through these plantations (e.g. Martínez et al., 2013). Plant diversity promotes functional diversity of instream litter mixtures, usually boosting community productivity (e.g. Fernandes et al., 2013). Thus, the presence of different species intermingled within the plantation or in riparian areas may lesser the influence of plantations on stream functioning (Casotti et al., 2015; Ferreira et al., 2016; Larrañaga et al., 2021). For instance, alder species are usually considered key species in riparian ecosystems (Pérez et al., 2021), since they can stimulate breakdown of litter mixtures in two different ways: (i) directly, by supplying streams with nitrogen-rich and palatable leaves (e.g. Graça et al., 2015; Rubio-Ríos et al., 2021; Rubio-Ríos et al., 2022) which may attract detritivores (Ferreira et al., 2012) and promote nutrient transfer between litter types (Tiunov, 2009; Handa et al., 2014); or (ii) indirectly, through an increase in stream water N concentrations (Compton et al., 2003; Shaftel et al., 2012), therefore mitigating the usual N limitation to which microbial communities are subjected in Mediterranean headwater streams (Ferreira et al., 2006b). Such mechanisms point to a key role of alder on stream ecosystem functioning at two different scales: instream (e.g. Alonso et al., 2021; Alonso et al., 2022) and within the riparian area or catchment (e.g. Shaftel et al., 2012). However, to our knowledge, the relative importance of both mechanisms has not been tested simultaneously in field experiments.

Here, we aim to assess whether the presence of black alder, *Alnus glutinosa* (L.) Gaertn., in the riparian area and/or within the stream (in the form of leaf litter) can mitigate the negative effects exerted by pine plantations on stream ecosystem functioning. We carried out a field experiment using litter bag techniques and both monocultures (single species) and 5 different mixtures of 3 species: 2 species widely used in afforestation programs during the 1950s in southeastern Spain, the evergreen needle conifer *Pinus pinaster* Aiton and the deciduous broadleaf *Populus nigra* L.; and the key species *A. glutinosa*. The experiment was deployed in 6 headwater streams flowing through pine plantations differing in the presence of alder in their riparian areas. We tested the following hypotheses: (1) water N concentrations will be higher in streams with riparian alder stands (Compton et al., 2003; Shaftel et al.,

2012); (2) riparian alder will enhance microbial and total litter mass loss (Kominoski et al., 2011) and (3) microbial nutrient cycling via stream nutrient enrichment (Ferreira et al., 2006b); (4) riparian alder will promote diversity effects on litter mass loss and nutrient cycling; and (5) litter diversity effects on litter mass loss will be greater when alder litter is present in the mixture (Larrañaga et al., 2020; Rubio-Ríos et al., 2021).

2. Material and methods

2.1. Study region and streams

We conducted a field experiment in 6 low-order streams located in the Sierra Nevada mountains (southeastern Spain), at elevations ranging between ca. 1500–1700 m a.s.l. and located relatively close to each other (max. straight line distance 11 km) (Fig. 1; Table S1). These streams have their sources at altitudes of ~2500 m a.s.l., show steep topographic gradients, and pluvio-nival regimes. The stream bottom is composed of heterogeneous sediments of a siliceous nature dominated by sand and gravel along with large boulders. All the streams are located within the protected area of Sierra Nevada National Park. The climate is Mediterranean, with cold, wet winters and warm, dry summers (Esteban-Parra et al., 2022).

The vegetation of the Mediterranean region has changed over the last three millennia due to climate changes and human pressures. In the Sierra Nevada, some of the most profound modifications have occurred during the last hundred years. The abandonment of traditional dryland farming and pastures was followed, since the 1950s, by the development of ambitious afforestation programs. This caused a drastic transformation of the landscape, with pine forests now dominating at higher zones (below 2100 m a.s.l.) and in old abandoned farmlands (Padilla et al., 2010; Olivencia et al., 2015). A favorable climate and the lack of appropriate management resulted in the current dense, nearly monospecific, stands of pine plantations, which account for ~79% of the forested area of the natural-national park. Only the remaining ~20% is covered by native forests of the evergreen holm oak *Quercus rotundifolia* Lam. or the deciduous oak *Quercus pyrenaica* Willd. (Pérez-Raya et al., 2001). The main species used in afforestation programs were maritime pine (*Pinus pinaster* Aiton), Aleppo pine (*Pinus halepensis* Mill.), black pine (*Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco) and Scots pine (*Pinus sylvestris* L.), which were planted depending on the altitudinal preferences of each species (Arias Abellán, 1981; Gómez-Aparicio et al., 2009; Mesa Garrido, 2019).

At present, plantations located at the altitudinal range studied here are mainly composed of maritime pine, mixed with a few holm oaks, and black poplars (*Populus nigra* L.) in riparian areas (Arias Abellán, 1981; Padilla et al., 2010). Six streams were selected (Table 1), 3 with riparian zones that consisted mostly of naturally grown willows (*Salix atrocinerea* Brot.) and black poplars, adjacent to the plantations of maritime pines, and 3 with black alder stands mixed into the riparian zones (Table 1).

2.2. Stream water characterization

During the full period of the litter mass loss (LML) experiment (January–March 2020) we monitored water temperature hourly in each stream with HOBO Pendant® loggers (Onset Computer Corporation). At the beginning, middle and end of the experiment, in each stream we measured stream water pH, specific conductivity, dissolved oxygen concentration and dissolved oxygen saturation with a multiparametric probe (HACH® model HQ-30d, Loveland, CO, USA). Additionally, samples of filtered (47-mm diameter, 1.2-µm pore size, APFC, Merk Millipore) and non-filtered stream water were collected at the beginning and middle of the experiment into acid-washed plastic bottles and transported to the laboratory. There, total alkalinity was immediately measured in non-filtered samples, by acid titration to a pH endpoint of 4.25 (Wetzel and Likens, 1991). Filtered samples were stored frozen

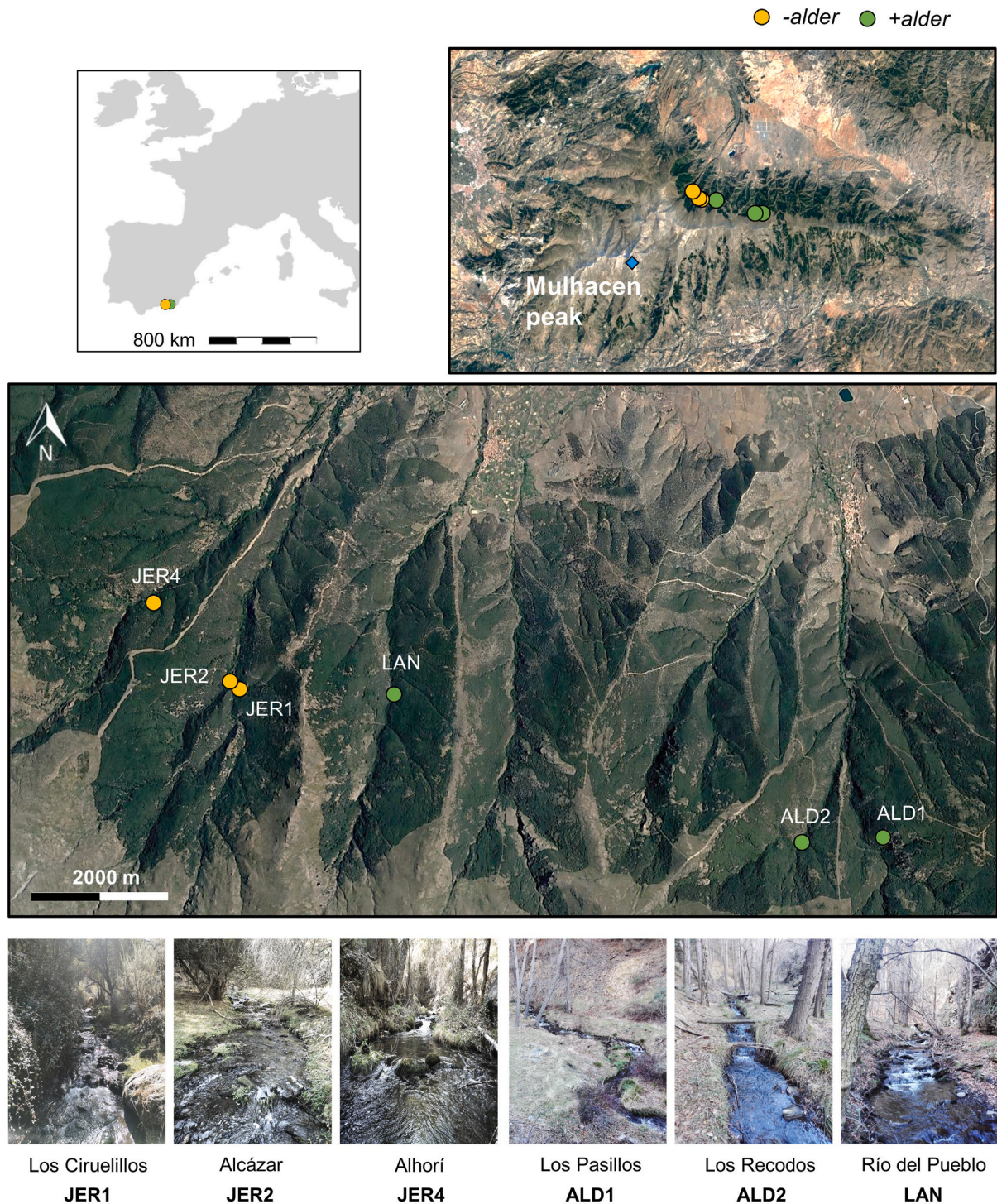


Fig. 1. Location of the six streams in Sierra Nevada, southeastern Spain.

(-20 °C) until used for nutrient analyses. Total dissolved nitrogen (TDN) and phosphorus (TDP), nitrates (NO₃-N), soluble reactive phosphorus (SRP) and ammonium (NH₄-N) were measured. For TDN and TDP an aliquot of 100 mL of filtered water was wet mineralized for 30 min at 120 °C in an autoclave. After cooling to room temperature, an aliquot (50 mL) was acidified with concentrated sulphuric acid to determine TDN (absorbance at 220 nm), whereas TDP, mineralized to phosphate, was determined in the remaining 50 mL (Wetzel and Likens, 1991). Nitrates were determined by the sodium salicylate method (APHA, 2005), SRP by the ascorbic acid method (Wetzel and Likens, 1991) and ammonium by the salicylate method (APHA, 2005). Streamflow was

estimated at the beginning and end of the experiment by measuring current velocity (SEBA Mini Current Meter M1, SEBA Hydrometrie GmbH & Co, Kaufbeuren, Germany) at multiple points along cross-sections of each stream.

2.3. Sampling of stream benthos and estimation of ecosystem attributes

In each stream we collected 10 sampling units of benthos using a Hess sampler (area 0.09 m², mesh size 0.5 mm), by means of a stratified random design, differentiating between two habitats: riffles and pools. Each sampling unit was divided in two fractions, coarse (>1 cm: leaves,

Table 1
Location, geographic characteristics and dominant tree species density (ind./dam²) in the riparian community of the selected streams.

