Land use drives detritivore size structure and decomposition through shifts in resource quality and quantity

Aitor Larrañaga [a],*, Daniel M. Perkins [b], Ana Basaguren [a], Santiago Larrañaga [c], Jesús Pozo [a], Jose M. Montoya [d]

[a] Department of Plant Biology and Ecology, Faculty of Science and Technology, University of the Basque Country (UPV/EHU), Barrio Sarriena s/n, 48940 Leioa, Spain
[b] School of Life & Health Sciences, University of Roehampton, London SW15 4JD, UK
[c] Escuela Universitaria de Magisterio Begoñako Andra Mari – BAM, Larrauri 1A, 48160 Derio, Spain
[d] Theoretical and Experimental Ecology Station, CNRS-UPS, 2 route du CNRS, 09200 Moulis, France

HIGHLIGHTS

- Links among land use, consumer size distribution and decomposition were assessed.
- Higher quantity of detritus increased the overall abundance of detritivores.
- Higher quality of detritus favoured more the largest detritivores.
- The proportion of the largest detritivores explained decomposition.
- Intra- and interspecific responses shaped the size distribution of detritivores.

GRAPHICAL ABSTRACT
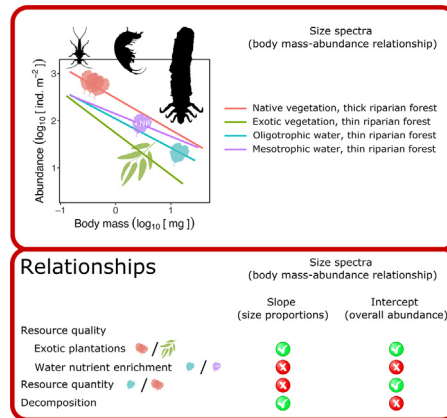
ABSTRACT

Land use change and nutrient pollution are two pervasive stressors that can modify carbon cycling, as they influence the inputs and the transformation of detritus. Understanding their impact on stream food webs and on diversity is particularly pressing, as streams are largely fuelled by detrital material received from the adjacent riparian environment. Here we assess how a switch from native deciduous forest to *Eucalyptus* plantations and nutrient enrichment alter the size distribution of stream detritivore communities and decomposition rates of detritus. As expected, more detritus resulted in higher size-independent, or overall, abundance (i.e. higher intercept of size spectra). This change in overall abundance was mainly driven by a change of the relative contribution of large taxa (Amphipoda and Trichoptera), which changed from an average relative abundance of 55.5 to 77.2 % between the sites compared for resource quantity differences in our study. In contrast, detritus quality modified the relative abundance of large vs small individuals (i.e. size spectra slopes), with shallow slopes of size spectra (proportionally more large individuals) associated with sites with nutrient-richer waters and steeper slopes (proportionally fewer large individuals) associated with sites draining *Eucalyptus* plantations. Decomposition rates of alder leaves due to macroinvertebrates increased from 0.0003 to 0.0142 when relative contribution of large organisms increased (modelled slopes of size spectra: −1.00 and − 0.33, respectively), highlighting the importance of large sized individuals for ecosystem functioning. Our study reveals that land

---

* Corresponding author.
  E-mail addresses: aitor.larranagaa@ehu.eus (A. Larrañaga), Daniel.Perkins@roehampton.ac.uk (D.M. Perkins), ana.basaguren@ehu.eus (A. Basaguren), slarranaga@bam.edu.es (S. Larrañaga), jesus.pozo@ehu.eus (J. Pozo), josemaria.montoyateran@sete.cnrs.fr (J.M. Montoya).

use change and nutrient pollution can greatly impair the transfer of energy through the detrital or 'brown' food web by means of intra- and inter-specific responses to quality and quantity of the detritus. These responses enable linking land use change and nutrient pollution to ecosystem productivity and carbon cycling.

