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Research article

Interactions among land use, climate, leaf litter traits, and consumers shape large-scale patterns of decomposition in streams of SW Europe

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ABSTRACT

Habitat degradation is one of the primary drivers of biodiversity loss and ecosystem alteration. In streams, leaf litter decomposition plays a key role in energy and nutrient cycling, which is influenced by leaf litter quality, microbial and invertebrate consumers, and environmental conditions. Land use changes alter stream habitats and can modify decomposition rates and dynamics, but large-scale assessments of these anthropogenic impacts remain limited. We explored the consequences of major land use changes (tree plantations, agricultural land, and urban settlements) on stream ecosystems by comparing sites in human-impacted catchments with reference unimpacted sites (i.e., surrounded by native vegetation) across several regions of southwestern Europe encompassing a wide climatic gradient. We quantified decomposition rates of multiple leaf litter types to evaluate the interaction between leaf litter traits and environmental variation, exploring changes in associated invertebrate assemblages. Overall, land use changes reduced total and microbial decomposition rates, with agriculture exerting the strongest effects, and caused marked shifts in invertebrate assemblages including replacement of sensitive by tolerant species and reduced detritivore richness, mainly in urban streams. Climatic variability seemed to modulate these responses, with seasonal climates showing higher vulnerability to impacts. Lastly, leaf litter types differed in their sensitivity to detect degradation, although no consistent trait-based patterns were observed. Our results show that land use changes alter stream ecosystems across climatic gradients, highlighting the urgent need to integrate environmental and biological drivers across spatial scales in watershed management and to provide actionable baselines to optimize riparian restoration and buffer the effects of ongoing climate change.

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1. Introduction

Stream ecosystems are subjected to multiple anthropogenic impacts, which can alter their proper functioning (i.e., the maintenance of ecosystem process rates) and their delivery of services such as water purification, habitat provisioning, or nutrient cycling (Ferreira et al., 2023a). Among these impacts, changes in land use (including the replacement of native forests by tree plantations, agricultural crops, or urban settlements) are known to affect stream ecosystems by altering hydrology, canopy cover and leaf litter inputs, and increasing nutrient and pesticide pollution (Oester et al., 2025). This, in turn, leads to changes in biological assemblages and key ecosystem processes (Paul and Meyer, 2008; Kominoski et al., 2013; Ferreira et al., 2019; Oester et al., 2025). Assessing the effects of land use changes on stream ecosystems is crucial for their conservation and management but not straightforward, because changes in land use can show complex interactions with natural environmental and biological variability at different spatial scales (Allan, 2004; Riato et al., 2023). Moreover, environmental stressors associated to land use changes are numerous and knowledge about their joint effects remains limited (Jackson et al., 2016; Bănăduc et al., 2024).

In headwater streams with heavy riparian shading and thus, limited primary production, leaf litter decomposition is a key component of ecosystem functioning, mediated by microbial decomposers and detritivorous invertebrates feeding on leaf litter (hereafter detritivores) (Marks, 2019). This process contributes the greatest inputs of carbon and nutrients for the food webs of these streams, and it is often used as an indicator of stream ecosystem integrity because of its relevance, its sensitivity to multiple impacts (Chauvet et al., 2016; Rojo et al., 2025), and because its measurement is relatively easy to implement (Bärlocher et al., 2020; Ferreira et al., 2020). Assessing impacts of land use changes on stream ecosystems through leaf litter decomposition is thus a useful approach (Paul et al., 2006; McKie and Malmqvist, 2009; Tiegs et al., 2024), although it requires knowledge of how the process varies across environmental gradients (Boyero et al., 2011b; Pérez et al., 2025) and how changes in decomposition are mediated by detritivores and microbial decomposers, which are often sensitive to environmental changes (Masese et al., 2014; Ferreira et al., 2015).

Here, we aimed to disentangle how the interactions between land use changes and environmental variability shape patterns of leaf litter decomposition across large scales. To do so, we conducted a field experiment in multiple streams across five regions of southwestern Europe encompassing considerable climatic differences (from oceanic to semiarid climates), measuring total and microbial decomposition and invertebrate assemblages associated to leaf litter. In each region, we compared streams surrounded by native vegetation (Nat) with streams affected by tree plantations (Pla), agricultural land (Agr), and urban areas (Urb). We hypothesized that land use changes in a catchment (Pla, Agr and Urb) would impair stream ecosystems compared to control sites flowing through native vegetation (Nat), which would be reflected in increasingly impoverished detritivore assemblages (i.e., lower abundance and taxon richness), and hence lower total decomposition rates; specifically, we predicted that these impacts would be most evident in urban areas, and least evident in plantations (i.e., Nat→Urb > Nat→Agr > Nat→Pla). In contrast, we expected that microbial decomposition would increase at impacted sites due to higher nutrient concentrations that would stimulate microbial activity. Moreover, as differences across regions could be expected to be related with their inherent environmental variability, we explored how multiple climatic and physicochemical variables would influence the patterns observed. Finally, we used several leaf litter types (including three species common to all sites and, at each site, one local species) to make our results more general, as different types of leaf litter are known to vary in their capacity to detect changes in environmental change depending on their traits (Pérez et al., 2021); with that in mind, we explored the role of multiple leaf litter traits on the patterns observed across regions and land use changes.

2. Methods

2.1. Study area characterization

The study was conducted in five regions of southwestern Europe spanning contrasting geoclimatic conditions: eastern France (FA), the Cantabrian coast in northern Spain (SC), central Portugal (CP), the Sierra Nevada mountains in southern Spain (SN), and Almería in southern Spain (SA) (see Table S1 in Supporting Information, Fig. 1). According to the Köppen classification (Beck et al., 2018), the regions comprised temperate oceanic (FA and SC; Cfb), warm-summer Mediterranean (CP; Csb), mountain Mediterranean (SN; Csa/Csb), and semi-arid Mediterranean (SA; BSk/BSh) climates. Four stream sites were studied in each region: one with mostly native vegetation in the catchment (Nat); one with tree plantations covering part of the catchment immediately upstream (Pla); one with agricultural land, including farms, crops or livestock, covering part of the catchment immediately upstream (Agr); and one with a human settlement immediately upstream (Urb). We focused on these three land-use types (tree plantations, agriculture, and urban settlements) because they represent the most widespread and well-documented forms of anthropogenic land-use change affecting stream catchments across our study regions, and because each is associated with a distinct combination of co-occurring stressors: plantations are typically linked to altered riparian leaf litter inputs and hydrological regulation; agricultural land to nutrient and pesticide inputs; and urban settlements to combined hydrological alteration, thermal modification, and pollution. This selection therefore allowed us to capture a broad and representative gradient of anthropogenic stressor combinations relevant to stream ecosystems in the region.

Each site comprised an approximately 50-m reach located in a low-order (<3) permanent stream, with alternating riffle and pool/run habitats. Within each site, we selected four consecutive pool/run habitats to conduct the experimental work. For each site, we recorded the decimal latitude and longitude and altitude (m a.s.l.) from Google Earth (Table S1). Climatic variables were obtained from global databases, and physicochemical parameters (water temperature, pH, conductivity, dissolved oxygen, nutrients, and discharge) were measured during the experiment following standard procedures (see Appendix S1).

