Leaf litter decomposition of native and introduced tree species of contrasting quality in headwater streams: How does the regional setting matter?

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HIGHLIGHTS

- We expected higher decomposition rates in regions receiving inputs of low quality.
- We expected greater evenness of decomposition among leaf species in these regions.
- Results supported the first hypothesis but not the second one.
- Caution is needed when introduced species replace native ones of higher quality.

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ABSTRACT

Terrestrial plant litter is important in sustaining stream food webs in forested headwaters. Leaf litter quality often decreases when native species are replaced by introduced species, and a lower quality of leaf litter inputs may alter litter decomposition at sites afforested with non-native species. However, since detritivore composition and resource use plasticity may depend on the prevalent litter inputs, the extent of the alteration in decomposition can vary between streams. We tested 2 hypotheses using 2 native and 3 introduced species of tree differing in quality in 4 Iberian regions with contrasting vegetational traits: 1) decomposition rates of all plant species would be higher in regions where streams normally receive litter inputs of lower rather than higher quality; 2) a higher resource-use plasticity of detritivores in regions vegetated with plants of lower litter quality will cause a greater evenness in decomposition rates among plant species compared to regions where streams normally receive higher-quality plant litter inputs. Results showed a highly consistent interspecific ranking of decomposition rates across regions driven by litter quality, and a significant regional effect. Hypothesis 1 was supported: decomposition rates of the five litter types were generally higher in streams from regions vegetated with species producing leaf litter of low quality, possibly due to the profusion of caddisfly shredders in their communities. Hypothesis 2 was not supported: the relative differences in decomposition rates among leaf litter species remained essentially unaltered across regions. Our results suggest that, even in regions where detritivores can be comparatively efficient using resources of low quality, caution is needed particularly when afforestation programs introduce plant species of lower litter quality than the native species.

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1. Introduction

The key role of headwater streams at the basin scale is emphasized in the hierarchical branching network perspective on fluvial ecosystems (Benda et al., 2004; Lowe and Likens, 2005). Headwater reaches represent over 70% of the total river length, and provide key linkages

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between stream networks and their surrounding land that might largely control the functional integrity of the whole river network (Meyer and Wallace, 2001; Gomi et al., 2002). Furthermore, headwater streams contribute disproportionately to regional biodiversity, due to their high β-diversity within and among catchments (Meyer et al., 2007; Clarke et al., 2008; Finn et al., 2011).

In many regions, headwaters drain forested catchments or are lined by gallery forests, and thus leaf litter is a major source of energy and matter for the food webs in such streams (Wallace et al., 1997; Gessner et al., 2010). Due to their small size and intimate connection to land, headwater streams are exceedingly vulnerable to changes in land use practices within their catchments (e.g. Vuori, 1996; Jackson et al., 2007). Although significant anthropogenic changes have affected headwaters only recently (in contrast to lower reaches), these changes have been so rapid and intense that Benke (1990) suggests that pristine streams are now rare.

Forestry practices, at the basin and riparian scales, are frequent sources of disturbance to headwaters. Forest plantations, although representing only 6.6% of the globally forested surface area, have expanded at a rate of 5 Mha per year during the last decade (FAO, 2010). In Europe, the size of plantations varies greatly among countries, with just 5 countries accounting for two-thirds of the area of forest plantations: Spain (2.7 Mha), UK (2.2 Mha), Portugal (0.8 Mha) and Bulgaria and France (1 Mha each). These European plantations consist of exotic or non-local native species of eucalyptus, pine, spruce and hybrids of poplar (FAO, 2010).

Riparian plantations can exacerbate impacts on headwater streams by compromising the maintenance or regeneration of buffer strips with natural vegetation. For instance, hybrids of poplar and syc-amore (i.e. *Platanus* spp.) are frequently planted in alluvial corridors, primarily for their higher resistance to diseases and herbivores, and higher growth rates, than native riparian trees (Casas and Gessner, 1999; Munné et al., 2003; Vanden-Broeck et al., 2005; Archaux and Martin, 2009).

Plantations usually include exotic species, non-local native species, or native species not naturally forming extensive pure stands (Hartley, 2002), consequently altering the timing, quantity, quality and diversity of leaf litter inputs into streams. Introduced species typically produce lower quality leaf litter (higher toughness and % lignin, and lower N contents) than that of the most common European native riparian species (such as alder, ash, willow and oak). The quality of leaf litter is a key factor controlling litter decomposition rates (Vitousek et al., 1997; Chapin, 2003; Cornwell et al., 2008), and hence, stream ecosystem functioning (Pozo et al., 1997; Graça et al., 2002; Leroy et al., 2006). Indeed, one of the main drivers of leaf-litter processing by stream invertebrates is litter quality and its stoichiometric nutrient imbalance in comparison to detritivores, regardless of the native or non-native origin of the resource (Hladyz et al., 2009).

Despite the high β-diversity of headwaters, a high degree of functional redundancy among detritivores has been suggested among catchments in temperate-humid European regions contrasting in vege-tation, which would override the effect of taxonomic compositional differences on leaf decomposition (Riipinen et al., 2010). But that might not be the case when dealing with more heterogeneous regions. For instance, Mediterranean regions are highly species diverse at multi-ple spatial scales (Blondel and Aronson, 1999), which can result in contrasting outcomes of the interactions between leaf litter quality, microbial decomposers and detritivores, even between relatively close areas (e.g. Casas et al., 2011).

Accordingly, it could be hypothesized that differences in taxonomic composition and functional capabilities of detritivores between contrast-ing regions – perhaps determined by adaptations to the quality of leaf litter inputs they normally receive (e.g. Gholz et al., 2000; Campos and González, 2009) – might cause differences in community efficiencies in the use of leaf litter of varying quality. Thus, contrasting responses to changes in resource quality among different regions might be expected.

A similar proposal might be made for microbial decomposers: for in-stance, Strickland et al. (2009) concluded that resource quality was a community-perceived trait, dependent on the quality of resource inputs that a microbial assemblage has experienced in the past.

Such ideas have recently been integrated into the SMI hypothesis (substrate quality–matrix quality interaction) (Freschet et al., 2012). This hypothesis predicts, for instance, that low-quality substrates will decompose faster than expected when incubated in a decompo-sition matrix of poor quality (e.g. ecosystems receiving low-quality inputs), and will decompose slower than expected in matrices of high-quality litters. For high-quality substrates a somewhat faster de-composition would be expected in low- than in high-quality matrices, particularly if detritivores were limited by food quality in the first resource-matrix type (high-quality food is always welcome). We expected therefore, (i) that in regions where streams normally re-ceive litter inputs of low quality, the decomposition rates of every litter species, but particularly those of low quality, would be higher than in regions with litter inputs of higher quality. Moreover, (ii) this acceleration in litter decomposition would be highest for spe-cies of low quality, causing greater evenness in breakdown rates across species differing in litter quality in regions receiving low-quality than in those receiving high-quality inputs.

We tested these hypotheses by comparing the breakdown rates of leaves of 5 tree species differing in quality, in four Iberian mountain regions with contrasting climates. We used leaf litter from two species native to the Iberian Peninsula, representing nearly the extremes of the quality range of native riparian trees in the study area (Molinero and Pozo, 2006), and from 3 non-native species of a lower quality com-monly used for plantations. We conducted our experiments in headwa-ter streams of similar size and chemistry (low aqueous mineral content and oligotrophic), but differing in riparian and/or catchment vegetation among regions.