1. Introduction

Understanding the global carbon cycle is becoming paramount as it is the foundation of climatic regulation and change (Cox et al., 2000). Among the various states in which carbon is stored, detritus (i.e. dead organic matter) is the key energy source in many ecosystems (Cebrian, 2004). For instance, food webs in low order forested streams are predominately fuelled by inputs of detritus from the surrounding vegetation, and the quantity of inputs they receive determine their productivity (Cummins et al., 1973; Wallace et al., 1997). In these ecosystems, detritivores are highly responsive to changes in the quality of detritus, as they face the largest stoichiometric difference between the consumer and its resource reported for any consumer-resource pair (Cross et al., 2005, 2003; Frost et al., 2006). Plant species release detritus that matches their ecological strategy in managing nutrients and energy. Thus, some plant species are able to grow fast and shed high quality detritus (e.g. *Alnus*), whereas other plant species manage their nutrient stocks more carefully, and thus, recover most of the nutrients invested on their leaves (e.g. *Quercus*). These two species epitomize the main axis of what has been coined "leaf economic spectrum" (Wright et al., 2004), which has a direct effect on the quality of the detritus and, consequently, on its consumption (Cornwell et al., 2008; de la Riva et al., 2019). As land use change is a common phenomenon worldwide (Foley et al., 2005), the quality and quantity of detritus that enter ecosystems are being modified globally with effects on communities and ecosystem functioning (Chauvet et al., 2016). Quality of detritus is, nonetheless, changed once microorganisms and detritivores start colonising and consuming it. In freshwater ecosystems microorganisms acquire nutrients from the water column and enrich the detritus, making it easier to be consumed by detritivores (Ferreira et al., 2014). The degree by which detritus is enriched is related to the availability of nutrients in the ecosystem (Pozo et al., 2011). Thus, both land use change and nutrient availability in the water can affect the quality of the detritus, with consequences on consumers.

The distribution of the abundance of organisms within body mass classes, known as the size spectrum, provides an integrated measure of diversity and food web structure (Kerr and Dickie, 2001). Building size spectra detaches from traditional taxonomical approaches as individuals are gathered by body mass instead of by identity, but has demonstrated to be a successful modelling approach to describe even the most complex ecosystems encompassing many orders of magnitude of body size, such as the open ocean (Hatton et al., 2021). Body size determines trophic links between predators and prey (Brose et al., 2006), which creates the foundation of size spectra (i.e. predators preying on more abundant and smaller prey). Although detritivores can show a large variation of body size (8 orders of magnitude in Potapov et al., 2019), they can feed on resources much larger than themselves and build communities that tend to be more weakly size-structured than those fuelled by within-system primary production (Blanchard et al., 2009; Dinmore and Jennings, 2004). A gathering body of evidence demonstrates interactions between environmental stressors and size spectra scaling, with size spectra slopes typically becoming steeper following disturbances, reflecting a reduction of the relative abundance or total withdrawal of the large organisms (Mor et al., 2022; Petchey and Belgrano, 2010; Pomeranz et al., 2019; Robinson et al., 2017). This has led to the use of size spectra as a quantitative measure of deviation of a natural community from a reference status as a result of environmental stressors (Jennings and Blanchard, 2004; Mulder and Elser, 2009; Ott et al., 2014). In streams, large and small detritivores can be constrained differently by the quality of the resource, which can bias the size spectra of the assemblage and thus its energy distribution. Small size consumers can more

easily have a high quality diet by selecting the high quality bits that are enriched by microbia within the overall low quality detritus, whereas large consumers are forced to feed on larger pieces that might not be totally conditioned or have toxic parts that they cannot avoid (Canhoto and Graca, 1999). Moderate environmental nutrient enrichment can enhance the quality of detritus and be more beneficial to larger consumers, increasing their relative abundance (Johnston and Sibly, 2020; Mulder and Elser, 2009; Ott et al., 2014), and thus, leading to a shallower size spectrum slope. Alterations in body size distributions and patterns of energy use are also associated with land use changes linked to changes in the quality of the detritus (Ehnes et al., 2014; Martínez et al., 2016). However, although a body of literature is building up on the response of size spectra to environmental stressors, the intraspecific or the interspecific mechanisms by which body size distribution is shaped are still not fully understood.