2.2. Leaf litter collection and initial processing

We used leaf litter from four plant species at each site. Three species not naturally present at the study areas were used across all sites: two American tree species (*Alnus acuminata* Kunth, Betulaceae; and *Quercus rubra* L., Fagaceae), collected in the field (see locations below); and *Musa balbisiana* Colla (Musaceae), which was commercially acquired. The fourth litter type was a local riparian tree species at each site, which hence differed across sites (FA: *Corylus avellana* L., Betulaceae; SC: *Salix atrocinerea* Brot., Salicaceae; SN: *Populus nigra* L., Salicaceae; SA: *Populus alba* L., Salicaceae; and CP: *P. nigra*). *Alnus acuminata* and *Q. rubra* were included because they were part of a larger study where these two species were used across 30+ regions globally distributed (GLoBE-LandComp, https://biodiversity.umbc.edu/landcomp/), representing two substrates of contrasting quality commonly used in decomposition experiments (Pérez et al., 2021). Moreover, both species were absent from all our study sites, avoiding any potential home-field advantage effects (Fenoy et al., 2024). *Musa balbisiana* provided a standardized substrate that was easy to acquire and process while remaining consumable by invertebrates, unlike other standardized substrates such as cotton strips, wood sticks, or tea bags (Ferreira et al., 2021; Rojo et al., 2025). The use of different local species in different regions did not allow within-species comparisons across regions, but it served to explore responses of invertebrates and microbial decomposers to an autochthonous substrate (see Appendix S1).

In the laboratory, leaves were air-dried until constant weight, weighed, sprayed with distilled water to avoid breakage, and enclosed in

coarse-mesh (6.5-mm opening, 20 × 15 cm) and fine-mesh (0.5-mm, 6 × 5 cm) litterbags, containing 3.0 ± 0.1 (target value ± precision) and 0.20 ± 0.01 g dry mass (DM), respectively. Litterbags were paired by enclosing each fine-mesh litterbag within a coarse-mesh litterbag, which was labelled and tied to a nylon rope. Sixty-four litterbags (i.e., 32 pairs: eight replicate pairs × four species) were prepared for each site, which resulted in 256 litterbags per region, and 1280 in total.

2.3. Leaf litter trait characterization

Extra subsets of leaves were used to estimate leaf litter mass loss due to leaching in microcosms (580-mL glass jars), with eight replicates per species. Each microcosm contained 2.00 ± 0.01 g (target value ± precision) of leaf litter and 400 mL of filtered (100 µm) stream water (from the Agüera stream in northern Spain), and were incubated for 72 h at 10 °C, with water renewal after 36 h. Leached leaf litter was used to determine leaf toughness using a penetrometer [pressure (kPa) required to pierce the leaf tissue with a 1.55-mm diameter steel rod (Boyero et al., 2011a)]; and specific leaf area (SLA), which is the ratio of leaf area (mm^2; calculated from leaf discs of known diameter) to leaf DM (mg). The material was then oven dried (60 °C, 72 h), weighed to estimate post-leaching DM, and each sample divided into two portions.

One subsample was incinerated (550 °C, 8 h) to calculate ash concentration (%) and initial ash-free dry mass (AFDM), and the other subsample was used to determine the rest of leaf litter traits in 4 replicates randomly selected. These traits were: carbon (C) and nitrogen (N) concentrations, measured with a Perkin Elmer series II CHNS/O elemental analyser (Perkin Elmer, Norwalk, CT, USA); phosphorus (P) concentration, measured spectrophotometrically following autoclave-assisted extraction (Rice et al., 2012); lignin concentration, determined by the Goering and van Soest method (Goering and Van Soest, 1970); polyphenol concentration, determined by the Folin-Ciocalteu method (Bärlocher et al., 2020); and concentrations of micronutrients and other elements (calcium, Ca; copper, Cu; iron, Fe; magnesium, Mg; potassium, K; silicon, Si; sodium, Na; sulfur, S; and zinc, Zn), determined with inductively coupled plasma optical emission spectroscopy (ICP-OES) using a THERMO ICAP 6500 DUO spectrometer. All leaf litter traits are listed in Table S3.

2.4. Experimental procedure

At each site, we deployed eight replicate litterbag pairs per species, two in each pool/run habitat (i.e., 32 pairs per site). All litterbag pairs in a pool/run were anchored to an iron bar or a rock, using stones as ballast if necessary. No litterbags were on top of each other, and large accumulations of leaf litter were avoided. Litterbags were left in the stream for 28-44 days (mean ± SD = 38 ± 5 days), with lower incubation time at higher temperatures (Table S1) to avoid complete loss of leaf material. Incubation generally lasted the same number of days within each region — 40 days at FA (mean temperature 9.95 – 11.35 °C), 41 days at SC (9.18 – 10.87 °C), 35 days at CP (10.13 – 15.26 °C), and 42 days at SN (5.47 – 9.02 °C) —, identical across all four land-use treatments within each of these regions, varying slightly among regions according to the temperature of their warmest site, so as to balance an accurate assessment of total and microbially mediated decomposition of the different substrates against sufficient time for litterbag colonization by the