2. Materials and methods

2.1. Study sites

The study was conducted in 12 low-order streams in the Iberian Peninsula. The streams were clustered into 4 regions, with 3 streams per region: (i) Cornisa Cantábrica [CC] in the north, (ii) Cordillera Litoral Catalana [CLC] in the northeast, (iii) Sierra de Guadarrama [SG] in the center, and (iv) Sierra Nevada [SN] in the south. All of the streams were similar in size, and flowed mainly over siliceous substrates, in catchments with sparse human settlements and activities (Table 1).

Annual precipitation and mean air temperature varied between 310 (SN) and 873 mm (CC), and 9 (SG) and 13 °C (CC and SN), respectively. The climate in CC and CLC was oceanic, while that in SG and SN was continental. Detailed information on the regional settings is given in Pozo et al. (2011).

2.2. Environmental variables

We used GIS-assisted topographic and land use maps to determine the local and mean altitudes of the upstream reach (between the exper-imental site and the source), channel slope, surface area, and % land uses of the basin drained at each experimental site. Four main land uses were differentiated across the 4 regions: native forests, native scrubland, forest plantations, and farming/ranching. The mean channel width (bank full) was determined in situ from 6 measurements.

At each experimental site, we characterized the riparian vegetation along a 50 m stream reach on 5 randomly selected belt-transects (10 m long × 1 m wide), perpendicular to the stream course and extending across both sides of the channel. We determined the total taxon richness and the density of woody species (trees and shrubs). Tree canopy cover was estimated using a spherical densiometer

Table 1
Basin, riparian and water quality characteristics of streams (n = 3 per region) in four regions of the Iberian Peninsula. Data given for each variable are mean, followed by the range in parentheses.

Parameters	Regions			
	Cordillera Cantábrica	Cordillera Litoral Catalana	Sierra de Guadarrama	Sierra Nevada
Local altitude (m asl)	378 (315–420)	508 (446–562)	1294 (1240–1322)	1431 (1403–1489)
Mean altitude (m asl)	557 (458–620)	863 (790–900)	1466 (1450–1500)	1927 (1854–2007)
Drainage area (ha)	314 (225–361)	838 (530–1260)	277 (98–419)	886 (167–1428)
Channel slope (%)	16.0 (13.3–20.5)	20.6 (13.3–33.9)	18.3 (11.9–31.0)	20.0 (18.3–20.9)
Channel width (m)	3.5 (3.3–3.7)	6.0 (4.9–7.1)	3.3 (1.7–5.1)	2.5 (2.2–3.3)
Land uses (%)				
Native forests	92.53 (90.3–94.6)	83.3 (74.4–90.5)	23.1 (11.3–33.9)	4.2 (0–12.5)
Native scrublands	5.8 (2.8–9.4)	5.0 (2.4–8.3)	44.9 (26.5–66.7)	23.0 (1.6–46.5)
Farming/ranching	0	11.7 (7.1–17.3)	5.3 (2.6–9.4)	0
Forest plantations	1.7 (0.3–2.6)	0	23.0 (19.3–30.2)	72.8 (53.5–98.4)
Riparian vegetation				
Tree canopy cover (%)	49.3 (42.2–55.0)	76.1 (60.0–88.7)	77.2 (56.77–94.58)	78.3 (72.3–86.7)
Richness of woody species	4.3 (2–6)	6.0 (6–6)	2.7 (2–3)	5.0 (5–5)
Density (indiv. m^{-2})				
Alnus glutinosa	0.08 (0–0.22)	0.14 (0.04–0.31)	0	0.12 (0.08–0.18)
Buxus sempervirens	0	0.20 (0–0.50)	0	0
Corylus avellana	0.05 (0–0.16)	0.02 (0–0.06)	0	0
Crataegus sp.	0.10 (0.02–0.17)	0	0	0
Fagus sylvatica	0.07 (0–0.16)	0	0	0
Ilex aquifolium	0	0.04 (0–0.09)	0	0
Quercus ilex	0	0.06 (0–0.17)	0	0.001 (0–0.003)
Quercus pyrenaica	0	0	0.08 (0.04–0.10)	0
Salix spp.	0.01 (0–0.03)	0.02 (0–0.04)	0.05 (0.01–0.09)	0.04 (0.02–0.07)
Total density	0.34 (0.18–0.61)	0.50 (0.28–0.89)	0.12 (0.05–0.16)	0.18 (0.16–0.21)
Aquatic environment				
Discharge (L s^{-1})	87 (50–128)	35 (26–49)	51 (22–78)	390 (221–560)
Mean temperature (°C)	6.4 (5.9–6.9)	6.3 (5.7–6.9)	4.7 (3.9–6.3)	5.2 (4.8–5.3)
pH	7.31 (7.07–7.62)	7.33 (7.11–7.51)	6.67 (6.32–7.14)	7.13 (6.80–7.32)
Conductivity (μS cm^{-1})	133 (109–164)	191 (142–233)	91 (48–138)	52 (40–71)
Alkalinity (meq L^{-1})	0.69 (0.35–1.13)	1.52 (1.12–1.90)	0.24 (0.12–0.46)	0.44 (0.37–0.51)
NO$_3$–N (μg L^{-1})	231 (3–627)	294 (207–455)	612 (505–680)	457 (398–565)
NO$_2$–N (μg L^{-1})	0.8 (0.6–1.1)	0.7 (0.6–0.8)	5.4 (5.0–6.2)	0.6 (0.5–0.6)
NH$_4$–N (μg L^{-1})	26 (25–27)	6 (4–8)	10 (6–15)	<1
PO$_4$–P (μg L^{-1})	16 (15–19)	15 (9–23)	14 (10–22)	9 (2–12)
DO (mg O$_2$ L^{-1})	12 (11–13)	12 (12–13)	11 (10–11)	10 (10–10)
DO (%)	104 (98–111)	100 (97–102)	99 (95–101)	98 (97–98)

(Model-A, Forestry Suppliers Inc., Jackson, MS, USA), as the mean of readings at 6 randomly selected points per stream reach.

During the study period of autumn–winter 2009–2010, we recorded 10 water quality parameters. Water temperature was recorded hourly with HOBO Pendant (Onset Computer Corporation, Bourne, MA, USA) or ACR Smart-Button (ACR Systems Inc., Surrey, British Columbia, Canada) temperature loggers. The following physical and chemical variables were measured three times over the course of the experiment. Electric conductivity (EC), pH and dissolved oxygen (DO) were measured with multiparametric sensors (WTW®, Weilheim, Germany; HACH® model HQ-30d, USA). Discharge was estimated from instantaneous records of mean water velocity (current-meters: FP311, Global Water, Gold River, CA, USA; SEBA M1 Kaufbeuren, Germany) obtained in a regular stream cross section of known area at each experimental site. For alkalinity and nutrient analyses, water was sampled and filtered through pre-ashed glass fiber filters (Whatman GF/F, Maidstone, UK). Alkalinity was determined by titration to a pH endpoint of 4.5 (APHA, 2005). NO$_3$–N concentration was determined by the sodium salicylate method (Monteiro et al., 2003) or by capillary ion electrophoresis (Agilent CE, Santa Clara, CA, USA), NH$_4$–N by the manual salicylate method (Krom, 1980), NO$_2$–N by the sulphanylamide method, and soluble reactive phosphorus (SRP) by the molybdate method (APHA, 2005).

2.3. Leaf litter decomposition experiment

We studied leaf litter decomposition of five species of tree with contrasting leaf quality, 2 species native to the Iberian Peninsula, alder (*Alnus glutinosa* L. (Gaertn)) and oak (*Quercus pyrenaica* Wild), and 3 introduced species, pine (*Pinus radiata* D. Don.), sycamore (*Platanus hispanica* Mill. ex Münchh.), and poplar (*Populus x canadensis* Moench). To obviate the effect of local differences in the initial intra-species leaf quality, all leaves of each species were collected at a single location: alder and pine in CC, oak in SG, sycamore in CLC, and poplar in SN.