Changes in the size distribution of consumers should have predictable impacts on rates of resource use. Individual consumer feeding rates correspond to mass-dependent metabolic requirements (Brown et al., 2004; Pawar et al., 2012). Scaling-up, the capacity of a community to process resources depends on both its total biomass, but also on how biomass is distributed among small or large individuals (Peralta-Maraver et al., 2021) as they show different metabolic demands. Consequently, size-corrected abundance (i.e. size spectrum intercept) and community size structure (i.e. size spectrum slope) should be important predictors of resource use and consumption. Furthermore, detritus offers some physical challenges for small individuals that are related to their difficulty to break through the hard cuticle of detritus, and thus, they select the most nutritious parts (Canhoto and Graca, 1999), but are not as efficient in processing detritus as larger individuals that cut larger parts. Indeed, there is a growing body of evidence to suggest that large individuals are the key players in detritus consumption (Chauvet et al., 2016; Handa et al., 2014; Tonin et al., 2018). With studies revealing a size specific response to land use change or to nutrient availability in the environment (Davis et al., 2010; Larrañaga et al., 2009; Merckx et al., 2018), the effect of large individuals on ecosystem functioning can be larger than a simple assemblage abundance, biomass or metabolism change could anticipate.

Here we test whether changes in resource quantity and quality can predict changes in the size distribution of their consumers. We explore the mechanism behind size distribution changes, separating intraspecific changes in body size (changes in the size of individuals within species) and interspecific changes in the relative abundance of the different taxa. Finally, we test whether decomposition rates are better predicted from consumer size spectra parameters (slope and intercept) or, alternatively, from the abundance, biomass or the metabolic capacity of the consumers. To do so, we characterised detritivore size spectra for 20 low-order streams: 5 flowing through native deciduous forests, another 5 flowing through eucalypt plantations offering a poor detritus, another 5 flowing through mixed land uses but with low levels of nutrients in the water and another 5 below small human settlements receiving moderate inputs of nutrients. Eucalypt plantations have long be known for offering a low quality detritus to streams below (Molinero and Pozo, 2004), while moderate nutrient addition into the water increases the nutrient concentration in detritus (Cross et al., 2003). We expect four outcomes. Firstly, changes in the quality of the detritus will modify the slope of the size spectra, with shallower slopes expected when the quality of the detritus is higher as big individuals will become relatively more abundant (Mulder and Elser, 2009; Ott et al., 2014). Secondly, changes in quantity of detritus will not affect the relative abundance of big vs. small individuals and, thus, will not change the size spectra slope, but will shape the overall carrying capacity for detritivores and modify the intercept of size spectra. Third, we expect the size spectra

slopes to be shaped both by interspecific responses, i.e. relative abundance of big and small taxa, and by intraspecific responses, i.e. body size changes within the detritivore taxa. Lastly, we anticipate decomposition rates of organic matter to be better explained by the relative abundance of big taxa, and thus, by the slope of the size spectra, than by the total number of detritivores (i.e. intercept).

2. Material and methods

2.1. Experimental design

The 20 low order streams were located in the north of the Iberian Peninsula (mean lat-long: 43° 17′N–3° 17′W). All sites were located over siliceous materials, and boulders, cobbles and pebbles were dominating the substrate. Sites were grouped into one of the following four site types: 1) streams flowing through native deciduous forests (hereafter *Native*) comprising mainly black alder (*Alnus glutinosa* Mill.), English oak (*Quercus robur* L.) and common hazel (*Corylus avellana* L.); 2) sites draining eucalypt plantations (*Eucalypt*) dominated by eucalypt (*Eucalyptus globulus* Labill.) with some presence of alder and hazel; 3) sites located upstream of small settlements with waters lacking human-derived nutrient inputs (*Oligotrophic*) and 4) sites downstream of these human settlements with waters receiving nutrient inputs from them, but with no sign of oxygen depletion (*Mesotrophic*). Thus, these two last types of sites were geographically paired within the same catchment; the rest of the sites were randomly located in different catchment of the study area. Riparian vegetation of these two last type of sites were comprised of narrow riparian forests with alder as the main species. Although dissolved inorganic nitrogen concentration in the former two type of sites were not as low as in the *Oligotrophic* sites, the concentration of soluble reactive phosphorus was even lower (Table S1).