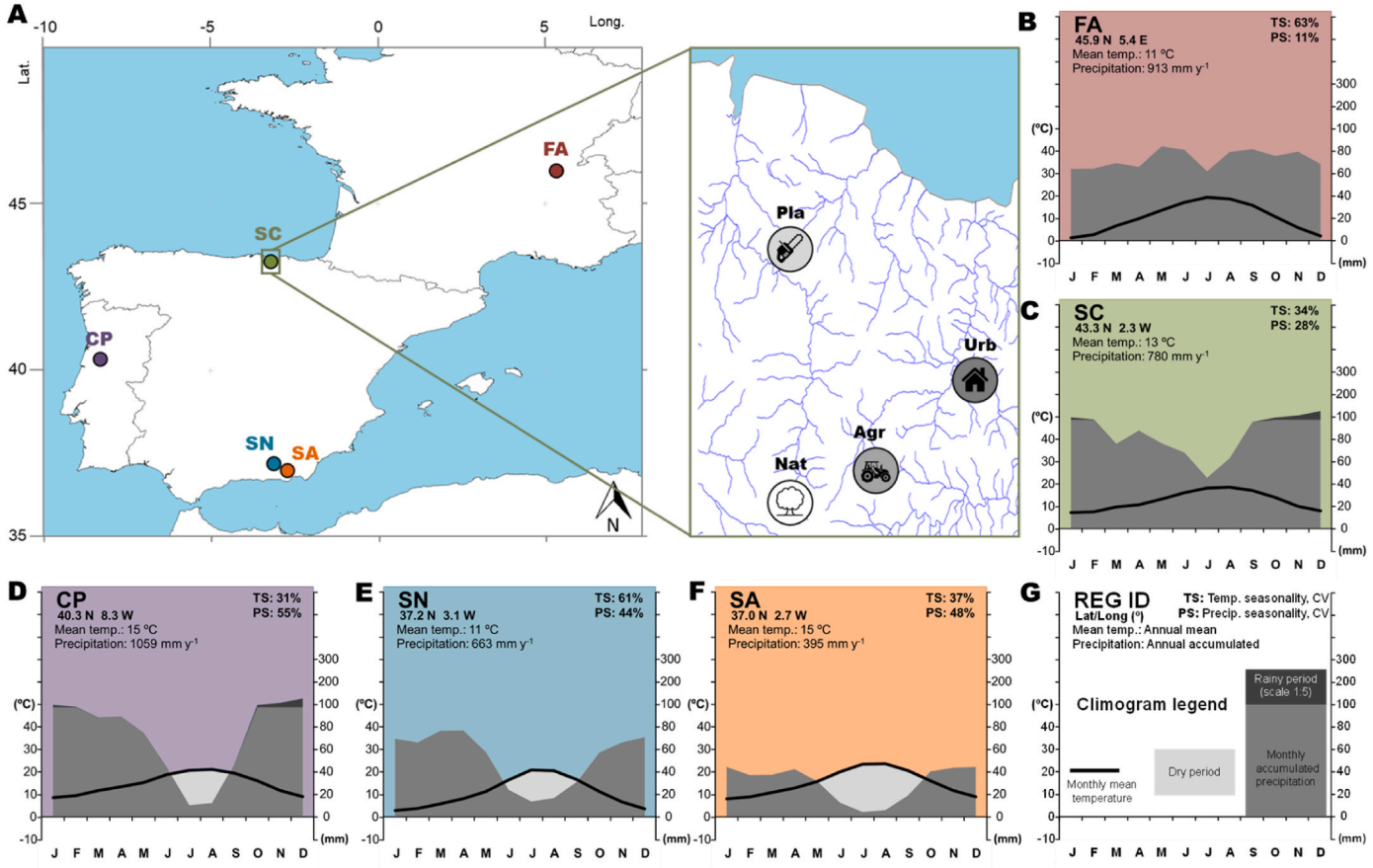


Fig. 1. (a) Map of southwestern Europe showing the five study regions (FA, eastern France; SC, Cantabrian coast in northern Spain; CP, central Portugal; SN, Sierra Nevada mountains in southern Spain; and SA, Almería in southern Spain)and an inset of four study streams (native, Nat; plantation, Pla; agricultural, Agr; and urban, Urb) at the SC region; (b–f) climograms of study regions showing monthly and annual values and seasonality (%) of temperature and precipitation; and (g) legend of the climographs.

associated fauna. At SA, incubation lasted 28 days for three of the four sites (12.10 – 15.73 °C), but 44 days at the tree plantation site (14.74 °C), after a flood event disrupted the original collection date; we thus allowed extra time after the return to baseflow conditions for the recovery of organism colonization (extended information on this aspect on Supporting Information). After the incubation period, the litterbags were collected by placing a 0.5-mm mesh hand net immediately downstream, thus avoiding the loss of leaf material and invertebrates, and they were individually introduced into plastic bags that were stored in a cooler and transported to the laboratory for processing within 24 h.

In the laboratory, each coarse-mesh litterbag was carefully opened and emptied onto a 500-μm sieve to rinse the leaf litter material and collect the invertebrates, which were preserved in a vial with 70% ethanol for further counting and identification. The process was repeated for fine-mesh bags, except that these contained no invertebrates. Leaf litter was transferred to labelled crucibles, dried in an oven (60 °C, 72 h), weighed to the nearest 0.001 g to estimate final DM, incinerated in a muffle furnace (550 °C, 8 h), and ashes weighed for estimation of final AFDM. Invertebrates were counted on a stereoscope at 50× magnification, identified with taxonomic keys (Tachet et al., 2010) to the lowest taxonomic level possible [often genus but sometimes family (e.g., Psychodidae), subfamily (e.g., Tanypodinae), or class (e.g., Oligochaeta)], and classified into leaf litter-feeding detritivores and others (Boyero et al., 2020). For each litterbag, we calculated the abundance and taxon richness (number of individuals and taxa per litterbag, respectively) of all invertebrates and detritivores.

2.5. Data analyses

We conducted several preliminary analyses to explore differences in climatic conditions and physicochemical variables across regions, as well as leaf litter trait variability across the plant species used in the experiment. To do so, we used principal component analysis (PCA; *prcomp* function of the "stats" package), after z-standardization of variables (*scale* function of the "base" package), to visualise the three datasets and thus improve the interpretation of results (Fig.S1, S2 and S3).

We quantified the leaf litter decomposition rate in each litterbag in terms of rates per degree day (k, dd^{-1}), derived from a negative exponential decay model (Bärlocher, 2020). This accounted for temperature differences across regions, a common procedure in large-scale studies (e.g., Woodward et al., 2012; Boyero et al., 2021). Before calculating decomposition rates, initial litter mass was corrected for remaining humidity, leaching losses and ash content, thus removing differences among species due to the rapid initial loss of soluble compounds (Bärlocher, 2020). Total and microbial decomposition rates were obtained from leaf litter enclosed in coarse-mesh and fine-mesh litterbags, respectively.

To test our hypotheses that land use changes would impair ecosystem functioning (measured through total and microbial decomposition) and associated assemblages (measured through invertebrate and detritivore abundance and taxon richness), we used effect sizes measured with the standardized mean difference Cohen's d. This was calculated as the difference between the mean of the altered site minus the mean of the control site, normalized by the pooled standard deviation using the Welch's approximation to adjust the degrees of freedom (West, 2021). As effects sizes are unitless, they allowed consistent comparison among response variables with different units across regions.

To further explore our hypotheses, we examined variation in invertebrate assemblage structure across regions with Principal Coordinate Analysis (PCoA) based on a Bray–Curtis dissimilarity matrix calculated from invertebrate abundances (*vegdist* function of the "vegan" package), using *cmdscale* function of the "stats" package. This was followed by permutational multivariate analysis of variance (*adonis2* function of the "vegan" package), to explore whether assemblages varied depending on land use or leaf litter type. The most representative taxa in each case were determined using an indicator value (IndVal) index (*multipatt* function of the "indicspecies" package) (De Cáceres, 2013).

To explore the contribution of different climatic and physicochemical variables and leaf litter traits to the patterns observed, we fitted forward stepwise linear models (*step* function in the "stats" package). We built one model for each response variable (i.e., total and microbial decomposition and invertebrate and detritivore abundance and taxon richness) and all predictor variables (i.e., climatic and physicochemical factors and leaf litter traits). Water temperature was not included in models explaining total and microbial decomposition, as decomposition rates were expressed per degree-day, which accounts for accumulated thermal exposure in the calculation of the response variable. For each response variable, the final model was selected based on the lowest Akaike Information Criterion (AIC); the contribution of each retained predictor was quantified as the proportion of variance explained, calculated as the ratio of its sequential sum of squares to the total sum of squares explained by the final model; and statistical significance was assessed using F-tests. All analyses were conducted in R version 4.4.1 (R Core Team, 2022).

3. Results

3.1. Effects of land use changes on leaf litter decomposition and associated assemblages

Leaf litter decomposition rates widely varied across land use types, regions, and leaf litter types (see Appendix S2, Table S4, Fig. S4), but effect sizes revealed a prevalence of negative effects of land use changes on both total and microbial decomposition. In all cases, significant effects showed large magnitudes according to established benchmarks (Cohen, 1988). Thus, in regions SC, CP, and SN, there was an overall reduction of total decomposition rates at impacted sites (Pla, Agr, and Urb) compared to control sites ($d \geq 0.8$; Fig. 2, Table S5). In contrast, total decomposition appeared to be unaffected by land use changes in FA, while in SA, it increased significantly at impacted sites, showing positive effect sizes (up to $d = 5.83$ in urban sites; Fig. 2, Table S5). Among the different impacts, Agr showed the greatest number of significant effect sizes for both total (e.g., $d = -2.88$ to -5.23 in CP and $d = -1.53$ to -2.40 in SN) and microbial decomposition ($d = 1.58$ to 2.43). This was followed by Urb, with significant effects for total ($d = -1.68$ to -3.18 in CP and SN, and up to $d = 5.83$ in SA) and microbial decomposition ($d = 1.54$ to 3.26). Finally, Pla showed fewer significant effects for total ($d = -1.47$ to -4.45) and microbial decomposition ($d = 1.38$ to 4.31; Fig. 2, Table S5). *A. acuminata* detected the greatest number of significant effects on total decomposition ($d = -1.31$ to -5.23), followed by the local species ($d = 1.24$ to 5.83), whereas for microbial decomposition, *M. balbisiana* ($d = 1.38$ to 2.53), *Q. rubra* ($d = 1.58$ to 2.78) and the local species ($d = 1.78$ to 4.31) showed more significant effects than the other species (Fig. 2).