Riparian type	With alder				Without alder			
	Stream ID	Stream	Municipality	Basin	Stream ID	Stream	Municipality	Basin
Stream	ALD1	ALD2	LAN	JER1	JER2	JER4		
Municipality	Barranco de los Pasillos	Barranco de los Recodos	Río del Pueblo	Barranco de los Ciruelillos	Barranco de Alcázar	Barranco de Alhorí		
Basin	Aldeire	Aldeire	Lanteira	Jerez del Marquesado	Jerez del Marquesado	Jerez del Marquesado		
Altitude (m a.s.l.)	1682	1643	1543	1519	1522	1507		
Geographic coordinates	37.12 N 3.07 W	37.12 N 3.08 W	37.14 N 3.16 W	37.14 N 3.18 W	37.14 N 3.19 W	37.15 N 3.19 W		
Plant community								
<i>Alnus glutinosa</i> (ind./dam ²)	11.76	2.56	30.19	0.00	0.00	0.00		Mean
<i>Populus nigra</i> (ind./dam ²)	5.88	33.33	9.43	14.84	6.06	25.93		0.00
<i>Pinus pinaster</i> (ind./dam ²)	1.96	5.13	1.89	16.22	3.03	9.26		11.36
<i>Betula pendula</i> (ind./dam ²)	15.69	0.00	0.00	2.99	0.00	0.00		4.10
<i>Quercus rotundifolia</i> (ind./dam ²)	1.96	5.13	0.00	5.23	0.00	0.00		0.00
<i>Salix atrocinerea</i> (ind./dam ²)	1.96	0.00	5.66	2.36	0.00	0.00		0.00
				29.17	15.15	12.96		19.09

twigs, cones...) and fine (>0.45 mm – 1 cm: macroinvertebrates, inorganic and organic particles of sediment) material, and transported to the laboratory on ice. There, instream leaf litter was sorted by plant species, rinsed with distilled water to remove sediment particles, oven-dried (70 °C, 72 h) and weighed to estimate the litter benthic composition and abundance in each stream.

Macroinvertebrates were sorted and identified to genus, or species level when possible, using identification keys (Tachet et al., 2010). Then, they were counted and assigned to functional feeding groups (FFG), oven-dried (24 h, 60 °C) and weighed to estimate the biomass of each FFG. Biomass of FFGs was used to estimate FFG ratios as indicators of stream ecosystem attributes (Merritt et al., 2017). Ratios estimated were the Autotrophy to Heterotrophy Index (Auto/Hetero), as *Scrapers to Shredders + Total Collectors* ratio; the Coarse Particulate Organic Matter to Fine Particulate Organic Matter Index (CPOM/FPOM), as *Shredders to Total Collectors* ratio; and the Top-Down Predator Control Index, as *Predators to All other groups* ratio.

2.4. Experimental design

We designed a field experiment to test the effects of black alder leaf litter on LML and nutrient dynamics of maritime pine, employed in extensive catchment plantations, and black poplar, used in riparian plantations (hereinafter alder, pine and poplar, respectively). We considered two experimental scales: stream and leaf-pack. We collected leaves of these three species just after abscission and dried them at room temperature (1 week) prior to initial weighing. We enclosed 5 g of litter (weighed to the nearest 0.1 mg) in each litter bag. Litter bags included single species (monocultures) and mixtures of all possible two species combinations (Fig. S1). We prepared 3 litter mixtures following the natural proportions of the litter benthic composition in streams with riparian alder (~25% out of the total for alder and ~3 times more poplar than pine; Fig. S2): ¼ poplar + ¼ alnus (PN + AG); ¼ pine + ¼ alnus (PP + AG); ¼ poplar + ¼ pine (PN + PP). Additionally, we prepared two extra mixture treatments using 3 × more alder than poplar (AG + PN) or pine (AG + PP) (Fig. S1). We constructed litter bags of two different mesh sizes, fine (1-mm) and coarse (5-mm), to isolate microbial from total LML. Fine-mesh bags only allow the access and activity of fungi and bacteria, whereas coarse-mesh bags allow access to all decomposers and detritivores. All litter mixtures were placed in the different mesh sizes and replicated 3 or 5 times for fine and coarse mesh, respectively (total of 384 bags) (Fig. S1). Sets of bags containing one replicate per treatment were incubated in separate riffle areas (distant ~10 m) in a reach of ~50-m long at each stream. Ninety extra litter bags of coarse mesh (5 per species and stream, each containing 1.66 g of leaves belonging to each plant species) were used to estimate initial (post-leaching, 48 h instream incubation) ash free dry mass (AFDM) of leaves. These leaves were used for initial leaf trait analyses (see Section 2.5).

The experiment lasted 61 days (from 8 January to 9 March 2020). Thereafter, litter bags were collected, stored individually in polyethylene zipper bags and transported to the laboratory on ice. There, remaining leaves were meticulously washed with stream water to remove fine particulate matter, sorted by species, oven-dried to constant mass (72 h at 60 °C), weighed to determine final dry mass (DM) and ground to leaf powder (Mixer Mill RETSCH MM 200). An aliquot of each sample was combusted (550 °C, 5 h), and re-weighed to determine ash concentration (% DM) and estimate final ash-free dry mass (AFDM). Another aliquot of each sample from those leaves incubated in fine mesh bags was stored for nutrient (CNP) analyses.

2.5. Litter trait characterization

Initial physical and chemical trait characterization (Table S2) was performed on post-leached litter (n = 6). Discs of each species were cut to measure specific leaf area (SLA) and leaf toughness. The remaining litter fragments were oven-dried (70 °C, 72 h), and ground for

subsequent litter chemical analyses. Specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) was estimated as the ratio of leaf disc area and disc DM. Leaf toughness (g) was measured using a Texture Analyzer (TA.XTPlus) equipped with a 0.7 mm \varnothing steel rod. Percentages of lignin were calculated as in Fenoy et al. (2016), using an ANKOM 200/220 fibre analyser (ANKOM Technologies, Macedon, NY, USA). Concentration of Ca and Mg (% DM) were determined by inductively coupled plasma mass spectrometry (ICP-MS, Perkin Elmer DRC II). Silicon (Si) concentration was measured using inductively coupled plasma atomic emission spectroscopy (Thermo ICAP 6500 duo, Thermo Fisher Scientific, Cambridge, UK), after microwave sample digestion in nitric acid (65%) and hydrogen peroxide (30%). Condensed tannins were estimated using the acid butanol assay (Gessner and Steiner, 2005). Total phenolics were determined following the Folin & Ciocalteu procedure as described in Bärlocher and Graça (2005). Concentrations of C and N (% DM) were estimated using a Perkin Elmer series II CHNS/O elemental analyser. P concentration (% DM) was measured spectrophotometrically after autoclave-assisted extraction (APHA, 2005). Concentrations of C, N and P were measured at the beginning (post-leached) and on litter in fine-mesh bags at the end of the experiment ($n = 3$). Molar ratios C:N, C:P and N:P were calculated.

2.6. Data analysis

Stream water characteristics were compared between riparian areas (- alder vs. + alder, $n = 3$) and among sampling dates using two-way ANOVAs and the *aov* function of the 'stats' R package (R Core Team, 2020). Differences between stream-riparian types in ecosystem attributes, deduced from FFG characteristics, were assessed using T-tests (*t.test* function of 'stats' package). Trait variability among species or mixtures was assessed using one-way ANOVA and post-hoc Tukey tests with the *anova* and *TukeyHSD* functions of 'stats' package. *Log* or *arcsin* transformations of variables were used when required.

We quantified the proportion of litter mass loss [LML = (initial – final AFDM)/initial AFDM; prop.], after correcting initial litter mass for humidity, ash content and leaching losses. To account for temperature differences among streams, LML was calculated in degree-days, dividing the mass loss by the sum of the accumulated mean daily temperature during the experiment. Changes in litter N (N change; prop.) and P (P change; prop.) were calculated as: (final – initial)/initial N or P content. Positive values represented nutrient immobilization, and negative ones nutrient mineralization. Changes in litter nutrients were only estimated from fine-mesh bags. The effect of leaf litter mixtures on LML and nutrient changes were explored through the net diversity effect (NDE). NDE is the difference between the observed (Obs.) value of the response variable in a mixture and the expected (Exp.) value, which is estimated as the weighted (by the initial proportion of species in mixture) average of the values obtained in the corresponding monocultures (species incubated alone) (i.e., $\text{NDE} = \text{Obs.} - \text{Exp.}$; Loreau and Hector, 2001). For example, a negative NDE in N change would indicate that mixtures gained less N (or lost more N) than expected based on monocultures.

We examined the effects of riparian type (- alder vs. + alder), litter species combinations and their interaction (riparian type \times litter mixture) on LML, nutrient (N and P) changes and net diversity effects using linear mixed effects regression (LMER) analyses at the leaf-pack level. All models included riparian type, litter mixture and their interaction as fixed factors and stream as a random factor nested within riparian type. Regressions were performed for each mesh size independently to avoid very complex models with many interactions (see Tonin et al., 2017). Linear models were fitted using the *lmer* function using restricted maximum likelihood (REML) estimation in the 'lme4' R package (Bates et al., 2015). Additionally, we assessed whether LML and nutrient changes differed between litter mixtures and riparian types (riparian area \times litter mixture as fixed factor) using linear models (Table S3; *lm* function of the 'stats' R package; R Core Team, 2020) followed by Tukey's HSD tests when significant differences were detected. In these analyses, each litter bag within each stream and

riparian area was considered a replicate (9 and 15 for fine and coarse mesh, respectively) for each litter mixture (Fig. S1). When necessary to meet ANOVA assumptions, LML, nutrient changes and NDE were transformed using the *orderNorm* function which was chosen by the *bestNormalize* function of the 'bestNormalize' R package (Peterson and Cavanaugh, 2020).

We explored differences in NDEs among treatments with nonparametric bootstrapped 95% confidence intervals using the BCa method in the *boot.ci* function of 'boot' R package (Canty and Ripley, 2019). For LML, the NDE was partitioned into complementarity and selection effects using the additive partitioning method (Loreau and Hector, 2001). Complementarity effects may derive from synergistic (positive) or antagonistic (negative) interactions; while selection effects represent positive (or negative) effects due to the presence of a dominant species in the mixture, which enhances (or inhibits) overall LML of the mixture (Handa et al., 2014). In addition, we compared LML for each species in monocultures and in each mixture where present using nonparametric bootstrapped 95% confidence intervals. Potential outliers were identified with boxplots (Ieno and Zuur, 2015) and were removed for subsequent analyses (approx. 5% of the data).

3. Results

3.1. Water physicochemical characteristics

Water temperatures for all streams ranged between 0.2 and 6.4 °C (mean: 3.5 °C \pm 0.06 SE) in January–March 2020, with a slightly, but significantly, higher mean temperature in streams without black alder (Table S1). Stream water of both riparian types was circumneutral (mean pH 7.45, range 7.10–7.95); soft (mean specific conductivity 35.5, range 25.5–48.3, $\mu\text{S cm}^{-1}$; mean alkalinity: 0.3, range 0.1–0.4, meq L^{-1}), and oligotrophic (mean nitrate-N 134, range 45–318, $\mu\text{g N L}^{-1}$; mean soluble reactive P: 6, range 2–12, $\mu\text{g P L}^{-1}$; mean $\text{NH}_4\text{-N}$ 20, range 0–69, $\mu\text{g N L}^{-1}$; mean total dissolved-N 0.72, range 0–2.29, mg N L^{-1} ; mean total dissolved-P 11, range 0–39, $\mu\text{g P L}^{-1}$; Table S1). Streams with alder had significantly higher dissolved N, with on average double nitrate-N and 1.4 times more total dissolved-N concentrations than their counterparts without alder (Table S1).