2.2. Detritivore assemblages

In each site, 5 benthic Surber samples (0.09 m², sieved through 0.5 mm mesh) were taken in randomly selected riffles in February–March 2003 and processed straight away in the laboratory. Benthic coarse particulate organic matter (> 1 mm) of the 5 samples in each site was lumped together. This bulk sample was then sorted into three categories: native leaves (mainly *Alnus glutinosa*, *Quercus robur*, *Castanea sativa* and *Corylus avellana*), eucalypt leaves and other material. All material was dried (70 °C, 72 h), weighed, combusted (500 °C, 8 h) and reweighed to estimate as ash free dry mass. Taxa comprising the shredder feeding guild (coarse organic matter feeders following Tachet et al., 2002) were sorted, identified (typically to genus level) and body length was measured in a stereomicroscope with a calibrated ocular micrometre. Body mass was estimated from total body length following size-scaling equations from the literature (Baumgartner and Rothhaupt, 2003; Benke et al., 1999; Burgherr and Meyer, 1997; Meyer, 1989), except for *Echinogammarus* sp. For this genus we constructed our own equation (lnMass = ln(0.0136) + 2.5674·lnLength; n = 593; r^2 = 0.97, $p < 0.0001$). Although shredders comprise a specific feeding group within the detritivores (there are also collector gatherers and filterers), they are tightly linked to the dynamics of the coarse particulate organic matter, which was the resource quantified in the present study. Thus, for the sake of simplicity we refer to these taxa as detritivores henceforth.

2.3. Size spectra construction

We observed that the sieve used (0.5 mm) was not able to create a clean break in body sizes as very small individuals were trapped by residues in the samples with the consequent underrepresentation of the abundance of the smallest body size categories (Fig. S1). To solve this sampling artefact, we decided to establish an a posteriori lower body mass limit for the individuals being considered in our analysis (see also Estévez et al., 2020; Maxwell and Jennings, 2006). From body dimension equations in literature

and the retentions observed in our meshes, we estimated that virtually all individuals above 0.1 mg of body mass were retained and we chose that value as the threshold (Martínez et al., 2016). Size spectra relationships were derived by creating bins of equal size for the log10 transformed range of body mass values and regressing log10 counts against the midpoint of the log10 body mass in each bin (Edwards et al., 2020). The total range of log10-transformed body masses for each sampling site was divided into seven bins of equal width. This number of bins minimised the number of empty bins and maximized the statistical power of the comparisons. However, to assess the dependence of size spectra intercepts and slopes on the number of size bins, we explored the relationship between size spectra coefficients obtained for different number of bins (from 5 to 10 bins; Fig. S2). Since whole-organism metabolic rates scale predictably with body mass (Brown et al., 2004) the metabolic capacity of detritivore assemblages was estimated as the total of individual body masses scaled with an exponent of $3/4$ (Perkins et al., 2010).

2.4. Decomposition

Leaf bags containing alder (*A. glutinosa* (L.) Gaertn.) were deployed in each of the 20 sites to estimate decomposition rates. Freshly fallen leaves were collected at a single site, air-dried and stored. Incubations in two mesh sizes were carried out to be able to separate decomposition by detritivore consumption and by microbial activity. Microbial decomposition was estimated in bags with a 0.5 mm mesh that prevented invertebrate access to the litter; total decomposition was estimated in 10 mm mesh bags. Six bags of each mesh size were incubated in different riffles of each stream. Six extra bags per mesh size were taken to the field, submerged in stream water and brought back to the laboratory to estimate initial air-dry mass to ash-free dry mass (AFDM) and manipulation conversion factors. In one site of each type (4 sites in total) additional sets of bags were incubated and retrieved periodically. This enabled us to estimate the time needed for ~50 % initial litter mass lost for each mesh size, and decide when to retrieve bags in all 20 sites. Thus, alder bags from all other streams were retrieved after 28 or 31 days. After being collected, bags were individually enclosed in zip-lock bags and transported to the laboratory in coolers. Remaining alder was rinsed with tap water onto a 0.5 mm mesh to remove sediments, but retain litter fragments. Collected material was dried (105 °C, 24–48 h), weighed, combusted (550 °C, 4 h), and reweighed to determine remaining AFDM. The material retrieved from the 4 sites, where periodic sampling was performed, was ground into fine powder (1-mm screen) and nutrient analyses (N and P) were carried out. Nitrogen was estimated with a Perkin Elmer series II CHNS/O elemental analyser (Perkin Elmer, Norwalk, Connecticut). Phosphorus was determined spectrophotometrically after mixed acid digestion (molybdenum blue method; Allen et al., 1974). Nutrient content was expressed as % leaf-litter dry mass (DM).