Invertebrate abundance and taxon richness again varied widely across land use types, regions, and leaf litter types (Fig. S5 and S6), with impacts of land use changes being less evident than for decomposition. However, there was a trend towards reduced abundance in Pla and Agr, significant in regions CP ($d = -2.96$) and SA ($d = -1.25$ to -2.01), while abundance increased in Urb sites of regions SC, SN and SA ($d = 1.35$ to 3.04; Fig. 3, Table S5). For detritivores, abundance tended to decrease with all land use changes, although effects were greater in Urb (all regions but FA): SC ($d = -1.47$ to -4.78), CP ($d = -1.69$), SN ($d = -1.56$ to -2.20), and SA ($d = -1.60$ to -2.36). General trends were similar across leaf litter types (Fig. 3). Impacts on invertebrate richness were more common than on abundance, with negative effects in Pla [regions CP ($d = -2.14$ to -3.32), SN ($d = -1.18$), and SC ($d = -1.34$)] and Agr (SN, $d = -1.73$ to -2.49); and mixed effects in Urb, negative in SN ($d = -1.44$ to -2.23) and positive in SC ($d = 1.78$) and SA ($d = 1.20$ to 1.91) (Fig. 4). For detritivore richness, effects were negative across regions, with particularly high numbers of effects in Urb ($d = -1.47$ to

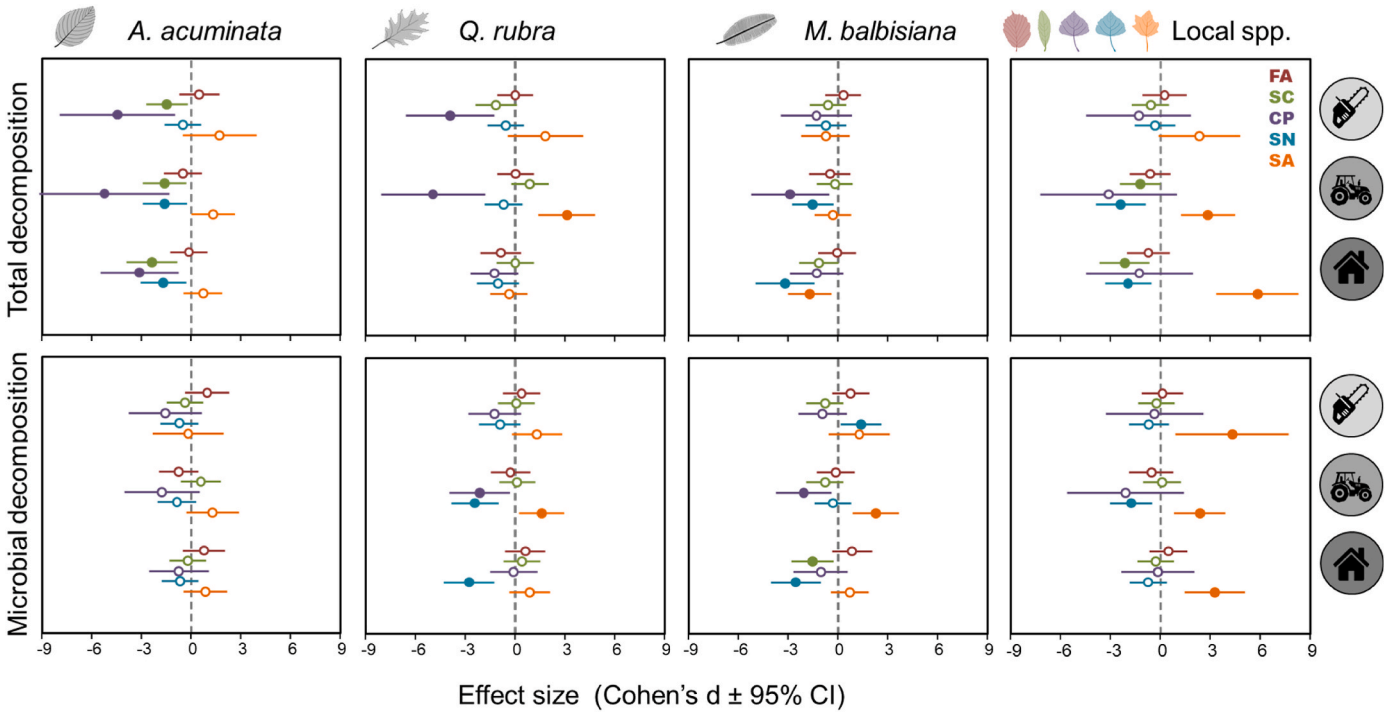


Fig. 2. Effect sizes (Cohen's d) measuring impacts of land use changes (plantation, agricultural, and urban) compared with control (native vegetation) streams, on total and microbial leaf litter decomposition, for different regions (FA, eastern France; SC, Cantabrian coast in northern Spain; CP, central Portugal; SN Sierra Nevada mountains in southern Spain; and SA, Almería in southern Spain) and leaf litter types (*Alnus acuminata*, *Quercus rubra*, *Musa balbisiana*, and the local species *Corylus avellana* in FA, *Salix atrocinerea* in SC, *Populus nigra* in SN and CP, and *Populus alba* in SA). Empty circles indicate no significant effects, whereas filled circles indicate significant positive (> 0; higher value at impacted sites) or negative size effects (< 0; lower value at impacted sites).