3.2. Stream ecosystem attributes based on macroinvertebrates

The Autotrophy to Heterotrophy Index (Auto/Hetero) indicated that all streams were heterotrophic-dependent on allochthonous organic matter inputs (Table S4). The CPOM/FPOM Index demonstrated that all streams were winter shredder streams, with macroinvertebrates mainly dependent on leaf litter. Streams with riparian alder presented higher values of CPOM/FPOM, but no significant differences were found compared to the other riparian type (T-test, $p = 0.1563$; Table S4). Overall, streams also showed a normal predator to prey balance (0.10–0.20; Merritt et al., 2017) based on the top-down predator control index (Table S4).

3.3. Initial litter traits across species and mixtures

Leaf litter of the 3 species selected differed in leaf traits (Fig. 2; Table S2). Alder litter exhibited the highest N and lignin concentrations and, C:P and N:P ratios, but the lowest P and tannin concentrations, C:N ratio and toughness (Fig. 2; Table S2). Poplar litter had the highest Ca, tannins and phenolics but the lowest Si and lignin concentrations (Fig. 2; Table S2). Pine litter had the highest toughness, C:N ratio and C concentration but the lowest SLA, Mg and Ca concentrations (Fig. 2; Table S2). Mixtures followed the patterns of the individual species making them up (Table S2).

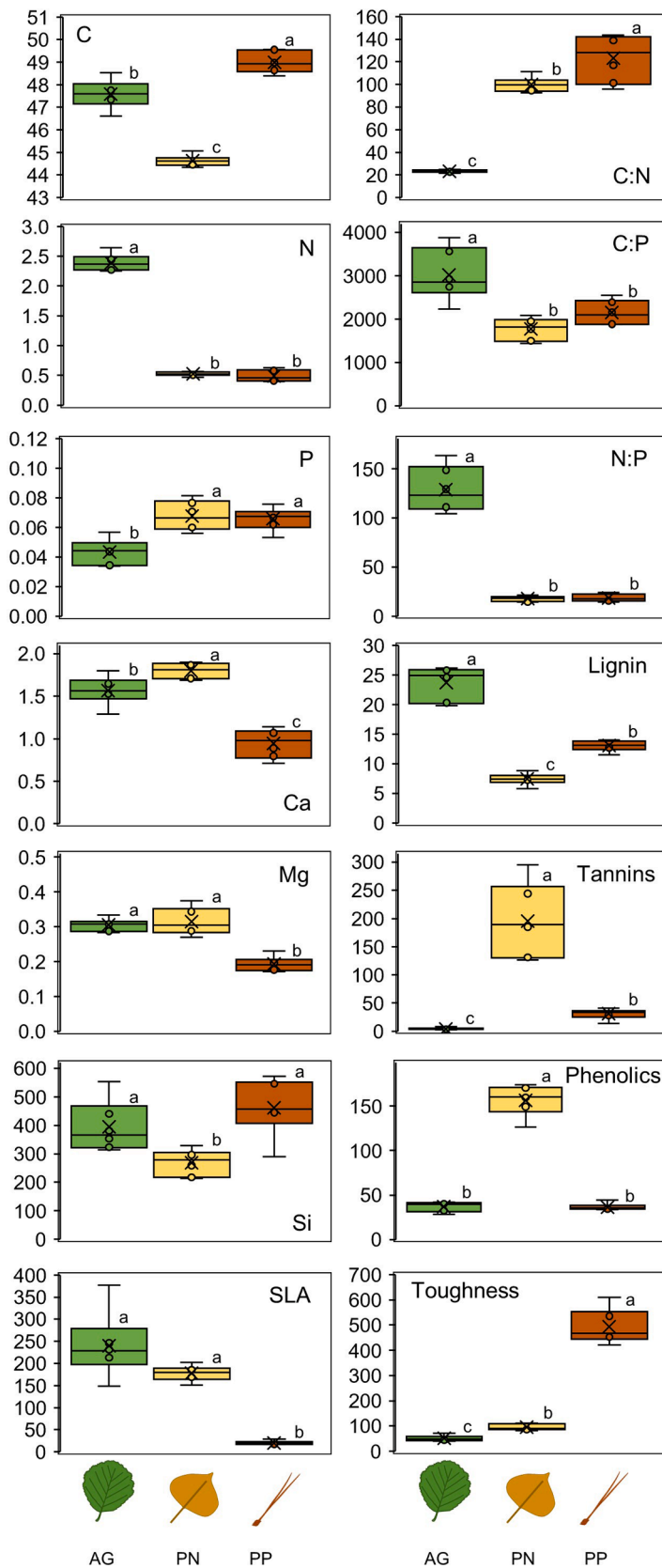


Fig. 2. Box-and-whisker plots for selected leaf trait variables of the three plant species studied (*Alnus glutinosa*, AG; *Populus nigra*, PN; *Pinus pinaster*, PP): carbon (C), nitrogen (N), phosphorus (P), calcium (Ca), magnesium (Mg) and silicon (Si) concentrations (% DM), molar elemental ratios (C:N, C:P and N:P), lignin concentrations (% DM), condensed tannins and total phenolics concentrations (mg g litter^{-1}), specific leaf area (SLA; $\text{cm}^2 \text{g}^{-1}$) and toughness (g) of each plant species. Box represents median and the interquartile range (25–75%), crosses are the mean, whiskers are the range, and dots are replicates. Different letters indicate significant differences ($p < 0.05$) among plant species, on the basis of linear models followed by pairwise multiple comparisons (Tukey test). Note that Y-axis in first panel (carbon, C) does not start at zero.

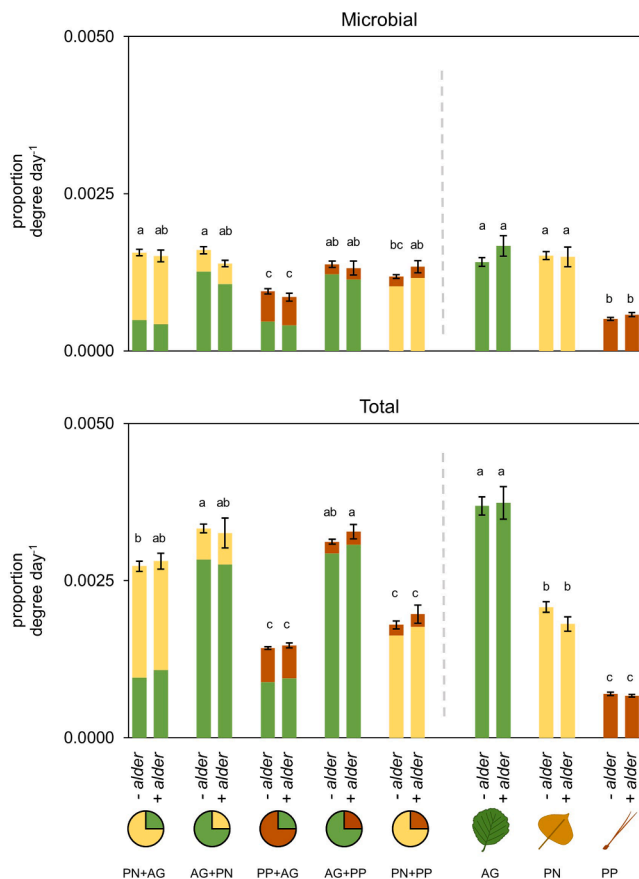


Fig. 3. Mean (\pm SE) litter mass loss (LML; proportion, prop.) of mixtures and monocultures. Different superscript letters indicate significant differences ($p < 0.05$) across single species and 2-spps (*Alnus glutinosa*, AG; *Populus nigra*, PN; *Pinus pinaster*, PP) litter mixtures independently on the basis of linear models followed by pairwise multiple comparisons. Streams with or without riparian alder are stated using + alder or - alder, respectively.

3.4. Litter mass loss

Microbial LML of monocultures was the lowest for pine (~35% lower in average), while higher, and very similar, for alder and poplar, independently of the riparian type (Fig. 3). Total LML of alder was 1.9 and 5.4 times higher than poplar and pine, respectively (Fig. 3). Microbial LML of litter mixtures, was affected by the type of mixture and the interaction riparian type \times litter mixture, whereas total LML was only significantly affected by the type of mixture (Table 2). Generally, microbial LML of mixtures containing alder was slightly faster. However, no significant differences were detected, except in the case of the mixture with a high proportion of pine (PP + AG), for which LML was significantly lower than most others (Fig. 3). Total LML of mixtures followed the pattern of monocultures, i.e., mixtures containing a high proportion of alder (AG + PN and AG + PP) lost more mass than mixtures without alder (PN + PP), or with a high proportion of pine (PP + AG), which lost the least mass (Fig. 3).

Net diversity effects (NDE) on microbial LML were significant for the interaction riparian type \times litter-mixture (Table 2). In riparian zones with alder, the AG + PN mixture (i.e., 75% alder + 25% poplar) exhibited negative NDE (Fig. 4-B), as a result of negative complementarity effects (Fig. 4-F). In streams without riparian alder, AG + PN, PP + AG and AG + PP exhibited a positive NDE (resulting from positive complementarity, Fig. 4-A,E), whereas PN + PP presented a negative NDE (Fig. 4-A) due to negative selection effects (Fig. 4-I). NDE in total LML were only affected by litter mixture (Table 2). These presented overall positive effects (Fig. 4-C, D) for both riparian types due to

positive complementarity effects (Fig. 4-G, H), except for PP + AG at both riparian types and for PN + PP at those without alder, for which the positive NDE appears to be derived from positive selection effects (Fig. 4-K, L).

Intraspecific comparisons of LML (i.e., comparison of LML of a particular species in monocultures and mixtures) highlighted significant mixing effects for some litter species (Fig. S3). One consistent pattern was shown for alder, which tended to lose more mass in mixtures than in monocultures, but only when incubated in streams without riparian alder (Fig. S3-A, B). Total LML of poplar was higher at riparian zones with alder when paired with pine (PN + PP; Fig S3-D), whereas at sites without alder, poplar lost mass similarly to its monoculture regardless of the mixture in which it was present (Fig S3-C). Pine exhibited higher microbial LML in the PP + AG mixture than in monocultures but only at riparian zones without alder (Fig. S3-E).

3.5. Litter nutrient dynamics

Nutrient changes were only assessed for fine-mesh bags. N concentrations increased in all the treatments independently of riparian type, except for the pine monoculture and the PP + AG mixture whose N concentration decreased ~19% and ~3%, respectively, at riparian areas without alder (Table S5). P concentrations increased in all treatments except for the pine monoculture (decrease of ~50%) and the PN + AG mixture (decrease of ~20%) independently of the riparian type and for the PN + PP mixture (decrease of ~4%) at streams without riparian alder (Table S5).

N change was affected by riparian type and litter mixture but not by their interaction (Table 2). Overall, N mineralization was observed in mixtures containing alder, exhibiting higher rates at streams without riparian alder (Fig. 5-A). Interestingly, each litter species acted differently: alder litter always lost N (mineralization) and poplar litter always gained N (immobilization), but pine needles either mineralized or immobilized N depending on the riparian type where they were incubated (Fig. 5-A). The NDE for N change was affected by the interaction between riparian types and litter mixtures (Table 2). The NDE for N change was overall negative when alder was present in the mixture independently of the riparian type, but positive when alder was absent in streams with riparian alder (Fig. 6-A).