2.5. Statistical analyses

All data needed to replicate the analyses shown in this paper can be accessed in Larrañaga et al. (2022). Variation in the quality and the quantity of the benthic organic matter in the 20 sites allowed us to test our hypotheses through three different comparisons among the four site types: two comparisons regarding changes in the quality of the resource and a third one regarding changes in quantity of the resource. The first comparison (called *Land use* throughout the paper), between native and eucalypt sites, addressed the effects of the reduction of the quality of detritus on the size spectra of detritivores. The validity of the comparison is supported by the reduction in the relative contribution of native leaf litter to the benthic resource stock (Table S1) and the differences in the upstream cover of eucalypt plantations (Larrañaga et al., 2009). The second comparison (called *Nutrient status*), between oligotrophic and mesotrophic sites, tested the effect of the increase in quality of detritus. Whilst we did not measure the quality of the benthic material directly, the faster enrichment in nutrients of the incubated alder leaves in the mesotrophic sites, mainly in terms of nitrogen, confirmed that nutrients were more readily available in

these sites (Table S1; Table S2; Fig. S3). The third comparison (called *Resource quantity*), between native and oligotrophic sites, allowed us to test the effect of the reduction in quantity, with negligible effects on the quality of the resource, as sites in these two categories showed similar levels of nutrients in the water and mostly differed in the quantity of organic matter (Table S1).

To test for differences in size spectra between these comparisons, we used linear mixed effects (LME) models (package "lme4", Bates et al., 2015), modelling $\log_{10}$ abundance values as a function of $\log_{10}$ body mass (*log M*), site type (*Type*) and the interaction between them, with *Stream* as a random factor. Random effects only for the intercept, for the slope, and for both terms (correlated and uncorrelated) were considered and models were compared with AIC. In all cases, a random effects term including only the intercept showed the lowest AIC, and thus, all the models shown include only random intercepts. Assumptions for applying LME models were met in all cases. For the comparison between the oligotrophic and mesotrophic sites, catchment was included in the random structure (*Stream* nested within *Catchment*) to account for the spatial correlation among the different sites sampled. However, this random term was not selected in the final models as it increased rather than reduced the AIC of the model, compared to the model with only the *Stream* as a random term. Goodness of fit for the three comparisons was given as R^2 following the method by Nakagawa and Schielzeth (2013) for linear mixed-effects models, in which marginal R^2 (variance explained by fixed factor) and conditional R^2 (variance explained by both fixed and random factors) are computed (package "MuMIn", Barton, 2023). We observed that linearity of the size spectra varied a lot among the four site types. To test for the presence of biases from linearity (i.e. secondary structures as in Kerr and Dickie, 2001), standard linear models were built for each site type, modelling $\log_{10}$ abundance values as a function of $\log_{10}$ body mass (*log M*), stream and the interaction between them. R^2 values for each of the 4 models were used to report linearity of size spectra of each site type.