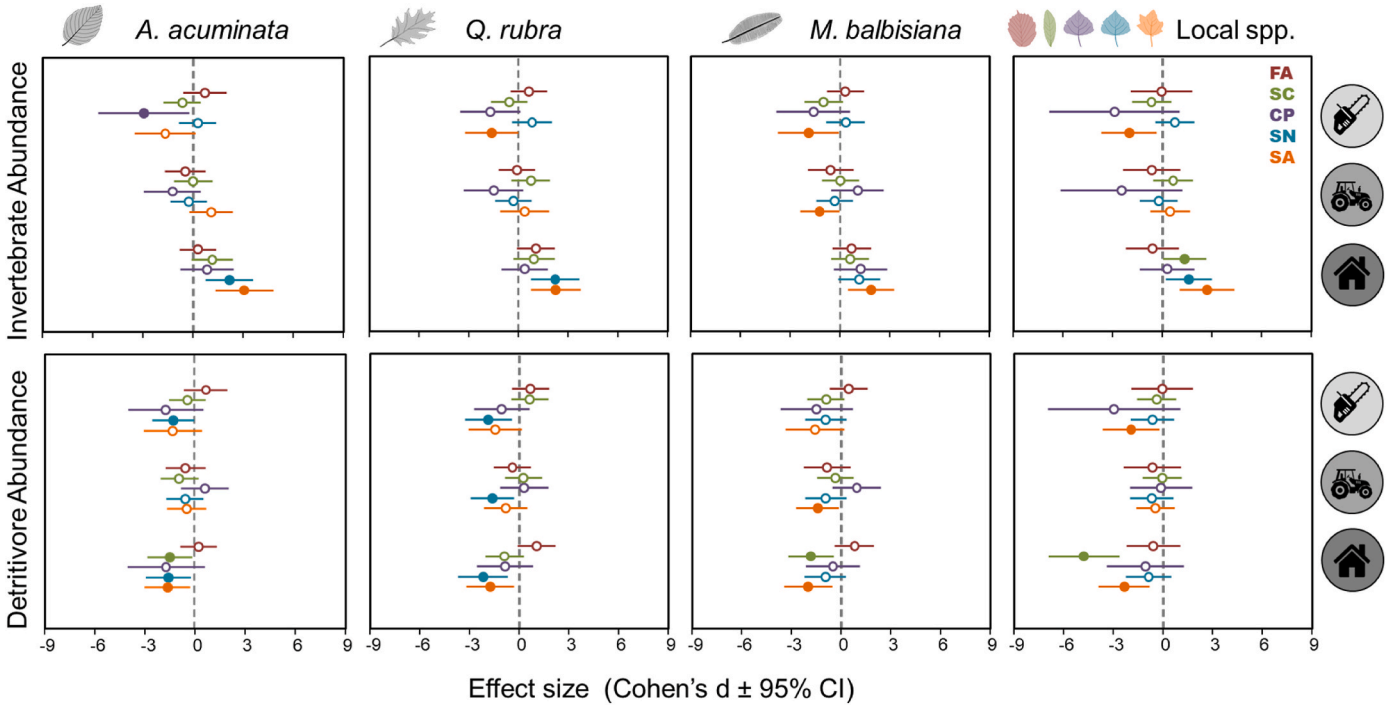


Fig. 3. Effect sizes (Cohen's d) measuring impacts of land use changes (plantation, agricultural, and urban) compared with control (native vegetation) streams, on invertebrate and detritivore abundance, for different regions (FA, eastern France; SC, Cantabrian coast in northern Spain; CP, central Portugal; SN Sierra Nevada mountains in southern Spain; and SA, Almería in southern Spain) and leaf litter types (*Alnus acuminata*, *Quercus rubra*, *Musa balbisiana*, and the local species *Corylus avellana* in FA, *Salix atrocinerea* in SC, *Populus nigra* in SN and CP, and *Populus alba* in SA). Empty circles indicate no significant effects, whereas filled circles indicate significant positive (> 0; higher value at impacted sites) or negative size effects (< 0; lower value at impacted sites).

−5.35) followed by Pla (d = −1.33 to −3.18), which were reflected by all leaf litter types, especially *A. acuminata* and *M. balbisiana* (Fig. 4; Table S5). In all cases, significant effects showed large magnitudes according to established benchmarks (Cohen, 1988). The composition of invertebrate assemblages also responded to land use changes, with clear clusters associated with each land use type, sensitive taxa associated to Nat, and tolerant taxa to Agr and Urb (see Appendix S2, Fig. 5, Tables S6 and S7).

3.2. The role of environmental variation and leaf litter traits on the patterns observed

The model for total decomposition explained 61% of the total variance and was mainly predicted by three factors, which together accounted for >50% of explained variance: precipitation seasonality (with a negative influence, hereafter "–") and the concentrations of two leaf micronutrients, Na (positive influence, hereafter "+") and K (−). Other leaf traits and environmental factors presented much lower contributions (Table S8). For microbial decomposition, total variance explained by the model was 51% and the largest contribution was made by lignin concentration (−), followed by ash concentration (+).

Total variation in invertebrate and detritivore abundance explained by the models were low (15% and 13%, respectively), and were mainly determined by several leaf litter traits and water physicochemical factors, which in both cases included SLA (+), polyphenol concentration (−), and Na concentration (+). Nitrogen availability in the water (by means of NO_3 concentration) only affected (+) invertebrate abundance, whereas detritivore abundance was influenced by other leaf litter traits such as Cu concentration (−) and toughness (−). For invertebrate richness, the model explained 42% of the total variation and the main predictors were water flow (+) and other environmental (pH and SRP) and climatic factors (isothermality and precipitation of the driest quarter; all –). Finally, variation in detritivore richness (46% of total variance explained) was mostly influenced by the same climatic factors as invertebrate richness (isothermality and precipitation of the driest quarter) and by NH_4 concentration in the water (all –).

4. Discussion

4.1. Land use changes impair stream ecosystems

Our large-scale experimental study across five regions in southwestern Europe evidenced strong impacts of major anthropogenic land use changes (i.e., plantations, agriculture, and urbanization) on leaf litter decomposition, a key component of stream ecosystem functioning, and its associated invertebrate assemblages, mainly the leaf litter-feeding detritivores. As we expected, there was a preponderant reduction in rates of leaf litter decomposition mediated by both detritivores and microorganisms (i.e., total decomposition) at altered sites, compared to sites surrounded by native vegetation, despite some inter-regional variability. Leaf litter decomposition rates often decrease in response to anthropogenic impacts, such as heavy organic pollution (Woodward et al., 2012; Martinez-Sanz et al., 2024), inorganic pollutants (e.g., pesticides; Dawoud et al., 2017; Cornejo et al., 2020), loss of riparian vegetation (Neres-Lima et al., 2017; López-Rojo et al., 2019), or the replacement of native forest by exotic plantations (Ferreira et al., 2019; Oester et al., 2025). Some or all these impacts may have been present across the land use changes studied here and could help explain the observed patterns, potentially contributing to the expected reductions in this key ecosystem process.

The above effects could be expected to be mediated by detritivores, many of which are sensitive to pollution and other environmental changes (Boyero et al., 2012; Cornejo et al., 2019; Larrañaga et al., 2023). We observed overall reductions in the number of detritivores in terms of individuals and taxa, and shifts towards more tolerant invertebrates at impacted sites, which replaced sensitive taxa, as shown elsewhere (Friberg et al., 2010; Cornejo et al., 2019). Beyond direct sensitivity to pollution, detritivore abundance and behaviour can also be