Litter mixture significantly affected P change (Table 2). Most mixtures exhibited P mineralization independently of the riparian type, except AG + PN (Fig. 5-B). P followed the opposite pattern of N, with alder litter immobilizing P, but poplar and pine litter mineralizing it (Fig. 5-B). NDE for P change was affected by the interaction between riparian types and litter mixtures (Table 2) and followed a similar pattern of that of N change, with overall negative effects, except for the PN + PP mixtures in streams with riparian alder (Fig. 6-B).

4. Discussion

Pine plantations cover millions of hectares in the Mediterranean basin (Barbéro et al., 1998). However, their influence on the functioning of stream ecosystems draining through these forests is still unclear due to the report of contradictory outcomes by different studies (see Larranaga et al., 2021), which sometimes may derive from the presence of broadleaf riparian forests. Here we assessed if *A. glutinosa* can mitigate the negative effects exerted by pine plantations on stream ecosystem functioning. Riparian alder did not exert an obvious effect on LML but exhibited a crucial role on litter N cycling and in regulating diversity effects.

4.1. Streams flowing through plantations with and without alder differ in water nitrogen concentrations

Water physicochemical characteristics were very similar across the six streams studied. Their proximity, shared lithology and pluvio-nival

Table 2

ANOVA results for the effects of riparian type (- alder vs. + alder) and litter mixture on litter mass loss (LML), N and P changes, and net diversity effects (NDE) of mixture treatments. Each variable was tested against three fixed factors (Riparian type, Litter mixture and their interaction) and a random factor (Stream nested within Riparian type). Analyses were carried out separately for each mesh type.

Factor	Fixed/Random	Microbial LML					Total LML				
		χ^2	df	p-value	R ² marginal	R ² conditional	χ^2	df	p-value	R ² marginal	R ² conditional
LML											
(Intercept)		1040.28	1	<0.0001	0.54	0.80	55.64	1	<0.0001	0.62	0.81
Riparian type	F	2.39	1	0.1223			0.03	1	0.8651		
Litter mixture	F	111.70	4	<0.0001			203.23	4	<0.0001		
Riparian type × Litter mixture	F	12.45	4	0.0143			0.87	4	0.9287		
Stream (Riparian type)	R	–	2	0.1148			–	2	0.0517		
NDE on LML											
(Intercept)		8.05	1	0.0045	0.27	0.68	2.97	1	0.0851	0.11	0.56
Riparian type	F	6.59	1	0.0103			0.00	1	0.9597		
Litter mixture	F	25.08	4	<0.0001			11.31	4	0.0233		
Riparian type × Litter mixture	F	28.88	4	<0.0001			6.86	4	0.1433		
Stream (Riparian type)	R	–	2	0.1145			–	2	0.0667		
N change											
(Intercept)		2.49	1	0.1144	0.74	0.81					
Riparian type	F	4.55	1	0.0330							
Litter mixture	F	114.68	4	<0.0001							
Riparian type × Litter mixture	F	6.50	4	0.1650							
Stream (Riparian type)	R	–	2	0.9847							
NDE on N change											
(Intercept)		53.90	1	<0.0001	0.61	0.72					
Riparian type	F	7.32	1	0.0068							
Litter mixture	F	108.50	4	<0.0001							
Riparian type × Litter mixture	F	49.07	4	<0.0001							
Stream (Riparian type)	R	–	2	0.9834							
P change											
(Intercept)		1.70	1	0.1917	0.39	0.61					
Riparian type	F	0.00	1	0.9921							
Litter mixture	F	38.17	4	<0.0001							
Riparian type × Litter mixture	F	1.78	4	0.7770							
Stream (Riparian type)	R	–	2	0.6843							
NDE on P change											
(Intercept)		0.06	1	0.8020	0.51	0.69					
Riparian type	F	2.16	1	0.1416							
Litter mixture	F	12.69	4	0.0129							
Riparian type × Litter mixture	F	20.71	4	0.0004							
Stream (Riparian type)	R	–	2	0.6523							

origin of water may explain this similarity. Mean water temperature was slightly, but significantly, higher in streams without riparian alder. However, the difference between the mean temperatures of riparian types was <0.2 °C, which appears to be insufficient to significantly affect the community of decomposers and detritivores or stream ecosystem functioning (e.g. Ferreira and Canhoto, 2015; Ferreira et al., 2015b). Likewise, although non-statistically significant, we observed higher streamflow in streams without riparian alder.

More importantly, the main difference observed between the two types of riparian areas was related to water N concentrations. According to our first hypothesis, streams with alder stands in their riversides presented higher concentrations in water of both nitrate-N and total dissolved N (TDN) forms. This agrees with previous studies suggesting that riparian alder could be an important source of N to stream water (Compton et al., 2003; Shaftel et al., 2012), and with other reporting higher nitrate and dissolved inorganic N concentrations in streams with their riparian areas invaded by the N-fixing *Acacia melanoxylon* R. Br. (Pereira and Ferreira, 2021). The season of the study (end of winter) could have promoted such differences in N concentrations between our riparian types. Streams surrounded by alder trees may receive higher N inputs when snow starts to melt and sweeps along the N mineralized under the snowpack during winter (Devotta et al., 2021). No differences in stream water P concentrations were observed between riparian types. However, since alder presence influence stream water N concentration, it can influence N:P ratios and may result in P limitation (Devotta et al., 2021) and consequently in an inhibition of biological N immobilization (Stewart et al., 2019). The TDN:TDP ratios of our streams (~74 and ~47 for streams with and without alder, respectively), suggest potential P

limitation independently of alder presence (Sterner and Elser, 2002; Güsewell and Gessner, 2009).

Macroinvertebrate FFG ratios, used as surrogates of ecosystem attributes (Merritt et al., 2017), indicated high similarity among streams. Accordingly, all streams were heterotrophic, with “normal” shredder associations linked to fall-winter functioning riparian systems and normal predator–prey balances. Although non-significant, those streams flowing through riparian zones with alder stands maintained slightly higher shredder relevance (high CPOM/FPOM Index values) than those without riparian alder, which agrees with studies reporting lower shredder biomass in streams flowing through conifer plantations (Whiles and Wallace, 1997; Riipinen et al., 2010). This may be related to the accumulation of high-quality organic matter stocks from alder.

4.2. Litter mass loss did not differ between riparian types but it did among litter mixtures

Higher N concentrations are expected to promote LML (Ferreira et al., 2015a; Rosemond et al., 2015; Pereira and Ferreira, 2021), due to stimulation of microbial decomposer activity (Gulis and Suberkropp, 2003; Ferreira et al., 2006b; Pereira and Ferreira, 2021; Pereira et al., 2021) and a reduction of nutrient imbalance for shredders (Cross et al., 2005; Lauridsen et al., 2012). In this study, contrary to our second hypothesis, neither microbial nor total LML significantly differed between riparian types, despite the significantly higher water N concentration in streams with riparian alder. This contrasts with previous studies (Kominoski et al., 2011; Pereira and Ferreira, 2021) but agrees with others reporting similar LML in streams flowing through conifer

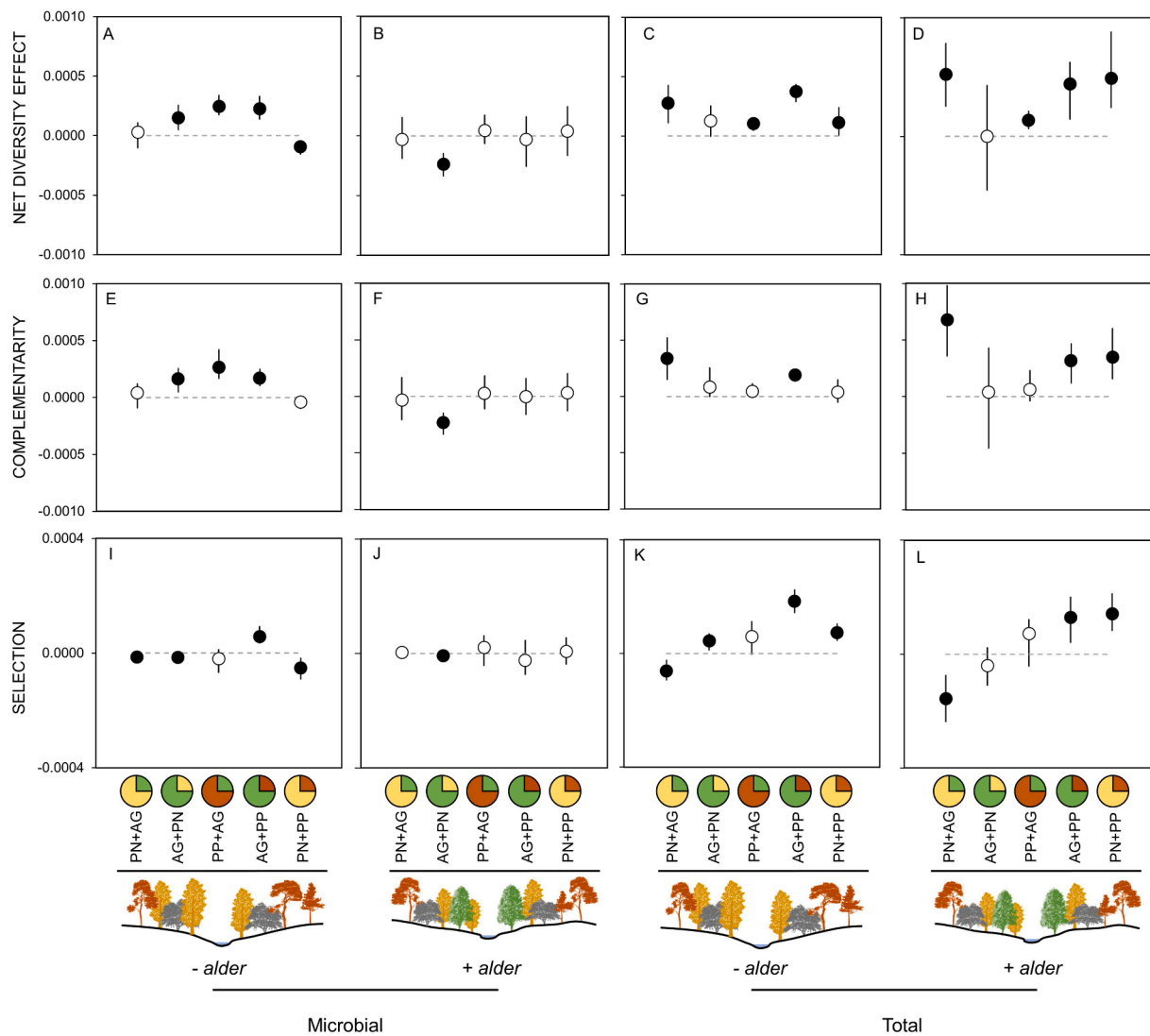


Fig. 4. Net diversity, complementarity and selection effects on microbially-mediated (A, B, E, F, I and J) and total (C, D, G, H, K and L) litter mass loss (LML; proportion degree day⁻¹) after a 61 days incubation in streams with (+ alder) and without (- alder) alder in their riverbanks. Mean values (circles) and upper and lower limits of 95% nonparametric bootstrapped confidence intervals (whiskers) are presented. Dashed lines denote no-effect, i.e., the null expectation that mixtures do not differ from expected ones, estimated from monocultures. Closed circles represent intervals that reject the null hypothesis (i.e., confidence interval do not contain the 0-value) and open circles represent intervals that accept the null hypothesis.

plantations and broadleaf forests (Riipinen et al., 2010; Ferreira et al., 2017). Probably, low mean water temperatures prevented a stimulation of litter mass loss in streams with riparian alder (Ferreira and Chauvet, 2011). Likewise, despite higher N concentrations in streams with riparian alder, both riparian types were close to the oligotrophic-mesotrophic boundary (~700 mg TN L⁻¹) according to the classification of stream trophic state suggested by Dodds et al. (1998). This situation may also have prevented effects of higher N concentrations on LML.