We were interested to know if the changes in the size spectra were based on a change of the structure of the assemblage, i.e. a change of the relative abundance of species of different size, or on intraspecific changes of body size, with larger or smaller individuals within taxa depending on the resource quality and/or quantity. To do this, first the composition of the assemblage was compared across the 20 sites with a non-metric multidimensional scaling (NMDS) using the average per site values for all the taxa and based on the Bray-Curtis dissimilarity matrix (package "vegan", Oksanen et al., 2022). A PERMANOVA test was performed to assess differences among site types (10^6 permutations). To further test for differences in assemblage structure, the relative abundance of big taxa (Amphipoda and Trichoptera) was calculated for each site and regressed against the slope and the intercept of the size spectra in each site. These two groups showed a larger average size and bigger individuals than the rest of the groups, which can originate less steep size spectra, but they also had individuals in the smallest size categories (Fig. S4), which can preserve the slope of the size spectra and have an effect on the overall abundance. Secondly, to investigate intraspecific responses that could affect size spectra, we needed a taxa that had a wide range of body sizes, that was abundant enough to get unbiased descriptors of their body size

variables and that was present in a number of sites of our study. Following these three criteria, we assessed the change in maximum body size of the most widespread and abundant shredder (*Echinogammarus berilloni*), which occurred in 18 out of 20 sites, and its relationship with the coefficients (slope and intercept) of the size spectra of the entire detritivore assemblage. The largest individuals of a big taxa like *E. berilloni* can potentially determine size spectra slopes as they have a big leverage on the regression. Nevertheless, the maximum body size is a variable that is prone to bias due to outliers, and thus, we took three precautions when extracting this value and relating it to the parameters of the size spectra. First, we used the 90th percentile as the approach for maximum body size to avoid including outlying large individuals in our analyses. Secondly, we assumed that sample size should have a relationship with the accuracy of the 90th percentile. To test this we calculated the 90th percentile and the median, and related the difference between these two metrics with the number of *E. berilloni* individuals in each site (Fig. S5). This relationship showed that the difference between the 90th percentile and the median was extremely reduced with little data (<16 individuals), i.e. the low number of individuals made estimating percentiles inaccurate, and thus, we only considered sites with >16 individuals of *E. berilloni* (13 sites in total). Thirdly, when building the linear models between the 90th percentile and the coefficients of the size spectra, we performed ordinary least square regressions, but we retested the relationship by weighing the datapoints by the sample size (number of *E. berilloni* individuals) following again the assumptions that increasing sample size would increase the precision of the percentile, i.e. reduce the variance of the estimate, and that sample size would be the inverse of the variance as commonly is accepted in metaanalyses (Borenstein et al., 2009).

For each of the 20 sites, an exponential decomposition rate (k, dd^{-1}) was calculated for each coarse and fine mesh bag as the slope of linear regressions of ln-transformed fraction of remaining AFDM over the accumulated mean daily temperature for the duration of the incubation (degree-days, °C), with the intercept fixed at Ln(1). Then, using the values for coarse and fine mesh bags decomposition by macroinvertebrates, i.e. fragmentation, was calculated following Lecerf (2017) and is used in this paper as the decomposition rate. For the sake of simplicity, original negative decomposition rates (material is being consumed) were transformed to positive for all the figures and statistical analyses. Comparisons of this decomposition rate among the different site types were again performed with linear mixed effects (LME) analysis, modelling decomposition rate values as a function of site type (*Type*), with *Stream* as random factor. Comparison of different random structures by means of AIC supported the use of a model with random intercept. The relationships among decomposition, total density, total biomass, metabolic capacity and size spectra parameters were performed with linear models, with decomposition considered as the response variable (y-axis) in all cases. In all models, behaviour of residuals was inspected to confirm the assumptions for linear models were met and log10 transformations applied when necessary. Cook's distance (D) (Cook, 1979) was used to estimate the leverage of each value in the models and highly influential values (D > 1) were excluded for the final models, although they are shown in the plots. All analyses were made in R (R Core Team, 2019).

Table 1
Estimates from linear mixed effect models for the intercept and slopes of detritivore size spectra in the three comparisons of the study. Standard deviation of the random term, and, marginal (variance of the fixed effects) and conditional (variance of the fixed and random effects) R^2 values are given. Note that estimates for Native and Oligotrophic sites are given for both comparisons they are used in, but the variation for the estimated parameters is negligible.