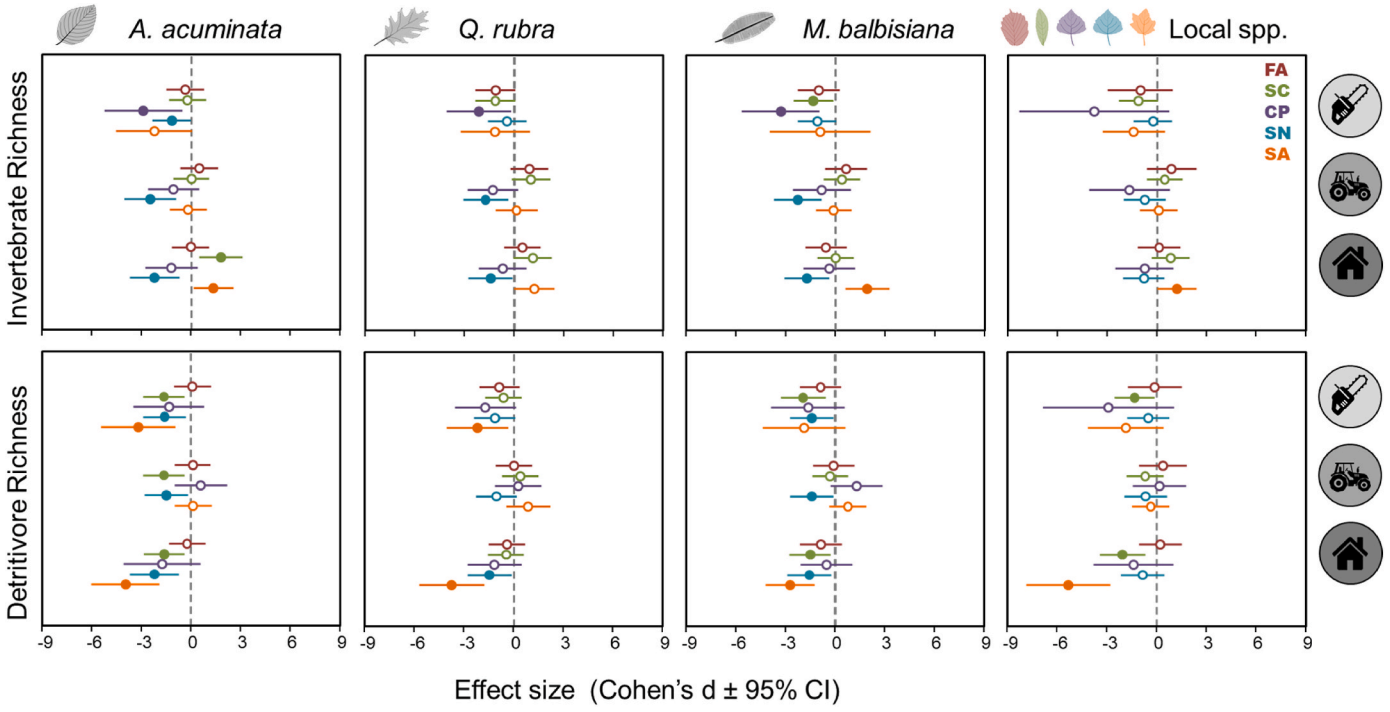


Fig. 4. Effect sizes (Cohen's d) measuring impacts of land use changes (plantation, agricultural, and urban) compared with control (native vegetation) streams, on invertebrate and detritivore taxon richness, for different regions (FA, eastern France; SC, Cantabrian coast in northern Spain; CP, central Portugal; SN Sierra Nevada mountains in southern Spain; and SA, Almería in southern Spain) and leaf litter types (*Alnus acuminata*, *Quercus rubra*, *Musa balbisiana*, and the local species *Corylus avellana* in FA, *Salix atrocinerea* in SC, *Populus nigra* in SN and CP, and *Populus alba* in SA). Empty circles indicate no significant effects, whereas filled circles indicate significant positive (> 0; higher value at impacted sites) or negative size effects (< 0; lower value at impacted sites).

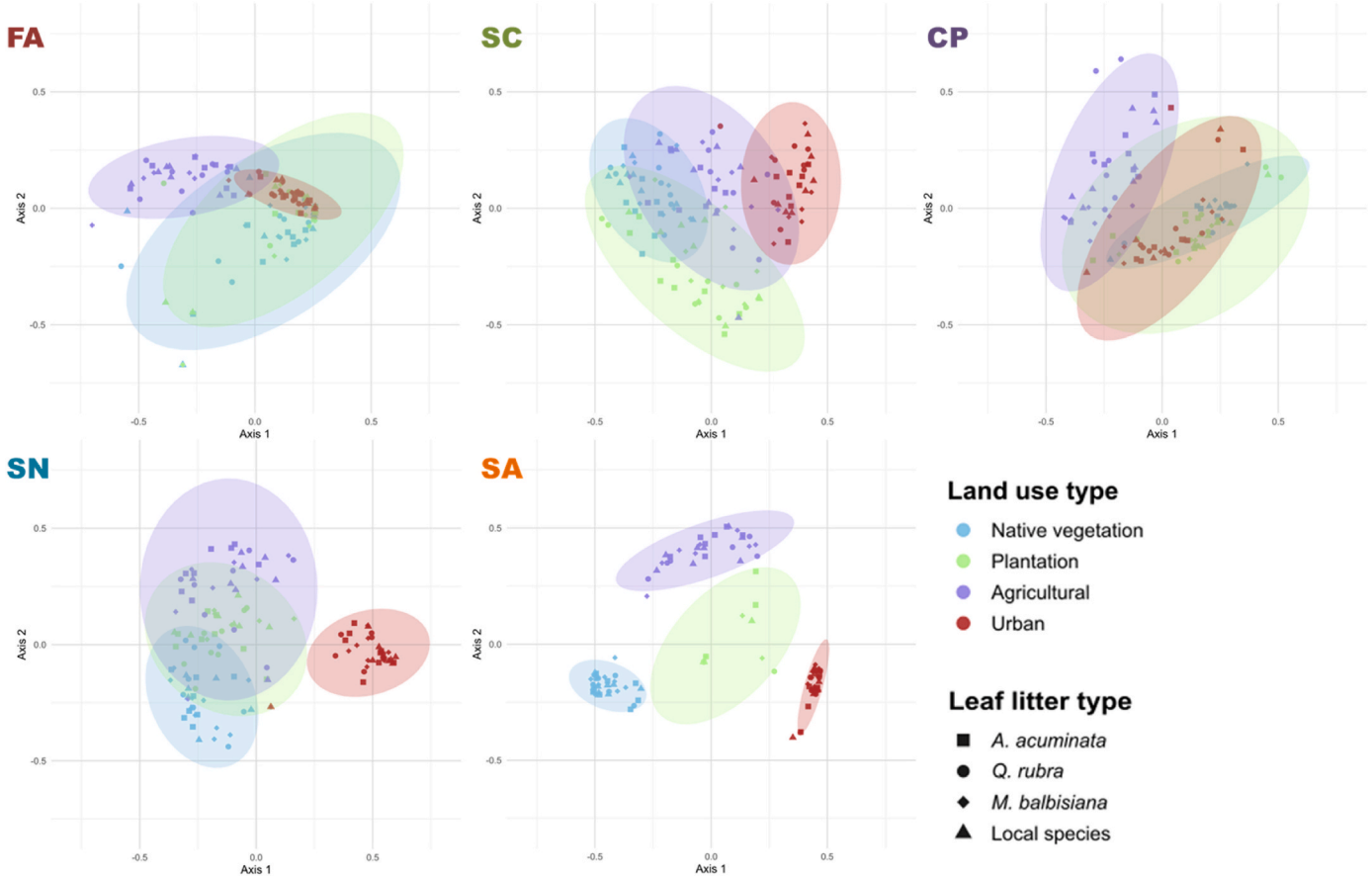


Fig. 5. Principal Coordinate Analysis (PCoA) plots of invertebrate assemblages from coarse-mesh litterbags collected from each region (FA, eastern France; SC, Cantabrian coast in northern Spain; SN, Sierra Nevada mountains in southern Spain; SA, Almería in southern Spain; and CP, central Portugal), land use type and leaf litter species (*Alnus acuminata*, *Quercus rubra*, *Musa balbisiana*, and the local species *Corylus avellana* in FA, *Salix atrocinerea* in SC, *Populus nigra* in SN and CP, and *Populus alba* in SA).

shaped by top-down control from vertebrate predators such as fish and amphibians, which can alter invertebrate abundance, foraging activity, and feeding rates both through direct consumption and through non-consumptive, risk-related effects (Preisser et al., 2005). Given that predator loss has been shown to alter stream ecosystem functioning and structure through such top-down pathways (Alonso et al., 2024), variation in predator presence across our study sites may have represented an additional, unmeasured source of variability in detritivore-mediated decomposition.