Leaves were collected in autumn 2009 just after abscission (except for pine needles, which were collected from dry branches), air-dried to constant weight, distributed among the four regions and stored until needed. Portions of 5.0 ± 0.25 g were weighed, moistened until pliable and inserted into mesh bags (15 × 25 cm, 5 mm mesh). To prevent accidental losses, pine needles were grouped into tied packs weighing 1 g. Leaf bags, 5 per leaf species and stream, were submerged and tied with nylon lines to iron bars driven into the streambed in 5 riffle sections along 50-m stream reaches. The bags were pooled into 5 sets, each composed of 5 bags of different species. An extra set of five bags per species was submerged for 24 h (T$_1$) in the most oligotrophic stream of each region to correct initial mass values for leaching (Gessner et al., 1999). Leaf submersion in the streams was initiated on 23 November 2009.

Leaf litter bags at each site were retrieved on dates that corresponded to approximately 50% (T$_{50}$) initial mass loss of alder (range 26–66 days, depending on the stream), as estimated in a parallel experiment. Thus the experiment was terminated at about the same stage of litter decomposition in each region. The initial mass was considered to be the initial ash-free dry mass (AFDM) corrected for leaching. After retrieval, litter bags were placed individually in zip-lock bags and transported in refrigerated containers to the laboratory, where they were immediately processed.

The leaf material was rinsed with filtered stream water, and the fauna was collected on a 0.5 mm sieve and preserved in 70% ethanol for later analyses. Macroinvertebrates were identified to family level with a dissecting microscope, counted, and sorted into functional feeding groups (FFG) according to Merritt and Cummins (1996) and Tachet et al. (2002). Individuals within each FFG were dried at 70 °C to constant weight (72 h) to determine dry biomass. The remaining material in each litter bag was oven-dried (70 °C, 72 h), weighed, a portion used for nutrient analyses, and the rest incinerated (550 °C, 4 h) to determine the remaining AFDM. These data were expressed as % leaf mass loss (%LML), per day or degree-day, of the initial AFDM.

2.4. Quality measurements of leaf litter

The toughness of 12 leaves per plant species was measured on leached material, as a trait of their initial quality, using a calibrated texturometer (TA.XT2 Plus, Stable Micro Systems, London, UK). A constant needle tip surface area (0.38 mm^2) was used throughout all measurements, thus differences in toughness were expressed in units of mass (g).

After leaching, portions (n = 3 per species, ~450 mg each) of leaf litter were dried (70 °C, 72 h) and ground to pass through a 0.25 mm pore sieve to measure acid detergent lignin (ADL) concentration by means of an ANKOM 200/220 fiber analyzer (ANKOM Technologies, Macedon, NY, USA). Lignin was estimated gravimetrically, as % leaf dry mass, by subtracting ash content (combustion at 550 °C, 3 h) of the remaining sample following ADL extraction.

Portions of leaf material, after leaching (n = 5 per species and region) and at T_{50} (n = 15), were ground to a fine powder (to pass through a 1 mm pore sieve) for determining nutrient concentration. Carbon (C) and nitrogen (N) were determined with a Perkin Elmer series II CHNS/O elemental analyser. Phosphorus (P) was determined spectrophotometrically after a mixed acid digestion (the molybdenum blue method, Allen et al., 1974). Results were expressed as %C, %N and %P of leaf dry mass. For bags retrieved at T_{50}, the N and P concentrations were expressed as the difference between the final (T_{50}) and initial (after leaching) percentages, which was taken as a proxy of nutrient change caused by microbial colonization.

2.5. Data analysis

To compare environmental distance among streams from the four regions, a similarity matrix was computed using the Bray–Curtis metric with basin or local-scale (riparian and water chemistry) variables, after $\ln(x + 1)$ or $\arcsin\sqrt{x}$ (for %) transformation for normalization. To visualize intra- and inter-regional distances among streams, a Principal Coordinate Analysis (PCoA) was performed on the similarity matrix, using PRIMER v6.0. (Clarke and Gorley, 2006). The significance of differences of intra- and inter-regional Bray–Curtis mean distances was determined using t-tests, both for the complete data set and for pair-wise comparisons. Similarity percentages were arcsin-transformed prior to these analyses.

Five parameters of the initial quality of leaf litter after leaching, ((i) leaf toughness, (ii) % lignin, (iii) % C, (iv) % N and (v) % P), were compared among species using one-way ANOVA and Tukey test for post-hoc pair-wise comparisons. Transformations were required for each variable: $\ln(x + 1)$ for toughness, and $\arcsin \sqrt{x}$ for %.

We carried out mixed, partially nested, analyses of variance (ANOVA) to assess the relative importance of leaf species, region and stream on the variability of leaf mass loss (%LML per day or degree-day), and on the variables involved in the process (N and P changes, density, biomass and taxon richness of total invertebrates and shredders) obtained on T_{50}. These analyses were initially performed for the entire data set (comprehensive model), using leaf species and region as fixed factors, with stream treated as a random factor nested within region. Data used for the comprehensive

models were examined for normality and homogeneity of variances and were found to be suitable for applying parametric tests. A Principal Component Analysis (PCA) was performed to illustrate the results of the ANOVAs, using as input data the % variance explained by different independent factors.

Subsequently, we tested separately for each leaf litter species (simpler component sub-models of the comprehensive models), the effects of region and stream on (i) %LML (per d^{-1} or d d^{-1}), (ii) shredder biomass (log [x + 1] transformed), and (iii) the relative leaf N change (the best predictors of %LML, see below), using mixed nested ANOVA, with region as a fixed factor and stream as a random factor nested within region. When significant differences were observed, post-hoc Tukey tests were used for pair-wise comparisons among species and regions in the comprehensive model, and among regions in component submodels.

Multiple regression models were carried out to explore the trends across and within regions in %LML d^{-1} (dependent variable) of all species pooled, and separately by species, and its dependence on invertebrate variables and relative N and P changes in leaf litter (predictor variables). Pearson correlations were calculated between predictor variables to check their co-linearity. Within highly correlated ($r > 0.70$) predictor pairs, we selected only the one with the higher functional meaning. Therefore, biomass and richness of total invertebrates were discarded because they were highly correlated with the more functionally meaningful predictors of shredder biomass and shredder richness ($r = 0.71$ and 0.75, respectively). For each dependent variable, the best subset of fitted models was initially selected using the Akaike information criterion (AIC). The model with the highest adjusted r^2 value was finally selected among models with Δ AIC < 2 (Burnham and Anderson, 2002), and with a significant ($P < 0.05$) likelihood ratio Chi^2.

We calculated the evenness of %LML d^{-1} across the five leaf species for each region (mean of the 3 streams per region) by means of the Simpson evenness index ($E_{1/D}$; Beisel et al., 2003). This was used to compare evenness of leaf litter decomposition across the range of litter quality among regions, using one-way ANOVA.

We tested the influence of dissolved nutrients (mean of 3 measures of DIN and SRP per stream) on the relative N and P change of leaf litter by ANCOVA, separately for each nutrient. Stream water nutrient concentration (Log-transformed) was included as the covariate, and region and leaf species as factors. This analysis was conducted for each leaf species separately, with region as factor and nutrient level as covariate. ANOVA, ANCOVA, multiple regression and correlation analyses were performed using Statistica (version 7.0; StatSoft, Tulsa, OK, USA).

To visualize macroinvertebrate assemblage-wide responses to treatments (leaf species, region and stream[region]), using both density data of taxa (60 taxa overall) and functional feeding groups (5 groups overall), we used a non-metric multidimensional scaling (NMDS) ordination method based on the Bray–Curtis distance measure. To omit noise caused by rare taxa and the overwhelming effect of very abundant taxa, density data were standardized by relativization to the maximum (Noy-Meir et al., 1975), and 14 rare taxa (found in <5% bags) were removed from the taxonomic data set prior to analyses.