Higher flow has been also reported to enhance LML (dos Santos Fonseca et al., 2013). Therefore, the higher streamflow reported for streams without riparian alder could have attenuated the effects promoted by alder-derived N taking place in those with riparian alder. Recent studies have suggested that this promotion of LML is likely derived from indirect positive effects of current velocity on shredder richness and abundance (Cristiano and Di Sabatino, 2023) more than due to direct physical abrasion, which appears to be irrelevant (e.g. Ferreira et al., 2006a). Nonetheless, it does not seem to be our case since streams with riparian alder (i.e., those with the lowest flow) maintained higher shredder relevance (see section 4.1) than streams without riparian

alder (i.e., those with the highest flow).

Litter mass loss differed among monocultures as expected based on litter differences in physical and chemical traits (Casas et al., 2013; Zhang et al., 2019). Alder lost mass the fastest and pine the slowest, although poplar litter in fine mesh bags lost mass as fast as alder, despite its high tannin and phenolics concentrations, which could have leached during the first weeks of litter incubation (Gessner, 1991; Schofield et al., 1998). These results are similar to previous studies reporting a significant relationship between litter quality and total and detritivore-mediated LML (Rubio-Ríos et al., 2021). As our streams appear to be P-limited (see section 4.1), higher P concentrations in poplar leaves may have favored their use by microbial decomposers to overcome potential stoichiometric imbalances (Gessner et al., 2010; Tonin et al., 2017) in agreement with the Growth Rate Hypothesis (Elser et al., 2000). Nonetheless, pine needles, with similar P concentrations as poplar leaves, exhibited much slower microbial LML. It is possible that higher concentrations of other nutrients in poplar litter, such as Ca which is known to promote aquatic hyphomycete performance (Jenkins and Suberkropp, 1995; García-Palacios et al., 2016) and have been reported as an important driver of litter diversity effects on decomposition

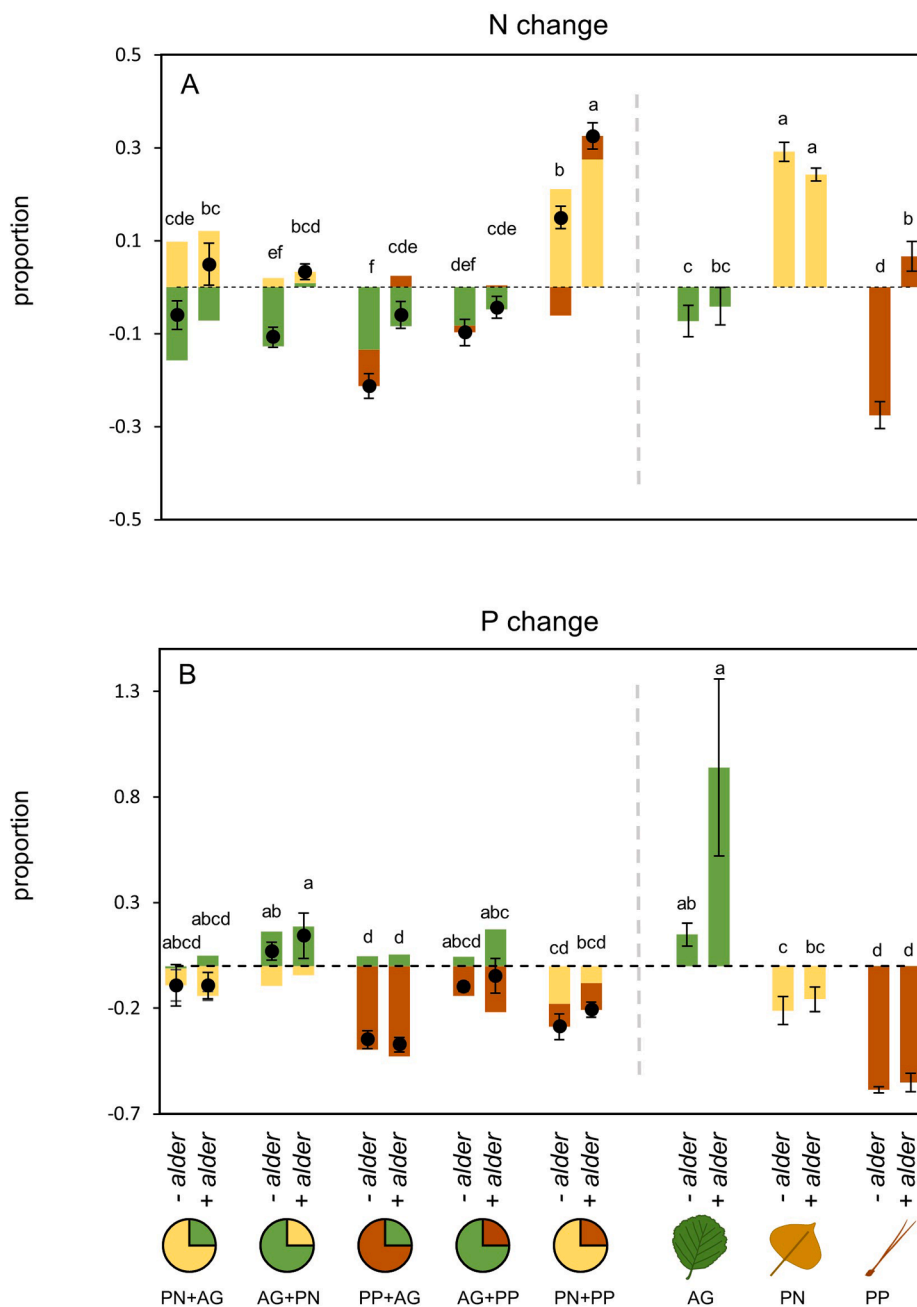


Fig. 5. Mean (\pm SE) N and P change (proportion, prop.) of mixtures and monocultures after 61 days incubation in fine mesh bags in streams with (+ alder) and without (- alder) alder in their riverbanks. Different superscript letters indicate significant differences ($p < 0.05$) across single species and 2-spps (*Alnus glutinosa*, AG; *Populus nigra*, PN; *Pinus pinaster*, PP) litter mixtures independently on the basis of linear models followed by pairwise multiple comparisons. Note that positive and negative values represent microbial immobilization and mineralization, respectively (i.e., increase or decrease of N or P content), respectively. When necessary (coexistence of negative and positive values) a black circle shows the mean value for the mixture.

(Santonja et al., 2019), can help accelerate mass loss. Besides, presence of antifungal compounds in pine needles (Bärlocher and Oertli, 1978) probably reduced its LML.

Microbially-mediated LML of mixtures apparently followed the patterns observed for monocultures. Except for the mixture containing high proportion of pine needles (PP + AG) which lost the least mass, our results are in line with others reporting similar microbial LML of mixtures independently of the amount of alder litter (from 0 to 50%) they contain (Alonso et al., 2022). On the other hand, total LML of mixtures did not totally follow the trend of monocultures since, for example, the PN + AG mixture which contained only 25% of alder litter, lost mass similarly to mixtures containing three times more alder (i.e. AG + PN and AG + PP). This result contrasts with a recent study, which reported differences in LML between litter mixtures containing 0–15% and those containing 50% of alder litter (Alonso et al., 2022). In accordance with that study, we found significant differences between LML of PP + AG (25% alder) or PN + PP (no alder) and the other three mixtures.

Nonetheless, such differences can be explained by the consistently reported lower LML of pine needles when compared to deciduous leaves (e.g. Albariño and Balseiro, 2002; Hisabae et al., 2011; Casas et al., 2013; Martínez et al., 2013). These results may indicate that small proportions of alder litter (~25%) can exert a similar effect on total LML of the whole mixture than very high proportions (~75%) when mixed with other deciduous species, but not when mixed with coniferous needles. Presumably, continuous water flow may provide microbial decomposers with the dissolved N supply necessary to cope with nutrient imbalances in the litter (Suberkropp, 1998; Cheever et al., 2012), whereas detritivores' feeding strategies rely exclusively on litter resources present in the stream.

4.3. Riparian alder modulates diversity effects on microbial litter mass loss

The presence of alder in riparian areas did not appear to affect LML

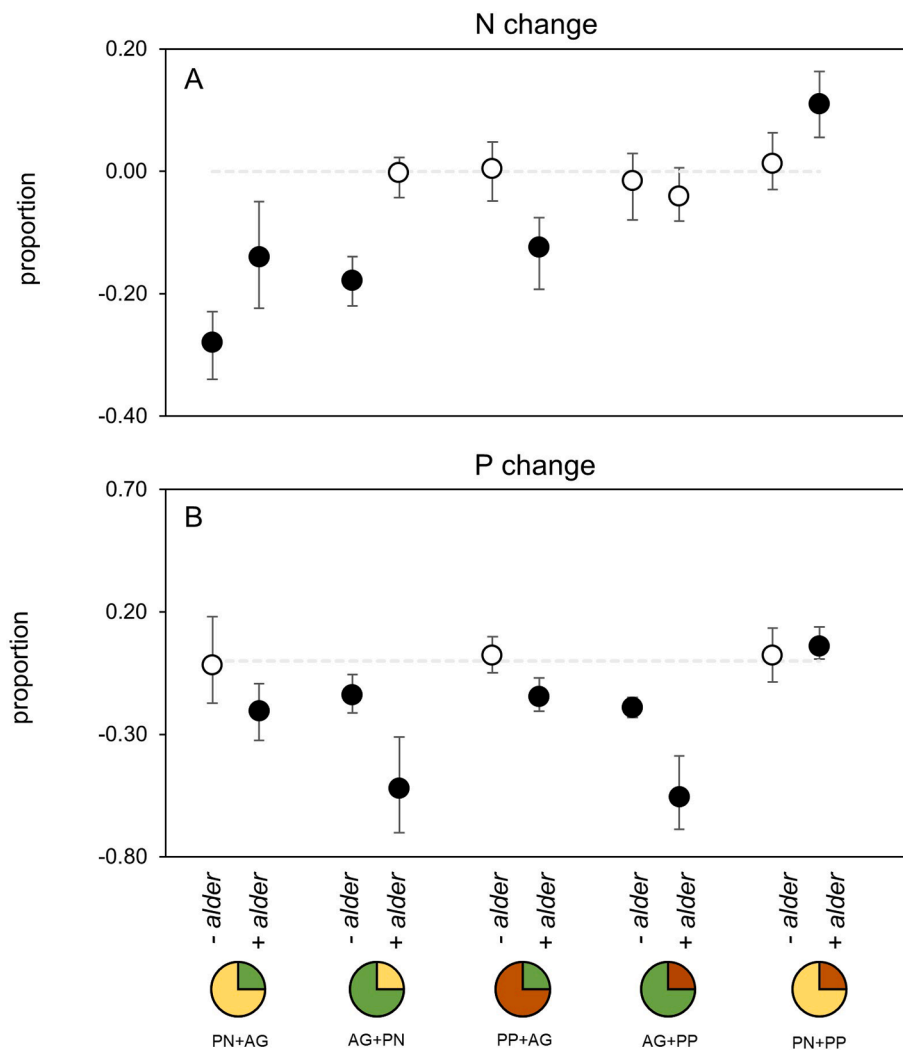


Fig. 6. Net diversity effects (NDE; proportion) on microbially-mediated N (A) and P change (B) after 61 days incubation in streams with (+ alder) and without (- alder) alder in their riverbanks. Mean values (circles) and upper and lower limits of 95% nonparametric bootstrapped confidence intervals (whiskers) are presented. Dashed lines denote no-effect, i.e., the null expectation that mixtures do not differ from expectations, estimated from monocultures. Closed circles represent intervals that reject the null hypothesis (i.e., confidence interval does not contain the 0-value) and open circles represent intervals that accept the null hypothesis.