Contrast	Type	Intercept		Slope		SD of random term	R^2_m	R^2_c
		Estimate	95 % CI	Estimate	95 % CI			
Native vs Eucalyptus	Native	2.379	0.331	−0.674	0.105	0.372	0.621	0.896
	Eucalyptus	1.606	0.333	−0.884	0.147			
Oligotrophic vs Mesotrophic	Oligotrophic	1.948	0.275	−0.616	0.168	0.291	0.422	0.681
	Mesotrophic	2.074	0.273	−0.477	0.163			
Native vs Oligotrophic	Native	2.380	0.253	−0.672	0.115	0.275	0.637	0.836
	Oligotrophic	1.948	0.253	−0.616	0.130			
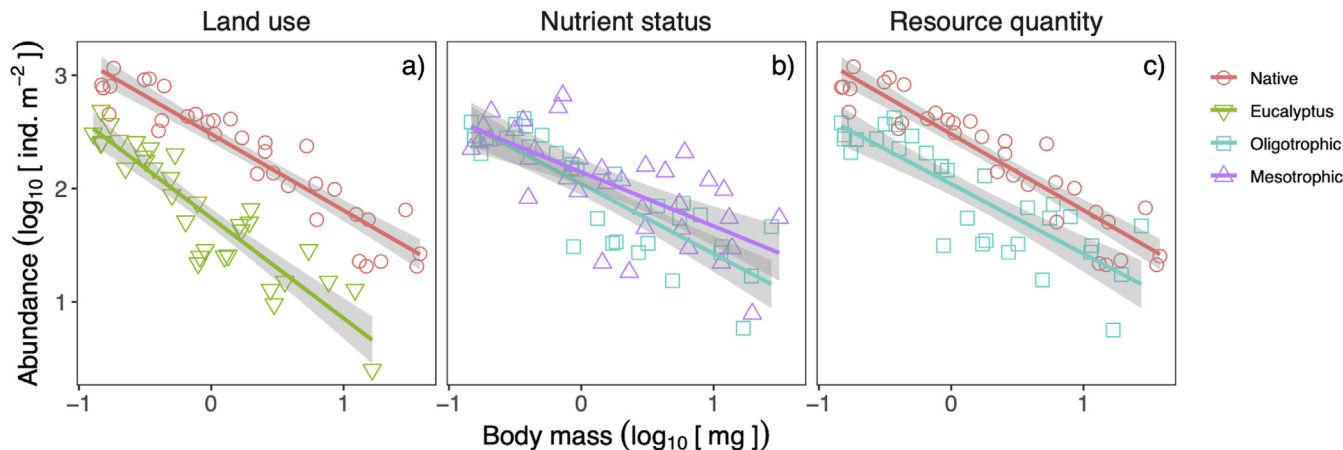
Fig. 1. Detritivore size spectra in streams from native deciduous forests and eucalypt plantations, and in oligotrophic and mesotrophic stream reaches. The first two comparisons represent changes in detritus quality (a: eucalypt lower than native; b: mesotrophic higher than oligotrophic) and the third comparison shows a change in detritus quantity (c: native higher than oligotrophic). Note that the oligotrophic and the native sites are present in two comparisons and data are slightly jittered from one to the other due to the slightly different random parameters.

3. Results

Linear mixed effects models for size spectra were able to explain over 80 % of the variation in the data in the Land use and Resource quantity comparisons, but only explained 68.1 % for the Nutrient status comparison, mainly because of the reduction of the variance explained by fixed factors (i.e. by the marginal R^2; Table 1). Refitting linear models for each site type with body size, stream and their interaction showed that these three sources of variation were able to explain 92.0 % of the variation for the Native sites, although only 80.1 % for the eucalypt sites. Linear models showed an even poorer fit for the oligotrophic and mesotrophic sites, explaining only 70.7 % and 70.2 % of the variation, respectively.