To determine whether significant differences in assemblage composition occurred among regions, streams nested within regions, and among leaf species across and within regions, we used the analysis of similarities test (ANOSIM). The number of Monte Carlo permutations was set at 9999. When global rho (R) was statistically significant ($P < 0.05$), pair-wise ANOSIM comparisons between regions and leaf species were performed to distinguish possibly contrasting effects. The multivariate similarity percentages procedure (SIMPER) was then applied to determine which taxa or FFG contributed most to the observed differences in multivariate community structure between these pairs of regions or leaf species showing significant R. The NMDS, ANOSIM and SIMPER analyses were conducted using PRIMER v6.0. (Clarke and Gorley, 2006).

3. Results

3.1. Regional environmental settings

The environmental characteristics of the streams differed greatly among the four regions (Table 1). The first factorial plane of the PCoA explained 72% of the total inertia (Fig. 1). The first axis (52.5% of total inertia) strongly separated CC and CLC streams (both characterized by low altitude, high EC, and a relatively high % of deciduous or mixed native forest in their basin) from SN streams, which were primarily associated with high altitudes and with basins with abundant pine plantations (mostly *Pinus sylvestris* L.). The second axis (19.7% of total inertia) separated SG streams from other regions mainly due to its riparian vegetation dominated by oak (*Quercus pyrenaica* Willd.) vs. a general dominance of alder and/or willow species in the other regions (Table 1).

Overall, the mean intra-regional environmental Bray–Curtis similarity (streams within a region) (0.95 ± 0.05 SE) was significantly greater than the inter-regional one (streams among regions) (0.89 ± 0.03 SE) ($t = 8.0$, d.f. = 64, $P < 0.0001$). Furthermore, most pair-wise comparisons showed a significantly higher ($P < 0.001$) environmental similarity of streams within than among regions (the exception was the comparison within CC vs. between CC-CLC ($t = 2.2$, d.f. = 10, $P = 0.051$)).

3.2. Initial leaf litter quality

The five species spanned a wide range of initial quality (Table 2), particularly for toughness and nutrient content (N and P), which varied over a 3- and 5-fold range, respectively. The native species alder and oak showed lower toughness and % lignin, and higher N and P contents, compared to the introduced poplar, sycamore and pine species. However, differences were not statistically significant for % lignin among alder, oak and poplar; for N among oak, poplar and sycamore; nor for P between oak and poplar (Tukey tests, $P > 0.05$; Table 2). Generally, sycamore and pine showed the poorest initial quality.

3.3. Leaf litter decomposition and potential biotic predictors across and within regions

Decomposition was strongly dependent on species, with this factor explaining approximately 65% of the total variability of percent leaf
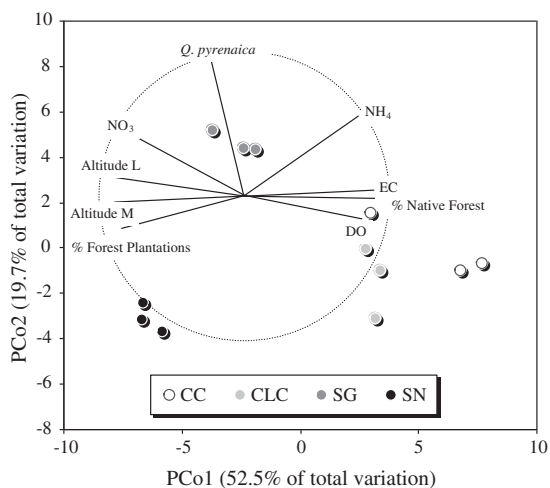

Fig. 1. Projection of the first factorial plane of PCoA showing environmental distance among streams of the 4 regions studied based on a Bray–Curtis similarity matrix. Vector overlay represents environmental variables with Pearson correlation over 0.8 ($P < 0.01$) on any of the two coordinate axes. The circle is a unit circle (radius = 1). CC, Cordillera Cantábrica; CLC, Cordillera Litoral Catalana; SG, Sierra de Guadarrama; SN, Sierra Nevada.

mass loss per day (%LML d^{-1}) (Fig. 2), and with a highly significant effect ($F_{4,32} = 79.96$, $P < 0.001$). Similar results were obtained when decomposition was expressed as % LML d d^{-1} (data not shown). Overall, the higher the initial leaf quality the higher the decomposition rate was. Thus, the % LML d^{-1} of alder was the fastest (1.22 ± 0.15 SE), followed by poplar (0.98 ± 0.07 SE), oak (0.77 ± 0.05 SE), pine (0.29 ± 0.07 SE) and sycamore (0.26 ± 0.04 SE), with statistically significant differences ($P < 0.05$) in all pair-wise comparisons except between the last two species.

Region explained a low, but still statistically significant, proportion (7.3%) of the total %LML d^{-1} variability (nested ANOVA: $F_{3,8} = 6.13$, $P = 0.018$; post-hoc Tukey tests: SG > SN > CLC = CC) (Fig. 2). The magnitude of regional differences in decomposition was species-dependent (Fig. 3). The general pattern of differences among species was essentially the same for all regions ($P > 0.05$ for region × species interaction in the comprehensive model (Fig. 2)), but not for all streams ($P < 0.001$ for stream (region) × species interaction) (Fig. 2). The highest evenness of decomposition among species (%LML d^{-1}) was recorded in SN (0.796 ± 0.027 SE), followed by SG (0.762 ± 0.015 SE), CLC (0.757 ± 0.010 SE) and CC (0.744 ± 0.025 SE), though differences among regions were not statistically significant ($F_3 = 2.34$, $P = 0.146$).

Species explained a high proportion of total variability of the relative N and P changes in the leaf litter, with highly significant effects on both nutrients ($F_{4,32} = 27.67$; $F_{4,32} = 17.62$; respectively, both $P < 0.001$) (Fig. 2). All species showed a net N enrichment, the magnitude of which was dependent on their initial quality: the highest for alder (0.53 ± 0.26%), which was significantly different (Tukey tests, $P < 0.05$) from the intermediate values for poplar and oak (0.40 ± 0.21% and 0.35 ± 0.25%, respectively), which in turn were significantly higher than the lowest values registered for sycamore and pine (0.12 ± 0.17% and 0.06 ± 0.08%, respectively). Conversely, a net P loss (range −0.0083% to −0.0008%) was detected for species with a higher initial P content (alder, oak and poplar) compared to the species with a low initial P content (sycamore and pine), in which there was a slight P gain (0.0018% and 0.0004%, respectively) (Tukey tests; alder = oak = poplar < sycamore = pine).

The stream (region) factor, but not region, and the interaction stream (region) × species had significant effects on the relative change of both nutrients (this was contrary to their effects on the %LML) (Fig. 2). For instance, the relative N change was significantly affected by region only in pine (component submodel), while there was a high intra-regional among-stream variability in the other species (Fig. 3). This variability could have been caused by differential availability, in the water, of nutrients for microbial activity; indeed, the relative N change was significantly and positively related to water DIN concentration (ANCOVA considering all species and regions, and fitting nutrients in the water as covariate: $F_{1,38} = 12.55$, $P = 0.001$). This overall trend also occurred for alder, oak and sycamore, when a similar analysis was performed for each leaf species separately. However, similar analysis for P (fitting SRP as a covariate this time) showed no significant relationship between relative leaf P change and aqueous phosphorus availability, whether all leaf species were considered together ($F_{1,38} = 0.91$, $P > 0.05$) or separately.