but seems to influence litter diversity effects on microbially-mediated LML. Interestingly, we observed an overall positive NDE at streams without riparian alder, when this species was present in the litter mixtures (according to our 5th hypothesis), but non or negative NDE at streams with alder (in opposition to our 4th hypothesis). These results are fundamentally opposed to those reported by a microcosm study (Tonin et al., 2017), observing positive NDE on microbial LML when water NO₃-N was increased 5 times over natural concentrations (~10-fold higher than our streams with riparian alder) but no effects at natural concentrations (2-fold higher). Possibly, weekly water renewal was insufficient to prevent nutrient limitation for microorganisms in microcosms receiving water with natural nutrient concentrations, whereas in the field, continuous flow of low nutrient concentrations, often precludes such strong limiting conditions (Suberkropp, 1998; Cheever et al., 2012). Previous results (Larrañaga et al., 2020; Rubio-Ríos et al., 2021) point to a threshold of litter quality dissimilarity above which diversity effects would be detectable. Here, we have probably exceeded that threshold in those treatments containing alder litter. However, higher water N concentrations at streams with riparian alder may have reduced the interspecific variability among plant litters, thus altering the way litter species interacted. This may have suppressed the positive complementarity effects (and thus NDE) found at streams without riparian alder (Rosemond et al., 2010). Conversely, in the mixture without alder litter (PN + PP), higher N concentrations in stream water appeared to compensate for negative NDE through a reduction of negative selection effects, which were probably derived from the low microbial LML of

pine needles, due to their antifungal compounds (Bärlocher and Oertli, 1978).

The overall positive NDE found for total LML (contrary to our 4th hypothesis) agrees with many other studies (e.g. Tonin et al., 2017; López-Rojo et al., 2018), but contradicts the results of a field study assessing the effects of alder loss on LML (Alonso et al., 2021). The length of their study (42 days) may have prevented the observation of positive NDEs in mixtures with alder, as they reported a significant increase of complementarity effects with incubation time. Furthermore, a microcosm study assessing a similar topic observed a positive NDE on total LML after 42 days (Rubio-Ríos et al., 2021). Presumably, such effects are more likely to be detected in shorter times in microcosm experiments where detritivores have no other food available. These results manifest the ability (or the need, given the general lack of compensatory feeding mechanisms in insect shredders; Fenoy et al., 2020; Fenoy et al., 2021) of detritivores to feed simultaneously on resources of contrasting quality to balance their diet (LeRoy and Marks, 2006; Carvalho and Graça, 2007), independently of water N availability.

4.4. Riparian alder can influence stream N budgets

Higher nitrate-N and TDN water concentrations at streams with riparian alder manifest the importance of alder as a source of N to streams (Compton et al., 2003; Shafiel et al., 2012). Such inputs can have considerable implications for the energy flow and nutrient cycling of recipient streams depending on the stream nutrient conditions.

Oligotrophic streams have been suggested as the most vulnerable to nutrient enrichments (Ferreira et al., 2015a), however, if the trophic state of a stream is already high, the input of additional nitrogen derived from riparian N-fixing trees may cause eutrophication issues. Furthermore, eutrophication could be promoted if leaf abscission of deciduous species come early as a consequence of the forecasted warming (Lupon et al., 2017), and if leaf N of non-fixing species is increased due to the higher soil N under N-fixing stands (Hellmann et al., 2011). This being especially notable downstream, since in headwaters riparian shading may mitigate stream eutrophication (Burrell et al., 2014) and P limitation may attenuate biological immobilization of N (Stewart et al., 2019), which will be exported downstream.

In our experiment, inputs of alder-derived N did not affect LML and litter mixtures exhibited similar LML at both riparian zones. These results may derive from the ability of microbial decomposers to use either stream water N or leaf litter N when required (Vitousek and Hobbie, 2000; Cheever et al., 2013). This was evidenced by how alder litter lost N in all cases, but at lower rates in streams with riparian alder (Fig. 5-A). It seems that microorganisms at streams without riparian alder might increase N assimilation from litter to compensate for the lower N concentrations in stream water. This inference is further supported by the N gain and loss undergone by pine litter at streams with and without riparian alder, respectively. Likewise, the overall higher N gain for poplar litter in streams with riparian alder (in support of our 3rd hypothesis) support the alternation of immobilization of exogenous N and assimilation of endogenous N as a potential strategy for microorganisms to avoid N limitation (Cheever et al., 2013). Nonetheless, poplar presented an interesting pattern, gaining more N the less alder litter accompanied it within the mixture. This trend could be explained given that N transfer is stoichiometrically controlled and depends on the demand for N relative to the availability of C (Handa et al., 2014). Thus, the higher C quality of poplar litter (e.g., lower lignin content; Jabiol et al., 2019) may have favored rapid microbial growth and, consequently, higher N demand, promoting fungal N assimilation from other litter species (Tiunov, 2009) or from stream water.

In general, we observed non or negative NDEs on N change in mixtures containing alder, what agrees with other field studies reporting non or mainly positive diversity effects on litter N loss (Handa et al., 2014; López-Rojo et al., 2020). Further, Handa et al. (2014) observed that litter from N-fixing species tended to have higher N loss rates in mixtures than in monocultures, similar to what we found. On the other hand, the positive NDE on N change observed for the PN + PP mixture at streams with riparian alder (supporting our 4th hypothesis) shows the ability of microorganisms to immobilize exogenous N when N-rich litter is lacking. Overall, mixtures containing alder exhibited negative NDEs on P change, but of higher magnitude at streams with riparian alder (supporting our 4th hypothesis). The combination of an isolated N-rich litter with high-water N concentrations likely promoted microbial immobilization of P from water on alder monocultures. This result finds support in other study (Stewart et al., 2019) which showed a negative correlation between instream nitrate and dissolved reactive phosphorus concentrations, probably due to an increase of microbial P uptake. In mixtures, the presence of other P-rich litter may have reduced P immobilization. At streams without riparian alder, only mixtures with high proportions of alder presented negative NDEs on P change. Presumably, high proportions of the N-rich alder litter promoted P assimilation from other species. These results show that the presence of riparian alder may influence not only N, but also instream P cycling.

5. Conclusion

The presence of riparian alder increased water N concentrations (Compton et al., 2003; Shaftel et al., 2012) but did not affect LML in streams flowing through pine plantations. Nonetheless, our results underscored the key role of alder in driving ecosystem N dynamics in headwater streams. Previous studies have pointed to a threshold of alder

riparian cover (ca. 20–30%) above which the profile of stream N can be altered (Compton et al., 2003; Shaftel et al., 2012; Devotta et al., 2021). Our results suggested that, even relatively low covers of *A. glutinosa*, can promote microbial nutrient cycling through a moderate increase of water N concentrations in oligotrophic systems if they are close enough to provide the streams with substantial amounts of litter (24–37% of the litter stocks in our streams; Fig. S2).

We suggest thinning of pine plantations in combination with planting of native broadleaved species (e.g., oaks; Pausas et al., 2004) to further alleviate the effects of pine plantations on Mediterranean streams and promote the action of riparian buffers. In addition, planting alder trees in the riparian zones could promote nutrient cycling in streams both, through an increase of water N concentrations (Ferreira et al., 2006b; Ferreira et al., 2015a) and through a promotion of litter diversity effects (Rubio-Ríos et al., 2021). However, managers should cautiously plan the magnitude of such planting programs depending on the background stream nutrient concentrations, since the nutrient enrichment derived from too high densities of alder stands may cause undesired effects in streams.

CRedit authorship contribution statement

Juan Rubio-Ríos: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing, Visualization. **María J. Salinas-Bonillo:** Investigation, Visualization, Writing – review & editing. **Javier Pérez:** Formal analysis, Methodology, Visualization, Writing – review & editing. **Encarnación Fenoy:** Investigation, Writing – review & editing. **Luz Boyero:** Writing – review & editing. **J. Jesús Casas:** Conceptualization, Funding acquisition, Investigation, Supervision, Visualization, Writing – review & editing.

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.

Data availability

Data will be made available on request.

Acknowledgements

This study was funded by grants to JJC from the Spanish Ministry of Science and Innovation, project RIBARID (CGL2012-39635; MICINN; EU FEDER), and from the 2014-2020 FEDER Operative Program Andalusia, project RIOVEGEST (FEDER-UAL18-RNM-B006-B). JRR was supported by a FPU grant from the Spanish Ministry of Education, Culture and Sports (ref. FPU16/03734).

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.121072>.

References

- Albariño, R.J., Balseiro, E.G., 2002. Leaf litter breakdown in Patagonian streams: Native versus exotic trees and the effect of invertebrate size. *Aquat. Conserv. Mar. Freshwat. Ecosyst.* 12 (2), 181–192.
- Alonso, A., Pérez, J., Monroy, S., López-Rojo, N., Basaguren, A., Bosch, J., Boyero, L., 2021. Loss of key riparian plant species impacts stream ecosystem functioning. *Ecosystems* 24 (6), 1436–1449.
- Alonso, A., López-Rojo, N., Pérez, J., Boyero, L., 2022. Functional consequences of alder and oak loss in stream ecosystems. *Freshw. Biol.* 67 (9), 1618–1630.
- Andrés, C., Ojeda, F., 2002. Effects of afforestation with pines on woody plant diversity of Mediterranean heathlands in southern Spain. *Biodivers. Conserv.* 11, 1511–1520.