Contrary to our expectation, microbial decomposition was also reduced by land use changes, although the effect was weaker than for total decomposition. This pattern contrasts with previous studies reporting enhanced microbial activity under eutrophication (Manning et al., 2018; Rossi et al., 2019; Cornejo et al., 2020), as well as studies reporting non-detectable effects of riparian plant diversity loss (López-Rojo et al., 2019) or the replacement of native forest by plantations (Ferreira et al., 2019; Rubio-Ríos et al., 2023). Still, a recent study found a pattern similar to ours in agricultural and urban tropical streams (García et al., 2025), suggesting that some agricultural practices may exceed the pollutant levels that could be beneficial for microbial activity, or significantly enhance sedimentation, thereby increasing the toxicity on the system. An additional, often overlooked mechanism linking nutrient enrichment to microbial decomposition is the interaction between periphytic algae and litter-associated fungi. Algal growth stimulated by nutrient enrichment can itself account for mass changes independent of decomposition, sometimes resulting in null or even negative apparent mass loss, and algae can also interact with fungal decomposers both positively and negatively, stimulating or suppressing fungal activity through priming effects (Kuehn et al., 2014; Halvorson et al., 2019). Because these interactions are nutrient-dependent, incorporating periphytic algal biomass and activity in future studies could help disentangle the mechanisms underlying microbial decomposition responses to land use change. Microbial assemblages associated with leaf litter are often considered functionally redundant (Gessner et al., 2010) and more capable of species replacement than detritivores under changing environmental conditions (Fenoy et al., 2022). Nevertheless, our experimental study showed similar trends for total and microbial decomposition due to land use changes (although the latter were weaker in magnitude), suggesting that microbial activity may be impaired by anthropogenic impacts to a greater extent than normally believed. Additionally, other taxonomic groups not assessed here could further influence these processes. As said above, periphytic algae can interact with litter-associated fungi, sometimes decoupling apparent mass loss from true decomposition through priming effects modulated by nutrient availability (Rojo et al., 2025). Furthermore, other macroconsumers such as fish, amphibians, or crayfish can directly and indirectly affect decomposition through top-down effects on detritivore abundance and feeding behaviour (Ruetz et al., 2002; Carvalho et al., 2016).

4.2. *Agriculture had the greatest effects on leaf litter decomposition*

Different types of land use changes varied in the intensity of their impacts on decomposition and detritivores, but not always in the expected order. Thus, while we expected urban streams to show the highest impacts, agriculture had greater effects on both total and

microbially-mediated decomposition. Reductions in total decomposition have been reported before in agricultural catchments, largely attributed to negative effects on detritivores (Piscart et al., 2009; Cornejo et al., 2020). In our study, however, detritivore abundance and richness were less affected by agricultural land than by the other impacts, which may have been due to antagonistic effects of different stressors associated to agriculture (Cornejo et al., 2019). For example, nutrients might improve detritivore fitness at low concentrations (Woodward et al., 2012), whereas pesticides clearly impair their survival and performance (Cornejo et al., 2021). Microbial decomposition was mostly reduced at agricultural sites in our study (with the exception of Almería, discussed below), which agrees with some previous studies (Rasmussen et al., 2012; García et al., 2025), but not with others that have reported higher rates of microbial decomposition in agricultural compared to control streams (Cornejo et al., 2020). These contrasting results might be due to different characteristics of agricultural activities, with a prevalence of pesticide toxicity or sedimentation over eutrophication in some cases (Rasmussen et al., 2012) and, possibly, the opposite in others.

Our urban streams showed the greatest number of impacts on detritivores and strong effects on leaf litter decomposition. Environmental changes in urban streams often include not only pollution, but also altered thermal regimes and modified hydrology because of the increase in impervious surfaces, which are negatively related to leaf litter decomposition and detritivore numbers (Classen-Rodríguez et al., 2019). In contrast, invertebrate abundance increased in urban streams here and in other studies (Wiederkehr et al., 2020), possibly due to an overcompensating production of pollution-tolerant taxa (Friberg et al., 2010). Microbial assemblages can also be affected by urbanization, with studies reporting decreased fungal biomass (Martins et al., 2015) and changes in bacterial assemblage composition (Hosen et al., 2017), but in our study there were fewer effects of urbanization on microbial decomposition than those of other land use changes.

Our streams draining monoculture plantations showed reductions in total leaf litter decomposition, as shown elsewhere (Ferreira et al., 2016), although the number of significant effects was lower than for the other studied impacts. Importantly, the greatest effects occurred in central Portugal and the Cantabrian coast, where plantations were of *Eucalyptus globulus*, known for its toxic leaves that contain high concentrations of polyphenols and essential oils and a waxy cuticle that make them a poor resource for detritivores (Correa-Araneda et al., 2017; Ferreira et al., 2019). In contrast, the other streams flowed through conifer plantations (*Picea abies* in eastern France and *Pinus* spp. in Almería and Sierra Nevada), whose needles are also known to be a low-quality resource for detritivores (Martínez et al., 2013) but might not be toxic as *Eucalyptus* leaves. Moreover, needles could provide a more stable resource than broadleaves because they stay for longer on the streambed (Sakai et al., 2016), although this may vary across species (Ferreira et al., 2016). Nevertheless, detritivore richness was more strongly reduced in plantation than agricultural streams, suggesting that some detritivores but not others might adapt to consuming *Eucalyptus* leaves or coniferous needles, although it could also be related to the existence of deciduous trees near agricultural but not plantation streams that may be buffering its effects.

4.3. Inter-regional variability

As previously mentioned, despite a consistency of observed effects of land use changes on stream ecosystems, we found variation across regions, which could have been related to differences in environmental conditions. Thus, despite all our study regions being in southwestern Europe, they showed considerable variation in climatic conditions (Fig. 1, Table S2), and these may have a direct influence on streamflow regimes and hence stream ecological processes and assemblages (Yeste et al., 2018). For example, a striking result was the positive land use effects on decomposition found in Almería (where decomposition rates were in general very low), meaning that impacted streams showed higher rates of decomposition (both total and microbial) than the control site in this region. The fact that this pattern was found across land use changes suggests that environmental conditions at the control site may have driven exceptionally low decomposition rates, despite the absence of apparent human disturbances. For example, the control site showed very high conductivity (2535 $\mu S\,cm^{-1}$) compared to the impacted sites in this region (462–832 $\mu S\,cm^{-1}$), and extremely low flow ($<0.10\,L\,s^{-1}$), suggesting a situation of strong water limitation that could have severely limited decomposition (Monroy et al., 2016). The higher water availability in impacted streams, possibly coupled with higher nutrient inputs, could thus have resulted in a stimulation of instream processes and consequently in the positive effect sizes observed (Datry et al., 2018; Ferreira et al., 2023b).

Still, regardless of the regional differences observed, our results suggest a consistent pattern across the studied regions where natural climatic seasonality modulates the sensitivity of stream assemblages and ecosystem processes to land use changes. In our dataset, precipitation seasonality emerged as a major predictor of variation in total decomposition. This is exemplified by the contrast between France (11% seasonality), which showed high decomposition rates and no significant land use effects, and Portugal (56% seasonality), which exhibited lower rates and the strongest impacts. The consistency and biological magnitude of these negative impacts across contrasting geoclimatic regions are further supported by our forward stepwise linear models. Total decomposition was consistently predicted by precipitation seasonality and leaf micronutrients (Na, K), which together explained a substantial portion of the total variance (61%). Similarly, the reduction in detritivore richness followed a predictable pattern driven by climatic factors such as isothermality and precipitation of the driest quarter. By identifying these key environmental and trait-based drivers, our analysis demonstrates that land use effects follow consistent, non-random patterns across the studied climatic gradient. This aligns with large-scale studies that emphasize the consistency of leaf litter decomposition as a functional indicator across large spatial scales, supporting the robustness of our observed impacts despite regional variability (Woodward et al., 2012; Chauvet et al., 2016).