The variation of invertebrate parameters, particularly biomass, was much less dependent on leaf species than on region (Fig. 2). Total invertebrate and shredder biomass showed the highest unexplained variation; with only region explaining a moderate, but significant, % of their total variability ($F_{3,8} = 19.02$, $P < 0.001$ and $F_{3,8} = 11.13$, $P < 0.01$, respectively) (Fig. 2). The highest mean values of total invertebrate biomass were in SN (53 mg bag^{-1}) and CLC (37 mg bag^{-1}), and the lowest were in SG (14 mg bag^{-1}) and CC (13 mg bag^{-1}), with statistically significant differences in all pair-wise comparisons between regions. The mean shredder biomass in SN (35 mg bag^{-1}) was significantly higher than that of all other regions (range 6–11 mg bag^{-1}), particularly in oak and pine bags (component submodels) (Fig. 3).

Table 2
Mean values ($\pm$ 1SE) of five quality variables of leaf litter (initial after leaching) for five species of tree. n = sample size per species. For each quality parameter, different superscript letters indicate significant differences ($P < 0.05$) after ANOVA followed by post-hoc pair-wise comparisons using Tukey tests. F values: *** $P < 0.001$.

Quality parameter	Native species		Introduced species			n	F value (ANOVA)
	Alder	Oak	Poplar	Sycamore	Pine		
Toughness (g)	54.2 ± 5.4^d	66.3 ± 12.1^c	81.9 ± 6.8^b	94.7 ± 19.4^b	146.9 ± 24.5^a	12	87.8***
% lignin	17.4 ± 1.2^b	17.2 ± 0.3^b	20.8 ± 2.1^b	40.0 ± 3.0^a	36.2 ± 2.1^a	3	35.4***
% C	51.19 ± 1.13^a	46.11 ± 0.22^c	44.60 ± 0.64^d	49.11 ± 0.75^b	51.23 ± 1.66^a	20	70.1***
% N	3.32 ± 0.25^a	0.83 ± 0.08^b	0.74 ± 0.01^b	0.78 ± 0.04^b	0.63 ± 0.06^c	20	1223.9***
% P	0.052 ± 0.012^a	0.025 ± 0.016^b	0.024 ± 0.010^b	0.012 ± 0.004^c	0.011 ± 0.006^c	20	31.7***

A higher % of the total variability in density (total density and shredder density), than in biomass, was explained by the factors studied, with significant effects of stream (region) and species, but not region (Fig. 2). Generally, total invertebrate and shredder densities responded positively to leaf litter quality, with significantly higher numbers (post-hoc Tukey tests, $P < 0.05$) in bags with native species (oak or alder, 85 and 70 individuals bag^{-1}, respectively), than in bags with introduced species, poplar (59 individuals bag^{-1}), sycamore and pine
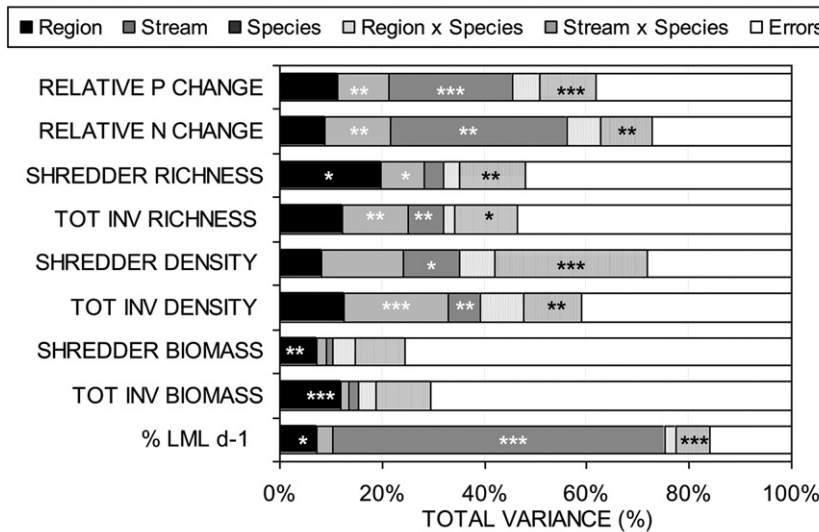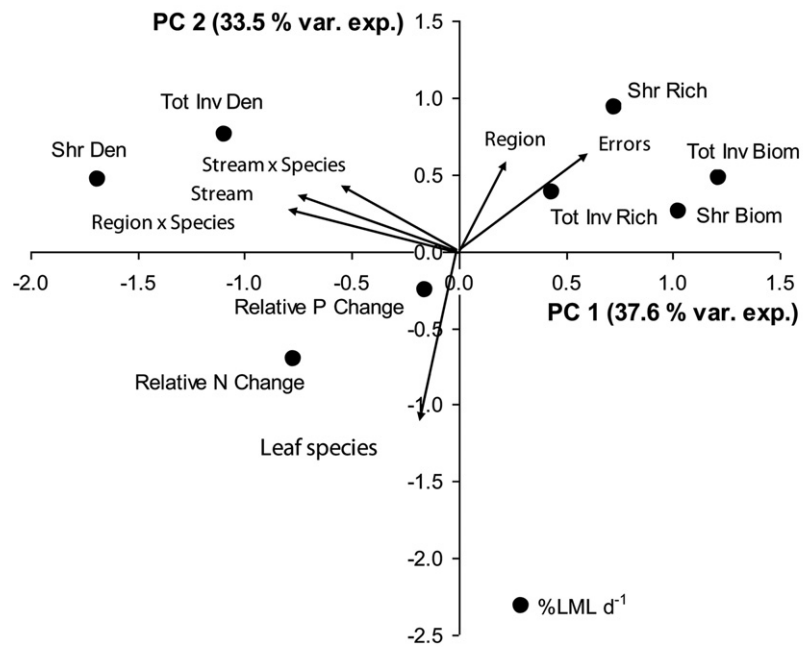