- Apha, 2005. Standard methods for the examination of water and wastewater. American Public Health Association (APHA), Washington, DC, USA.
- Arias Abellán, J., 1981. La repoblación forestal en la vertiente norte de Sierra Nevada. In: Cuadernos geográficos, pp. 283–306.
- Barbéro, M., Loisel, R., Quézel, P., 1998. Pines of the Mediterranean basin. In 'Ecology and Biogeography of Pinus' (Ed. DM Richardson) pp. 153–170. In: Cambridge University Press: Cambridge, UK.
- Bärlocher, F., Graça, M.A.S., 2005. Total phenolics. In: Methods to Study Litter Decomposition: a practical guide. In: Graça, M.A.S., Bärlocher, F., Gessner, M.O. (Eds.), Methods to Study Litter Decomposition. Springer-Verlag, Berlin/Heidelberg, pp. 97–100.
- Bärlocher, F., Oertli, J.J., 1978. Inhibitors of aquatic hyphomycetes in dead conifer needles. Mycologia 70 (5), 964–974.
- Bates, D., Mächler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67, 1–48.
- Boothroyd, I.K.G., Quinn, J.M., (Lisa) Langer, E.R., Costley, K.J., Steward, G., 2004. Riparian buffers mitigate effects of pine plantation logging on New Zealand streams: 1. Riparian vegetation structure, stream geomorphology and periphyton. For. Ecol. Manage. 194 (1–3), 199–213.
- Burrell, T.K., O'Brien, J.M., Graham, S.E., Simon, K.S., Harding, J.S., McIntosh, A.R., 2014. Riparian shading mitigates stream eutrophication in agricultural catchments. Freshwater Science 33 (1), 73–84.
- Canty, A., Ripley, B., 2019. boot: bootstrap R (S-Plus) functions. R package. version 1.3-22, 2019. In.
- Cristiano, G., Di Sabatino, A., 2023. How does water current velocity affect invertebrate community and leaf-litter breakdown in a physicochemically stable freshwater ecosystem? An experimental study in two nearby reaches (erosional vs depositional) of the Vera Spring 2023 (Central Italy) Ecohydrology, e2532.
- Carvalho, E.M., Graça, M.A.S., 2007. A laboratory study on feeding plasticity of the shredder *Sericostoma vittatum* Rambur (Sericostomatidae). Hydrobiologia 575 (1), 353–359.
- Casas, J.J., Larrañaga, A., Menéndez, M., Pozo, J., Basaguren, A., Martínez, A., Pérez, J., González, J.M., Mollá, S., Casado, C., Descals, E., Roblas, N., López-González, J.A., Valenzuela, J.L., 2013. Leaf litter decomposition of native and introduced tree species of contrasting quality in headwater streams: How does the regional setting matter? Sci. Total Environ. 458–460, 197–208.
- Casotti, C.G., Kiffer, W.P., Costa, L.C., Rangel, J.V., Casagrande, L.C., Moretti, M.S., 2015. Assessing the importance of riparian zones conservation for leaf decomposition in streams. Natureza Conservação 13 (2), 178–182.
- Cheever, B.M., Kratzer, E.B., Webster, J.R., 2012. Immobilization and mineralization of N and P by heterotrophic microbes during leaf decomposition. Freshwater Sci. 31 (1), 133–147.
- Cheever, B.M., Webster, J.R., Bilger, E.E., Thomas, S.A., 2013. The relative importance of exogenous and substrate-derived nitrogen for microbial growth during leaf decomposition. Ecology 94 (7), 1614–1625.
- Collen, P., Keay, E., Morrison, B., 2004. Processing of pine (*Pinus sylvestris*) and birch (*Betula pubescens*) leaf material in a small river system in the northern Cairngorms, Scotland. Hydrol. Earth Syst. Sci. 8, 567–577.
- Compton, J.E., Church, M.R., Larned, S.T., Hogsett, W.E., 2003. Nitrogen export from forested watersheds in the Oregon Coast Range: The role of N₂-fixing red alder. Ecosystems 6 (8), 773–785.
- Cornish, P., 1989. The effects of radiata pine plantation establishment and management on water yields and water quality. A review.
- Cross, W.F., Benstead, J.P., Frost, P.C., Thomas, S.A., 2005. Ecological stoichiometry in freshwater benthic systems: Recent progress and perspectives. Freshw. Biol. 50 (11), 1895–1912.
- Devotta, D.A., Fraterrigo, J.M., Walsh, P.B., Lowe, S., Sewell, D.K., Schindler, D.E., Hu, F. S., 2021. Watershed *Alnus* cover alters N: P stoichiometry and intensifies P limitation in subarctic streams. Biogeochemistry 153 (2), 155–176.
- Dodds, W.K., Jones, J.R., Welch, E.B., 1998. Suggested classification of stream trophic state: Distributions of temperate stream types by chlorophyll, total nitrogen, and phosphorus. Water Res. 32 (5), 1455–1462.
- dos Santos Fonseca, A.L., Bianchini, I., Pimenta, C.M.M., Soares, C.B.P., Mangiavacchi, N., 2013. The flow velocity as driving force for decomposition of leaves and twigs. Hydrobiologia 703 (1), 59–67.
- Dosskey, M.G., Vidon, P., Gurwick, N.P., Allan, C.J., Duval, T.P., Lowrance, R., 2010. The role of riparian vegetation in protecting and improving chemical water quality in streams 1. JAWRA J. Am. Water Resour. Assoc. 46 (2), 261–277.
- Elsler, J.J., Sterner, R.W., Gorokhova, E., Fagan, W.F., Markow, T.A., Cotner, J.B., Harrison, J.F., Hobbie, S.E., Odell, G.M., Weider, L.W., 2000. Biological stoichiometry from genes to ecosystems. Ecol. Lett. 3 (6), 540–550.
- Esteban-Parra, M.J., García-Valdecasas Ojeda, M., Peinó-Calero, E., Romero-Jiménez, E., Yeste, P., Rosa-Cánovas, J.J., Rodríguez-Brito, A., Gámiz-Fortis, S.R., Castro-Díez, Y., 2022. Climate Variability and Trends. In: In, The Landscape of the Sierra Nevada. Springer, pp. 129–148.
- FAO, 2015. Global Forest Resources Assessment 2015: How are the World's Forests Changing?.
- FAO, UNEP, 2020. The State of the World's Forests 2020. Forests, biodiversity and people.
- Fenoy, E., Casas, J.J., Díaz-López, M., Rubio, J., Guil-Guerrero, J.L., Moyano-López, F.J., Nakatsu, C., 2016. Temperature and substrate chemistry as major drivers of interregional variability of leaf microbial decomposition and cellulolytic activity in headwater streams. FEMS Microbiol. Ecol. 92 (11), fiw169.
- Fenoy, E., Moyano, F.J., Casas, J.J., 2020. Warming and nutrient-depleted food: Two difficult challenges faced simultaneously by an aquatic shredder. Freshwater Science 39 (3), 393–404.
- Fenoy, E., Rubio-Ríos, J., González, J.M., Salinas, M.J., Moyano, F.J., Casas, J.J., 2021. Strategies of shredders when feeding on low-quality leaf-litter: Local population adaptations or fixed species traits? Limnol. Oceanogr. 66 (5), 2063–2077.
- Fernandes, I., Duarte, S., Cássio, F., Pascoal, C., 2013. Effects of riparian plant diversity loss on aquatic microbial decomposers become more pronounced with increasing time. Microb. Ecol. 66 (4), 763–772.
- Ferreira, V., Canhoto, C., 2015. Future increase in temperature may stimulate litter decomposition in temperate mountain streams: Evidence from a stream manipulation experiment. Freshw. Biol. 60 (5), 881–892.
- Ferreira, V., Chauvet, E., 2011. Synergistic effects of water temperature and dissolved nutrients on litter decomposition and associated fungi. Glob. Chang. Biol. 17, 551–564.
- Ferreira, V., Graça, M.A.S., de Lima, J.L.M.P., Gomes, R., 2006a. Role of physical fragmentation and invertebrate activity in the breakdown rate of leaves. Arch. Hydrobiol. 165, 493–513.
- Ferreira, V., Gulis, V., Graça, M.A., 2006b. Whole-stream nitrate addition affects litter decomposition and associated fungi but not invertebrates. Oecologia 149, 718–729.
- Ferreira, V., Encalada, A.C., Graça, M.A.S., 2012. Effects of litter diversity on decomposition and biological colonization of submerged litter in temperate and tropical streams. Freshwater Sci. 31 (3), 945–962.
- Ferreira, V., Castagnyrol, B., Koricheva, J., Gulis, V., Chauvet, E., Graça, M.A.S., 2015a. A meta-analysis of the effects of nutrient enrichment on litter decomposition in streams. Biol. Rev. Camb. Philos. Soc. 90 (3), 669–688.
- Ferreira, V., Chauvet, E., Canhoto, C., 2015b. Effects of experimental warming, litter species, and presence of macroinvertebrates on litter decomposition and associated decomposers in a temperate mountain stream. Can. J. Fish. Aquat. Sci. 72 (2), 206–216.
- Ferreira, V., Koricheva, J., Pozo, J., Graça, M.A., 2016. A meta-analysis on the effects of changes in the composition of native forests on litter decomposition in streams. For. Ecol. Manage. 364, 27–38.
- Ferreira, V., Faustino, H., Raposo, P.M., Gonçalves, V., 2017. Replacement of native forests by conifer plantations affects fungal decomposer community structure but not litter decomposition in Atlantic island streams. For. Ecol. Manage. 389, 323–330.
- García-Palacios, P., McKie, B.G., Handa, I.T., Frainer, A., Hättenschwiler, S., 2016. The importance of litter traits and decomposers for litter decomposition: A comparison of aquatic and terrestrial ecosystems within and across biomes. Funct. Ecol. 30, 819–829.
- Gessner, M.O., 1991. Differences in processing dynamics of fresh and dried leaf litter in a stream ecosystem. Freshw. Biol. 26, 387–398.
- Gessner, M.O., Steiner, D., 2005. Acid butanol assay for proanthocyanidins (condensed tannins). Methods to study litter decomposition: a practical guide, pp. 107–114.
- Gessner, M.O., Swan, C.M., Dang, C.K., McKie, B.G., Bardgett, R.D., Wall, D.H., Hättenschwiler, S., 2010. Diversity meets decomposition. Trends Ecol. Evol. 25, 372–380.
- Gómez-Aparicio, L., Zavala, M.A., Bonet, F.J., Zamora, R., 2009. Are pine plantations valid tools for restoring Mediterranean forests? An assessment along abiotic and biotic gradients. Ecol. Appl. 19, 2124–2141.
- Graça, M.A., Cressa, C., 2010. Leaf quality of some tropical and temperate tree species as food resource for stream shredders. Int. Rev. Hydrobiol. 95, 27–41.
- Graça, M.A., Ferreira, V., Canhoto, C., Encalada, A.C., Guerrero-Bolaño, F., Wantzen, K. M., Boyero, L., 2015. A conceptual model of litter breakdown in low order streams. Int. Rev. Hydrobiol. 100, 1–12.
- Gulis, V., Suberkropp, K., 2003. Leaf litter decomposition and microbial activity in nutrient-enriched and unaltered reaches of a headwater stream. Freshw. Biol. 48, 123–124.
- Güswell, S., Gessner, M.O., 2009. N: P ratios influence litter decomposition and colonization by fungi and bacteria in microcosms. Funct. Ecol. 23, 211–219.
- Handa, I.T., Aerts, R., Berendse, F., Berg, M.P., Bruder, A., Butenschoten, O., Chauvet, E., Gessner, M.O., Jabiol, J., Makkonen, M., 2014. Consequences of biodiversity loss for litter decomposition across biomes. Nature 509, 218–221.
- Hellmann, C., Sutter, R., Rascher, K.G., Máguas, C., Correia, O., Werner, C., 2011. Impact of an exotic N₂-fixing *Acacia* on composition and N status of a native Mediterranean community. Acta Oecologica 37 (1), 43–50.
- Hisabae, M., Sone, S., Inoue, M., 2011. Breakdown and macroinvertebrate colonization of needle and leaf litter in conifer plantation streams in Shikoku, southwestern Japan. J. For. Res. 16, 108–115.
- Ieno, E.N., Zuur, A.F., 2015. A Beginner's guide to data exploration and visualisation with R. Highland Statistics Limited.
- Inoue, M., Shinotou, S.I., Maruo, Y., Miyake, Y., 2012. Input, retention, and invertebrate colonization of allochthonous litter in streams bordered by deciduous broadleaved forest, a conifer plantation, and a clear-cut site in southwestern Japan. Limnology 13, 207–219.
- Jabiol, J., Lecerf, A., Lamothe, S., Gessner, M.O., Chauvet, E., 2019. Litter quality modulates effects of dissolved nitrogen on leaf decomposition by stream microbial communities. Microb. Ecol. 77, 959–966.
- Jenkins, C.C., Suberkropp, K., 1995. The influence of water chemistry on the enzymatic degradation of leaves in streams. Freshw. Biol. 33, 245–253.
- Kominoski, J.S., Marczak, L.B., Richardson, J.S., 2011. Riparian forest composition affects stream litter decomposition despite similar microbial and invertebrate communities. Ecology 92, 151–159.
- Larrañaga, A., de Guzmán, I., Solagaistua, L., 2020. A small supply of high quality detritus stimulates the consumption of low quality materials, but creates subtle effects on the performance of the consumer. Sci. Total Environ. 138397.
- Larrañaga, A., Martínez, A., Albariño, R., Casas, J.J., Ferreira, V., Principe, R., 2021. Effects of exotic tree plantations on plant litter decomposition in streams. In, The Ecology of Plant Litter Decomposition in Stream Ecosystems. Springer, pp. 297–322.