4.4. Responses to land use changes varied among leaf litter types

We conducted our experiment with different leaf litter types because of their potential to reflect impacts in different ways, in relation to traits that determine their proneness to be decomposed or consumed by detritivores (García-Palacios et al., 2016). In fact, the species with fastest decomposition (*P. alba* and *A. acuminata*) were also those detecting the greatest number of land use impacts. In other studies, *A. acuminata* also detected agricultural impacts on decomposition better than others (Cornejo et al., 2020; Pérez et al., 2023), as did other species of the genus such as *A. glutinosa* (Pérez et al., 2021; Rojo et al., 2025).

However, the leaf traits mostly driving decomposition in our study were not those often associated to palatability, such as N and P concentrations, SLA, or toughness (Danger et al., 2012; López-Rojo et al., 2021). Instead, they were concentrations of some micronutrients such as Na (+influence) and K (−), together explaining 28% of the model variance for total decomposition. Other studies have found micronutrients such as Mg and Ca to be major decomposition drivers, possibly through effects on microbial decomposer growth and activity (García-Palacios et al., 2016; Santonja et al., 2019). However, there is little information about Na and K, which are normally involved in osmotic regulation (Herrmann et al., 2022). *Alnus acuminata* showed the lowest K concentration among our studied species, but it also had relatively low Na concentration, so the role of these micronutrients in decomposition remains unclear.

On the other hand, microbial decomposition was mainly driven by lignin concentration (– influence), a structural trait known to limit microbial colonization and slow down decomposition (Zhang et al., 2008; Schindler and Gessner, 2009; Marks, 2019); and ash concentration (+),

which is related to mineral elements, including nutrients and micronutrients (Yang et al., 2022). Again, the mechanisms driving these relationships are unclear because species with the highest microbial decomposition rates showed either low (*P. alba*), intermediate (*M. balbisiana*) or high (*A. acuminata*) lignin concentrations, and relatively low (*A. acuminata*) or high (*P. alba* and *M. balbisiana*) ash concentrations. In this case, *A. acuminata* detected fewer land use impacts than other species, likely because increased nutrient availability reduced differences in microbial decomposition rates by disproportionately enhancing the decomposition of chemically recalcitrant litter (Marks, 2019). The commercial leaf litter type, *M. balbisiana*, although less prone to detect impacts in terms of total decomposition than *A. acuminata*, was efficient at detecting land-use effects on microbial decomposition and also reflected the reduction of detritivore richness at impaired sites, as observed elsewhere (Rojo et al., 2025).

4.5. Conclusions, study limitations, and future perspectives

Our study illustrates how globally widespread anthropogenic activities across stream catchments can substantially alter key ecosystem processes and the associated biological assemblages, even under diverse environmental conditions. Our main findings include (1) a general trend towards reduced decomposition rates, although with context-dependent exceptions; (2) a central role of invertebrates, evidenced by declines in detritivore numbers and shifts towards more tolerant species, but also of microorganisms, which are often assumed to be less sensitive to pollution and other stressors; (3) relatively consistent effects across different types of land use change, with agriculture exerting stronger pressure on decomposition and urbanization more strongly affecting detritivore assemblages; (4) the moderating influence of climatic variability, where more stable climates appear to enhance ecosystem resilience and thus reduce the magnitude of impacts; and (5) differences among leaf litter types in their ability to detect alterations, although no clear relationship with specific traits emerged. Taken together, these results reveal complex interactions among human activities, climate, and riparian vegetation that will be essential to understand for anticipating stream ecosystem responses under future global-change scenarios. Ultimately, these findings are consistent with biodiversity-ecosystem functioning (BEF) theory, showing that a greater functional diversity and redundancy within communities may buffer anthropogenic impacts on ecosystem processes. Thus, our study underscores the broader role of biodiversity in sustaining the integrity and stability of stream ecosystem functioning and structure under global-change scenarios.

While our study provides robust evidence of land-use impacts across a broad climatic gradient, some methodological limitations should be acknowledged. First, our design prioritized geographic extent and climatic diversity over within-region replication, representing each land-use category with a single representative site per region. While this approach focuses on identifying consistent large-scale patterns, we acknowledge that site-specific factors may contribute to local variability. Second, as is typical in real-world landscape studies, the land-use types examined involve complex suites of co-occurring stressors (e.g., altered hydrology and nutrient inputs); thus, our results reflect the integrated ecosystem response to these anthropogenic changes rather than the effects of isolated variables. Finally, incubation periods were adjusted to ensure comparable decomposition progress across different thermal regimes, a trade-off intended to minimize the risk of complete litter loss in warmer regions.

Despite these constraints, the robustness of our findings is supported by several rigorous methodological safeguards. We employed a high level of replication ($n = 8$ per species per site, totaling 1280 paired litterbags) and used multiple standardized substrates to ensure that the observed patterns were not specific to a single type of litter. Furthermore, the use of intra-regional comparisons through effect sizes (Cohen's d) allowed us to isolate land-use impacts from regional baseline variability; we acknowledge that degree-day-normalization is nonetheless a simplification (Pérez et al., 2011; Gessner and Peeters, 2020), but this standardization provided comparable results across a broad climatic gradient. It is precisely the combination of these measures that enables the remarkable consistency of responses across five biogeographically distinct regions, underscoring the strength of our conclusions and their relevance for understanding land-use impacts at a broad geographical scale.

Future studies addressing similar questions could further strengthen this approach through several methodological refinements. First, replicating multiple sites within each land-use type and region would enable a clearer statistical separation of broad land-use effects from site-specific variability and singularities (Ferreira et al., 2016). Second, incorporating multiple incubation periods would allow the assessment of different stages of decomposition, as the sensitivity of this process to environmental stressors may vary over time (Bärlocher, 2020). Third, including additional biological components, such as fish, biofilm or algal assemblages, would provide a more comprehensive representation of trophic interactions and ecosystem-level responses to land-use change (Medina Madariaga et al., 2024). Finally, expanding the climatic and geographic scope beyond southwestern Europe would help evaluating the generality of these patterns across a wider range of environmental context, particularly in tropical and other understudied regions where land-use impacts may follow different trajectories.

CRediT authorship contribution statement

Diana Rojo: Writing – review & editing, Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. **Javier Pérez:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Project administration, Methodology, Investigation, Data curation, Conceptualization. **Naiara López-Rojo:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation. **Alberto Alonso:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation. **Verónica Ferreira:** Writing – review & editing, Resources, Methodology, Investigation. **Juan Rubio-Ríos:** Writing – review & editing, Resources, Methodology, Investigation. **Encarnación Fenoy:** Writing – review & editing, Resources, Methodology, Investigation. **J. Jesús Casas:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition. **Juan Mateo Rivera-Pérez:** Writing – review & editing, Resources, Methodology. **Aydeé Cornejo:** Writing – review & editing, Resources. **Christopher M. Swan:** Writing – review & editing, Resources, Methodology, Funding acquisition. **Luz Boyero:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Methodology, Investigation, Funding acquisition, Formal analysis.

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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.jenvman.2026.131285.

Data availability

Data will be made available on request.

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