Fig. 2. Results of a PCA (upper panel) based on the % of total variance explained by independent factors (arrows)–region, stream nested within region, leaf species, interactions region × species and stream(region) × species, and errors–using mixed partially nested ANOVAs for % leaf mass loss (%LML d^{-1}) and other dependent variables (dots) involved in the process. Percentages of total variance explained by each independent factor are given for each dependent variable (lower panel): Levels of significance, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.
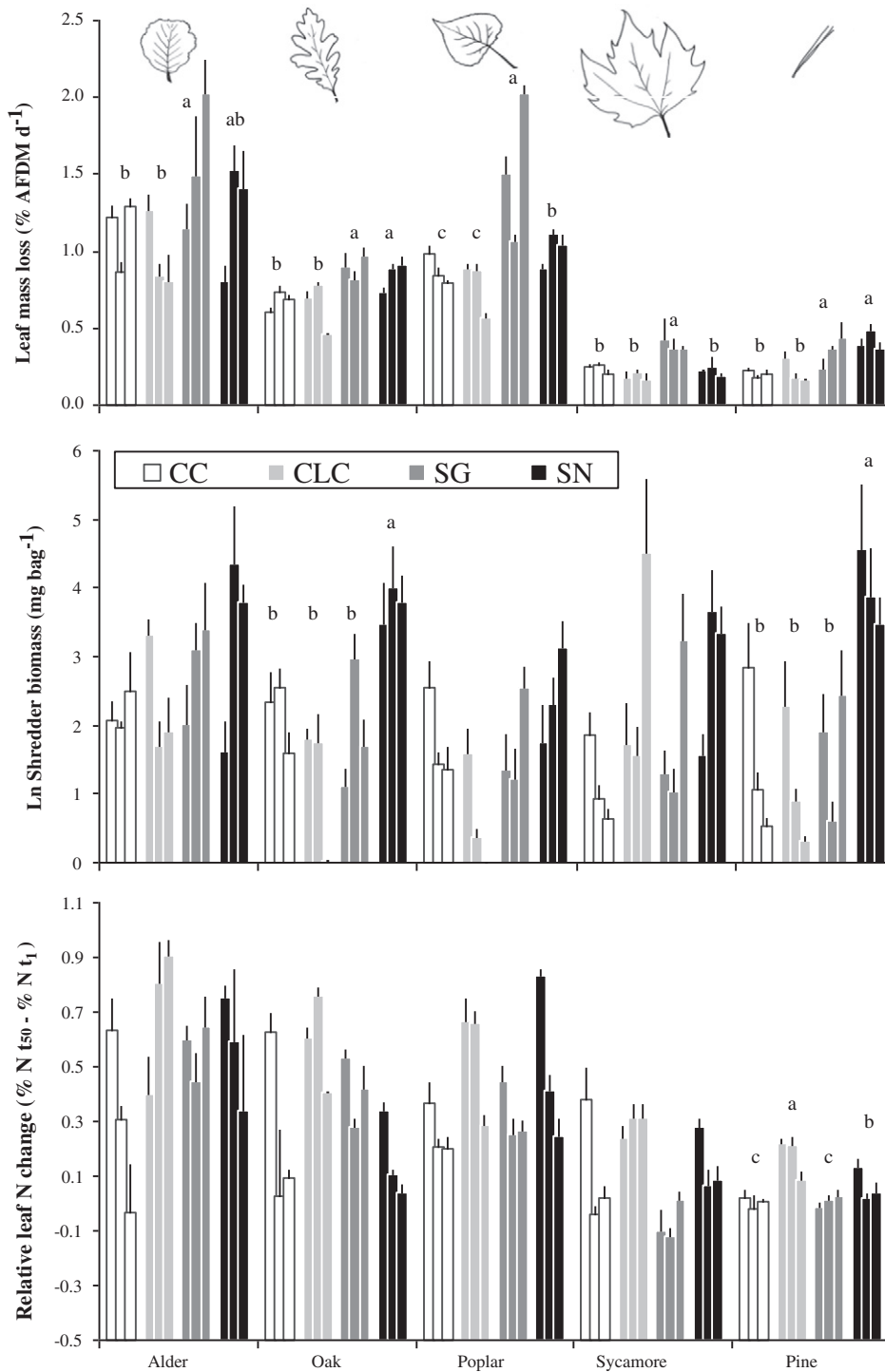
Fig. 3. Results (mean + SE) of %LML d^{-1}, relative N change of leaf litter, and shredder biomass bag^{-1} in each of the 3 streams studied per region. Streams are clustered in each one of the 4 studied regions. Results are presented separately for each of the 5 leaf litter species assayed. A different letter indicates statistically significant differences after mixed nested ANOVA, separately for each species, and post-hoc pairwise comparisons among regions using Tukey tests. The absence of a letter indicates no significant regional effect for the corresponding variable and species.

(44 and 39 ind. bag^{-1}, respectively). Stream (region) and the interaction stream (region) × species generally explained the highest % variation in density data (Fig. 2).

Stream (region) and the interaction stream (region) × species significantly affected taxon richness of both total invertebrates and shredders; but contrasting results were observed for other factors (Fig. 2). Total richness significantly depended on species but not on region, with bags containing oak having – on average – richer assemblages (10.1 taxa bag^{-1}) than did bags containing other tree species

(range 7.7–8.1 taxa bag^{-1}) (Tukey tests; $P < 0.05$). In contrast, the shredder richness was significantly affected by region, but not by species, with SN and CC having higher mean values (3.3 and 3.2 taxa bag^{-1}, respectively) than did SG (2.4 taxa bag^{-1}) and CLC (1.6 taxa bag^{-1}) (Tukey tests, $P < 0.05$).

Multiple-regression models when all species were pooled revealed that the best biotic predictors of %LML were the relative changes in N and P, which were in turn highly dependent on their initial quality. The minor contribution to the regression models, statistically significant, of

shredder biomass, tended to decrease or vanish when each region was considered separately (Table 3).

When species were analyzed separately, overall and by regions, there was a loss of explanatory power of the biotic predictors of leaf decomposition (%LML) with decreasing initial quality of leaf litter (Table 3). However, differences among regions and plant species are worthy of mention. (i) In SG, the region with the highest values of %LML, no significant model was obtained except for poplar (see below). (ii) In most regions, the decomposition of alder was related positively to shredder biomass and negatively to relative N change (Table 3), suggesting that shredder consumption was strong enough to mask or even reverse the expected relationship between microbial effects (i.e. N enrichment) and %LML. (iii) In oak, shredder biomass in CLC and total invertebrate density in SN, were positively related with %LML; and relative N and P changes were negatively related to %LML in CC and SN respectively, but this relationship was positive to N in CLC. (iv) For poplar, N change was positively related to %LML in all regions, suggesting that decomposition in this species was more substantially driven by microbial activity rather than is the case in alder and oak. (v) Shredder biomass or density contributed positively to %LML of poplar in CC, CLC and SN, but not in SG. (vi) The effect of biotic action on % LML was weak or nil for pine and sycamore, the two species of poorest quality (Table 3).

3.4. Responses of invertebrate assemblage composition to leaf litter species, stream and region

The NMDS ordination based on density data of invertebrate taxa and functional feeding groups (FFG) (Appendix A) provided interpretable two-dimensional ordinations of leaf bags (Fig. 4). Both the taxonomic and FFG composition of the invertebrate assemblages differed significantly among regions (ANOSIM: Global $R = 0.53$ and 0.45 respectively, $P < 0.001$). Streams nested within region (Global $R = 0.20$ and 0.22, respectively), and leaf litter species across regions (Global $R = 0.02$ and 0.01, respectively) showed no significant effects (all $P > 0.05$) on assemblage composition.

Pair-wise comparisons between regions showed that CC and SN were taxonomically well separated from each other (R ranging between 0.99 and 0.74) and from other regions (R ranging between 0.74 and 0.59) (all $P < 0.001$), in contrast to the high taxonomic overlap between CLC and SG ($R = 0.11$, $P > 0.05$). A similar pattern of pair-wise regional differences was detected for FFG, with the exception of the pair CC-SN, which were not separated functionally, even though distinctly separated taxonomically ($R = 0.22$, $P > 0.05$; $R = 0.74$, $P < 0.001$; respectively) (Fig. 4).

Comparison of invertebrate assemblages among leaf litter species within each region also reflects the weak effects of plant species on taxonomic and FFG composition, with all global $R < 0.1$, except for taxa in CC (with a Global $R = 0.26$, which was slightly over the threshold of interpretable differences). In CC, pair-wise comparisons among leaf species showed that only alder was colonized by taxonomically distinctive assemblages compared to other species (alder vs. other species: R range 0.50–0.56, all $P < 0.001$; pair-wise comparison among other species: R range 0.00–0.19, all $P > 0.05$).

Shredder taxa as a whole contributed mostly to regional pair-wise dissimilarity (Table 4). The population densities of Leuctridae, Nemouridae and total shredders were notably higher in CC and SN compared to CLC and SG (Table 3). Overall, stonefly shredders were more abundant in CC

Table 3

Multiple-regression models for the overall dataset (all regions together) and for each of the four regions, for the five leaf species assayed, testing the contribution of different predictor variables (regarding colonizing invertebrates and in-stream nutrient changes of leaf litter) to the % leaf mass loss per day. For each leaf species and data set, the table shows the model with the highest r^2 value adjusted within the best subset of models with ΔAIC < 2 and significant likelihood ratio Chi^2. The standardized regression coefficient (beta) is shown for each variable entering the model to evaluate its relative importance. Empty cells in the table indicate that the predictor was not included in the model. Missing lines for leaf species in a given region indicate that no significant model was found.