- Lauridsen, R.B., Edwards, F.K., Bowes, M.J., Woodward, G., Hildrew, A.G., Ibbotson, A. T., Jones, J.I., 2012. Consumer–resource elemental imbalances in a nutrient-rich stream. *Freshwater Science* 31, 408–422.
- LeRoy, C.J., Marks, J.C., 2006. Litter quality, stream characteristics and litter diversity influence decomposition rates and macroinvertebrates. *Freshw. Biol.* 51, 605–617.
- López-Rojo, N., Martínez, A., Pérez, J., Basaguren, A., Pozo, J., Boyero, L., 2018. Leaf traits drive plant diversity effects on litter decomposition and FPOM production in streams. *PLoS One* 13.
- López-Rojo, N., Pérez, J., Pozo, J., Basaguren, A., Apodaka-Etxebarria, U., Correa-Araneda, F., Boyero, L., 2020. Shifts in key leaf litter traits can predict effects of plant diversity loss on decomposition in streams. *Ecosystems* in press.
- Loreau, M., Hector, A., 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412, 72–76.
- Lupon, A., Sabater, F., Bernal, S., 2017. The influence of Mediterranean riparian forests on stream nitrogen dynamics: a review from a catchment perspective.
- Márquez, J.A., Principe, R.E., Cibils Martina, L., Albariño, R.J., 2017. Pine needle litter acts as habitat but not as food source for stream invertebrates. *Int. Rev. Hydrobiol.* 102, 29–37.
- Martínez, A., Larrañaga, A., Miguélez, A., Yvon-Durocher, G., Pozo, J., 2016. Land use change affects macroinvertebrate community size spectrum in streams: The case of *Pinus radiata* plantations. *Freshw. Biol.* 61, 69–79.
- Martínez, L.A., Pérez, J., Descals, E., Basaguren, A., Pozo, J., 2013. Effects of pine plantations on structural and functional attributes of forested streams. *For. Ecol. Manage.* 310, 147–155.
- Martín-Peinado, F.J., Navarro, F.B., Jiménez, M.N., Sierra, M., Martínez, F.J., Romero-Freire, A., Rojo, L., Fernández-Ondoño, E., 2016. Long-term effects of pine plantations on soil quality in southern Spain. *Land Degrad. Dev.* 27, 1709–1720.
- Merritt, R.W., Cummins, K.W., Berg, M.B., 2017. Trophic relationships of macroinvertebrates. In: *Methods in Stream Ecology*, Volume 1. Elsevier, pp. 413–433.
- Mesa Garrido, M.Á., 2019. Reforestación, silvicultura e incendios forestales en la dinámica del paisaje del Espacio Natural de Sierra Nevada (1881–2018). *Investigaciones Geográficas (Esp)* 209–234.
- Molina, A.J., González-Sanchis, M., Biel, C., del Campo, A.D., 2021. Ecohydrological turnover in overstocked Aleppo pine plantations: Does the effect of thinning, in relation to water, persist at the mid-term? *For. Ecol. Manage.* 483, 118781.
- Olivencia, Y.J., Rodríguez, L.P., Calvo, A.C., 2015. A half-century of landscape evolution in the Sierra Nevada (Spain). *Boletín de la Asociación de Geógrafos Españoles*.
- Padilla, F.M., Vidal, B., Sánchez, J., Pugnaire, F.I., 2010. Land-use changes and carbon sequestration through the twentieth century in a Mediterranean mountain ecosystem: Implications for land management. *J. Environ. Manage.* 91, 2688–2695.
- Pausas, J.G., Bladé, C., Valdecantos, A., Seva, J.P., Fuentes, D., Alloza, J.A., Vilagrosa, A., Bautista, S., Cortina, J., Vallejo, R., 2004. Pines and oaks in the restoration of Mediterranean landscapes of Spain: New perspectives for an old practice—A review. *Plant Ecol.* 171, 209–220.
- Pereira, A., Ferreira, V., 2021. Invasion of native riparian forests by *Acacia* species affects in-stream litter decomposition and associated microbial decomposers. *Microb. Ecol.* 81, 14–25.
- Pereira, A., Figueiredo, A., Ferreira, V., 2021. Invasive *Acacia* tree species affect in-stream litter decomposition through changes in water nitrogen concentration and litter characteristics. *Microb. Ecol.* 82, 257–273.
- Pérez, J., Basaguren, A., López-Rojo, N., Tonin, A.M., Correa-Araneda, F., Boyero, L., 2021. The role of key plant species on litter decomposition in streams: Alder litter as experimental model. In: Swan, C.M., Boyero, L., Canhoto, C. (Eds.), *The Ecology of Plant Litter Decomposition in Stream Ecosystems*. Springer, pp. 143–161.
- Pérez-Raya, F., López-Nieto, J., El Aallali, A., Hita-Fernández, J., 2001. Cartografía y evaluación de la vegetación del Parque Natural de Sierra Nevada. *Consejería de Medio Ambiente, Junta de Andalucía*.
- Peterson, R.A., Cavanaugh, J.E., 2020. Ordered quantile normalization: A semiparametric transformation built for the cross-validation era. *J. Appl. Stat.* 47, 2312–2327.
- Principe, R.E., Márquez, J.A., Martina, L.C., Jobbágy, E.G., Albariño, R.J., 2015. Pine afforestation changes more strongly community structure than ecosystem functioning in grassland mountain streams. *Ecol. Ind.* 57, 366–375.
- R Core Team, 2020. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing v. 3.6.3, Vienna, Austria.
- Riipinen, M.P., Fleituch, T., Hladyz, S., Woodward, G., Giller, P., Dobson, M., 2010. Invertebrate community structure and ecosystem functioning in European conifer plantation streams. *Freshw. Biol.* 55, 346–359.
- Rosemond, A.D., Swan, C.M., Kominoski, J.S., Dye, S.E., 2010. Non-additive effects of litter mixing are suppressed in a nutrient-enriched stream. *Oikos* 119, 326–336.
- Rosemond, A.D., Benstead, J.P., Bumpers, P.M., Gulis, V., Kominoski, J.S., Manning, D. W., Suberkropp, K., Wallace, J.B., 2015. Experimental nutrient additions accelerate terrestrial carbon loss from stream ecosystems. *Science* 347, 1142–1145.
- Rubio-Ríos, J., Pérez, J., Salinas, M., Fenoy, E., López-Rojo, N., Boyero, L., Casas, J., 2021. Key plant species and detritivores drive diversity effects on in-stream leaf litter decomposition more than functional diversity: A microcosm study. *Sci. Total Environ.*, 149266.
- Rubio-Ríos, J., Pérez, J., Salinas, M.J., Fenoy, E., Boyero, L., Casas, J.J., 2022. Climate-induced plasticity in leaf traits of riparian plants. *Divers. Distrib.* 28, 859–876.
- Sabater, F., Butturini, A., Martí, E., Muñoz, I., Román, A., Wray, J., Sabater, S., 2000. Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. *J. N. Am. Benthol. Soc.* 19, 609–620.
- Santonja, M., Rodríguez-Pérez, H., Le Bris, N., Piscart, C., 2019. Leaf nutrients and macroinvertebrates control litter mixing effects on decomposition in temperate streams. *Ecosystems* 1–17.
- Schofield, J.A., Hagerman, A., Harold, A., 1998. Loss of tannins and other phenolics from willow leaf litter. *J. Chem. Ecol.* 24, 1409–1421.
- Shaftel, R.S., King, R.S., Back, J.A., 2012. Alder cover drives nitrogen availability in Kenai lowland headwater streams, Alaska. *Biogeochemistry* 107, 135–148.
- Sterner, R.W., Elser, J.J., 2002. Ecological stoichiometry: the biology of elements from molecules to the biosphere. Princeton University Press.
- Stewart, S.D., Young, M.B., Harding, J.S., Horton, T.W., 2019. Invasive nitrogen-fixing plant amplifies terrestrial–aquatic nutrient flow and alters ecosystem function. *Ecosystems* 22, 587–601.
- Suberkropp, K., 1998. Effect of dissolved nutrients on two aquatic hyphomycetes growing on leaf litter. *Mycol. Res.* 102, 998–1002.
- Swank, W.T., Douglass, J.E., 1974. Streamflow greatly reduced by converting deciduous hardwood stands to pine. *Science* 185, 857–859.
- Tachet, H., Richoux, P., Bournaud, M., Usseglio-Polatera, P., 2010. *Invertébrés d'eau douce: systématique, biologie, écologie*. CNRS éditions Paris.
- Tiunov, A.V., 2009. Particle size alters litter diversity effects on decomposition. *Soil Biol. Biochem.* 41, 176–178.
- Tonin, A.M., Boyero, L., Monroy, S., Basaguren, A., Pérez, J., Pearson, R.G., Cardinale, B. J., Gonçalves Jr, J.F., Pozo, J., 2017. Stream nitrogen concentration, but not plant N-fixing capacity, modulates litter diversity effects on decomposition. *Funct. Ecol.* 31, 1471–1481.
- Vitousek, P.M., Hobbie, S., 2000. Heterotrophic nitrogen fixation in decomposing litter: Patterns and regulation. *Ecology* 81, 2366–2376.
- Wallace, J., Eggert, S., Meyer, J., Webster, J., 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. *Science* 277, 102–104.
- Wetzel, R.G., Likens, G.E., 1991. Inorganic nutrients: Nitrogen, phosphorus, and other nutrients. In: *Limnological analyses*. Springer 81–105.
- Whiles, M.R., Wallace, J.B., 1997. Leaf litter decomposition and macroinvertebrate communities in headwater streams draining pine and hardwood catchments. *Hydrobiologia* 353, 107–119.
- Wipfli, M.S., Musslewhite, J., 2004. Density of red alder (*Alnus rubra*) in headwaters influences invertebrate and detritus subsidies to downstream fish habitats in Alaska. *Hydrobiologia* 520, 153–163.
- Zhang, M., Cheng, X., Geng, Q., Shi, Z., Luo, Y., Xu, X., 2019. Leaf litter traits predominantly control litter decomposition in streams worldwide. *Glob. Ecol. Biogeogr.* 28, 1469–1486.