Region and species	Shredders			Total invertebrate density	Relative leaf nutrient change[a]		AIC	Likelihood ratio Chi^2	r^2 adj.
	Biomass	Richness	Density		N	P			
All regions									
All species	0.20***				0.32***	−0.32***	324.22	84.33***	0.26***
Alder	0.32*	0.32*	0.24		−0.30*		74.16	24.53***	0.27***
Oak	0.45**					0.18	−46.59	10.42**	0.14**
Poplar	0.34**			−0.19	0.26*		2.53	11.70**	0.14*
Pine	0.42**		−0.24				−61.88	8.50*	0.12*
CC									
All species	0.22				0.16	−0.35**	48.28	28.90***	0.27***
Alder	0.78**				−0.42*	0.73*	−53.43	7.85*	0.28[b]
Oak			0.15		−0.56*		−29.20	8.47*	0.30*
Poplar	0.72**				0.40*		−26.26	14.05***	0.53**
CLC									
All species	0.15				0.54***	−0.41***	23.85	45.01***	0.53***
Alder	0.33*				−0.57*		3.48	11.99**	0.46**
Oak	0.56***		−1.01**	0.33*	1.09***	0.21	−47.98	45.88***	0.94***
Poplar		0.32	0.61**		0.60**		−19.15	15.36**	0.58**
Pine		0.52*			0.47*	0.22	−31.57	13.38**	0.38*
SG									
All species				0.19*	0.59***		100.69	38.44***	0.41***
Poplar					0.70**	0.29	−5.76	11.65**	0.48**
SN									
All species					0.13	−0.66***	55.97	42.43***	0.42***
Alder	0.66**		−0.49*		−0.37*	−0.47**	3.24	27.69***	0.82***
Oak				0.42*		−0.56**	−29.30	12.20**	0.48**
Poplar			0.88**		0.38*		−18.89	6.86**	0.34*

CC, Cordillera Cantábrica; CLC, Cordillera Litoral Catalana; SG, Sierra de Guadarrama; SN, Sierra Nevada.

[a] % nutrient concentration at T_{50}–% nutrient concentration at T_1.

[b] Marginally significant, $P = 0.051$.

* $P < 0.05$.

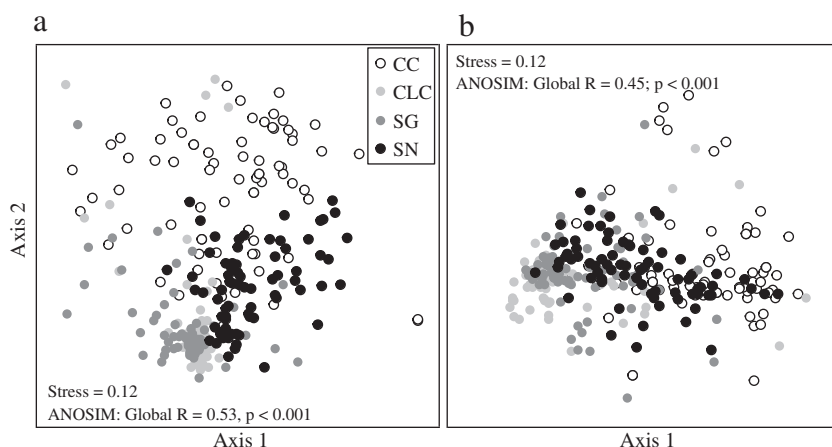** $P < 0.01$.

*** $P < 0.001$.

Fig. 4. NMDS ordination of leaf litter bags incubated in streams from four regions (different symbols) based on Bray–Curtis similarity matrices of density data of a) taxa (i.e. families) composition and b) functional feeding groups (FFG). Also shown are the stress value of the ordination and results of the test ANOSIM (global R) comparing regions.

and SN (19.02 ± 2.29 and 12.90 ± 1.62 individuals bag^{-1}; respectively) than in CLC and SG (3.49 ± 0.74 and 2.03 ± 0.22 individuals bag^{-1}; respectively). Sericostomatidae shredders, although numerically less abundant than other taxa, were characteristic of SG (Table 4). Overall, caddisfly shredders were relatively more abundant (40% of shredders in SG compared to 10–20% in other regions) and with a higher density in SG (3.84 ± 0.85 individuals bag^{-1}) than in SN (2.49 ± 0.44 individuals bag^{-1}), and were scarcest in CC and CLC (1.44 ± 0.27 and 0.61 ± 0.12 individuals bag^{-1}, respectively).

4. Discussion

Our results point to the strong effect of initial quality of leaf litter on decomposition rates, as would be expected from the large quality range of the species assayed (e.g. Schindler and Gessner, 2009). In all regions, decomposition rates across species were consistent with their initial quality, which was primarily related to the N and lignin content. This result supports the widespread notion of the strong control of initial quality over decomposition rates both in terrestrial (Aerts, 1997; Godoy et al., 2010; Makkonen et al., 2012) and aquatic ecosystems (Ostrofsky, 1997; Leroy and Marks, 2006).

Regional, but not stream, variability also contributed significantly to decomposition rates. This variability may have been mediated by terrestrial vegetation and its putative effects on invertebrates, since our regions primarily differed in catchment and riparian vegetation, with streams within each region being more similar to each other than were streams among regions. These findings are consistent with recent studies indicating that the variability of decomposition rates decreases with increasing spatial scale (from within reach towards stream or basin scales) within homogeneous regions (Tiegs et al., 2009),

Table 4
SIMPER comparison for mean density (SE in parentheses) of invertebrate assemblages between pairs of regions. Data presented are average percentage of Bray–Curtis dissimilarity, and the % contribution of the main taxa (families) and functional feeding groups (FFG) to assemblage differences between pairs of regions. Taxa and FFG are listed in approximately decreasing order of contribution to dissimilarity. Abbreviations: regions; CC Cordillera Cantábrica, CLC Cordillera Litoral Catalana, SG Sierra de Guadarrama, SN Sierra Nevada; functional feeding groups: SH shredders, CG collector–gatherers, CF collector–filterers, PR predators.

	Density (individual bag^{-1})				% contribution to pair-wise dissimilarity					
	CC	CLC	SG	SN	CC vs. CLC	CC vs. SG	CC vs. SN	CLC vs. SG	CLC vs. SN	SG vs. SN
Taxa										
Average dissimilarity					79.6	79.7	71.7	42.3	58.1	59.1
Chironomidae (CG)	5.13	76.25	26.00	17.13	19.4	18.5	14.9	7.8	8.9	7.0
	(0.81)	(11.59)	(3.55)	(1.39)						
Leuctridae (SH)	8.33	0.59	0.44	7.14	14.5	13.1	11.2	2.8	13.3	11.9
	(1.04)	(0.11)	(0.11)	(1.23)						
Nemouridae (SH)	8.65	1.07	0.33	5.38	13.4	12.6	10.6	7.5	10.7	9.1
	(1.37)	(0.71)	(0.08)	(0.87)						
Simuliidae (CF)	6.19	2.33	0.80	0.39	9.9	8.5	7.8	8.0	3.3	3.3
	(1.81)	(0.78)	(0.22)	(0.15)						
Hydropsychidae (CF)	0.91	0.97	0.79	5.44	2.4	2.5	6.8	3.5	11.2	9.9
	(0.18)	(0.27)	(0.27)	(0.69)						
Sericostomatidae (SH)	0.97	0.14	2.00	0.06	2.5	3.7	2.1	6.5	<1.0	3.4
	(0.23)	(0.05)	(0.58)	(0.02)						
FFG										
Average dissimilarity					54.4	49.3	37.1	26.6	35.7	32.0
SH	21.29	4.91	6.13	16.50	40.2	37.0	30.0	33.1	41.3	39.2
	(2.31)	(0.77)	(0.93)	(1.82)						
CG	12.92	78.12	28.04	24.16	27.4	29.0	32.0	9.9	12.9	12.4
	(1.41)	(11.74)	(3.61)	(1.67)						
CF	7.44	3.30	2.37	5.92	16.5	16.0	20.1	19.3	19.7	19.1
	(1.82)	(0.82)	(0.50)	(0.72)						
PR	3.55	4.32	1.93	6.36	10.7	11.8	17.0	20.1	18.9	20.2
	(0.77)	(0.45)	(0.26)	(0.61)						

but that a significant variability among regions emerges when they differ in critical environmental factors (Riipinen et al., 2010; Casas et al., 2011; Boyero et al., 2011a,b).

Decomposition rates within each plant species were generally lower in CC and CLC (with a high % of native deciduous and mixed forest in their catchments), than in SG and SN, where pine plantations were abundant or dominant. Furthermore, in the region with the highest decomposition rates (SG), the riparian vegetation was dominated by the native oak, while in the other three regions the riparian vegetation was dominated by species producing inputs of higher quality, such as alder. This pattern generally meets our expectation of higher decomposition rates in regions with litter inputs of a poorer quality. Similar differences in decomposition rates among the same regions studied here, but in different streams and testing only for alder leaves, were observed in a previous study (Pozo et al., 2011), which indicates that the pattern detected is rather consistent across species of contrasting quality, and across space and time scales, within and among regions.

Which proximate factors could have promoted the inter-regional differences in decomposition rates? Our results suggest that biotic factors played a major role, whereas only a minor role might be attributed to inter-regional differences in water chemistry (regions were selected to be homogeneous in this aspect). Among biotic factors, microbial decomposers are less likely to explain such differences than detritivores. The changes in litter nutrient concentration (taken as proxies of microbial activity) were significant predictors of litter decomposition in several species and regions. Yet, these changes were not always associated with faster decomposition: for example, in alder, litter N enrichment was negatively related to decomposition rates. Moreover, given that changes in litter nutrient concentrations did not differ among regions, they can hardly explain the observed inter-regional differences in decomposition rates. On the contrary, invertebrate biomass (total and shredder), shredder richness, and taxonomic composition of invertebrates significantly varied among regions. In oligotrophic headwater streams of temperate regions, detritivores often play a key role in leaf litter decomposition (reviewed by Graça, 2001). In experimental and correlational studies, decomposition rates were significantly related to various detritivore metrics such as per capita consumption rates, density, biomass or species richness and composition (Anderson and Sedell, 1979; Hieber and Gessner, 2002; Jonsson et al., 2001; Casas et al., 2011).

Our data indicate that variation of invertebrate biomass can partially explain inter-regional differences in leaf litter decomposition. Although in our study most of the total variance in total invertebrate biomass and in shredder biomass remained statistically unexplained (70–75%, respectively), perhaps due to prevailing small-scale variability (see Tiegs et al., 2009), region did explain a significant fraction of this variability, whereas stream and plant species did not. In addition, shredder biomass, more than richness, significantly contributed to decomposition rates of most plant species across regions.

Furthermore, our results suggest that inter-regional differences in leaf litter decomposition were not just driven by a unique detritivore metric. Thus, while shredder biomass can explain the higher decomposition rates in SN compared to those in CC and CLC, this variable cannot explain the highest rates found at SG. Although regions differed numerically in taxonomic composition of the invertebrates colonizing the leaf litter bags, for the most abundant taxa SG differed less from CLC with the lowest rates than it did from the other regions with higher decomposition rates. However, shredder composition differed markedly among regions, with the highest abundance of sericostomatids and shredding caddisflies at SG. In temperate regions, sericostomatids, and shredding caddisflies in general, can have higher per capita consumption rates than other shredder taxa (González and Graça, 2003; Graça and Canhoto, 2006; Boyero et al., 2012), even on leaf litter of remarkably low dietary quality (Friberg and Jacobsen, 1999; Campos and González, 2009). In addition to their feeding activities, case-bearing shredding

caddisflies also use recalcitrant litter (such as pine needles) for case building, thus contributing to the decomposition of low quality leaf litter (Whiles and Wallace, 1997).

Therefore, as suggested in Pozo et al. (2011) for the same regions studied here, the caddisfly shredders (i.e. lepidostomatids, limnephilids and sericostomatids), although numerically less abundant than other detritivores such as stoneflies, can accounted for the higher decomposition rates in SG, and perhaps also in SN, as compared to those in CC and CLC. Similar density-compensation effects among abundant stonefly and scarce caddisfly shredders have been argued to explain decomposition rates in other European regions (e.g. Riipinen et al., 2010).

If caddisfly shredders are generally less selective using leaf litter species of contrasting quality (high resource-use plasticity) than are other shredder taxa (Whiles et al., 1993; Friberg and Jacobsen, 1994, 1999; Carvalho and Graça, 2007; Boyero et al., 2012), a greater evenness in decomposition rates among plant species would be expected in regions with a higher abundance of caddisflies. Our results do not support this hypothesis: the highest evenness was found in the two regions with the highest caddisfly abundance, though no statistically significant differences were detected among regions, and the highest evenness (in SN) was not reported from the region with the greatest caddisfly density (SG).

Our results indicate that the outcome of introduced species of relatively low quality on leaf decomposition rates, and consequently on stream food webs, may vary from region to region, depending on shredder composition and biomass, and their species-specific capabilities to exploit scarcely palatable leaf litter. This inter-regional variation might be attributed to a shredder guild adapted to exploiting the assortment of litter quality commonly found in a given region (e.g. Lacán et al., 2010). However, more detailed information is needed to determine the ultimate causal factors driving interregional variation, for instance by means of inter-regional comparisons of the feeding behavior (e.g. Boyero et al., 2012), and of the physiology of shredders at the species level.

Our observation that in some regions leaf litter of low quality from introduced species can be more efficiently processed than in other regions, does not necessarily imply a negligible putative impact on stream food web in the former regions. The introduced species sycamore and pine showed a remarkably low rate of decomposition in all four regions compared to native species. Particularly, the lowest rate of decomposition and the lack of a significant contribution of biotic predictors for the decomposition of sycamore, across and within regions, denote the weak role that this species may play in stream food webs if it were introduced in riverine areas, regardless of detritivore idiosyncrasies. For the European species of sycamore, several studies in Mediterranean streams have shown that the introduced species *Platanus hispanica* has by far the lowest decomposition rate (Casas and Gessner, 1999) and enzymatic activity (Artigas et al., 2004) when compared to native riparian species. Moreover, the leaves of *Platanus orientalis* were not eaten by aquatic shredders (including caddisflies), even if the shredders came from the native geographical range of the plant species (island of Crete) (Malicky, 1990).

Our data indicate that leaf litter of the introduced *Populus x canadensis* appeared more readily utilizable by detritivores than that of *Platanus hispanica*. However, González and Graça (2003) concluded that to maintain the production of the caddisfly *Sericostoma vittatum* in a Portuguese stream, 53% more leaf litter mass would be needed if all the leaves were poplar (*P. x canadensis*) than if they were alder. These results suggest the need for energetic studies on detritivores to accurately evaluate the consequences of introduced species of trees on stream food webs, and that caution is needed in afforestation programs when introduced species, even those of intermediate leaf litter quality, replace native ones of higher litter quality such as alder.

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Acknowledgments

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