Detritivores in Eucalypt sites were less abundant overall irrespective of their body size (i.e. smaller intercept for the size spectra) than those from native sites, but largest individuals declined more their abundance (i.e. steeper slopes) (Fig. 1a, Table 2). The overall slope changed from −0.674 to −0.884, from native to eucalypt sites (Table 1). Eucalypt sites lacked the largest individuals observed in native sites, as shown by a truncated body size range compared to native sites, with the largest body mass bin centre being 1.07 and 1.29, respectively (log$_{10}$ values; 11.7 and 19.4 mg, respectively). Despite nutrient availability in the water and the enrichment rate of alder by nitrogen were higher in the Mesotrophic than in the Oligotrophic sites (Table S1, Table S2), size spectra only displayed a non-significant trend of increasing the relative abundance of the largest detritivores (Fig. 1b, Table 1, Table 2). For the Resource quantity contrast

size spectrum slopes did not differ between native and oligotrophic sites although the intercepts did, with higher overall abundances for native sites, which exhibited a significantly larger stock of benthic OM (Fig. 1c, Table 2).

The composition of the detritivore assemblages showed a large overlap among the different site types with only a slight separation between native and eucalypt sites (Fig. 2), but the overall separation among the site types was not significant (Permanova: PseudoF = 0.67, p = 0.742). Contrastingly, the relative abundance of large detritivores (Amphipoda + Trichoptera) ranged from 7 to 99 % of the total abundance and was positively related to the overall abundance (i.e. intercept of the size spectra) ($F_{1,18}$ = 46.65, p < 0.001), but not to the slope ($F_{1,18}$ = 0.44, p < 0.517; Fig. 3). Neither for Amphipoda nor for Trichoptera was the relationship between average body mass (in log10) and abundance (log-transformed) significant (Pearson correlation: Amphipoda: r = 0.12, p = 0.64; Trichoptera: r = −0.36, p = 0.14). On the other hand, the most abundant big taxa of our assemblages, the amphipod *E. berilloni* (relative density of 72.3 %, relative biomass of 65.3 % for individuals larger than 0.1 mg) occurred in 18 out of the 20 sites, missing from one of the eucalypt sites and one of the mesotrophic sites. Its maximum body size, estimated by the 90th percentile of the body mass, was able to significantly explain the variation of the size spectra slope ($F_{1,10}$ = 8.40, p = 0.016), but not of the intercept ($F_{1,11}$ = 2.34, p = 0.154; Fig. 3). A reanalysis with values weighted by the sample

Table 2
Comparison of linear mixed effect models with different sources of variation for the three comparisons of the study: streams with Native or Eucalypt riparian buffer, streams with Oligotrophic or Mesotrophic waters, and, streams with thick or thin riparian forests (Native and Oligotrophic sites, respectively). Chi square and *p*-values of likelihood ratio tests between the model in the line and the one below it are given.

Contrast	Driver	Model	AIC	Df	Chi sq	P-value
Native vs Eucalyptus	Resource quality	log M * Type	29.317	6	4.972	0.0258
		log M + Type	32.289	5	8.311	0.0039
	reduced	log M	38.601	4		
Oligotrophic vs Mesotrophic	Resource quality	log M * Type	64.829	6	1.373	0.2413
		log M + Type	63.202	5	0.516	0.4727
	increased	log M	62.718	4		
Native vs Oligotrophic	Resource quantity	log M * Type	33.989	6	0.409	0.5222
		log M + Type	32.399	5	5.181	0.0228
	reduced	log M	35.579	4		
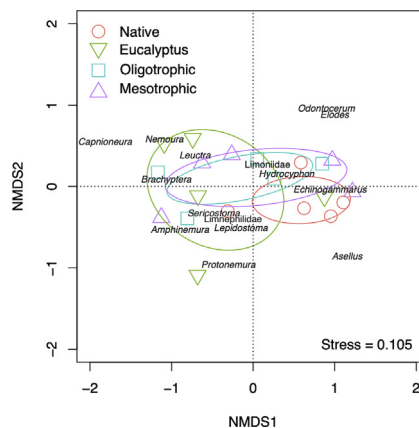
Fig. 2. Non-metric multidimensional scaling of the detritivore assemblages of the 20 stream sites. Ellipses display the 95th confidence interval of the standard error of the centroid. Permanova analyses revealed no statistical difference among the 4 different groups (see text).
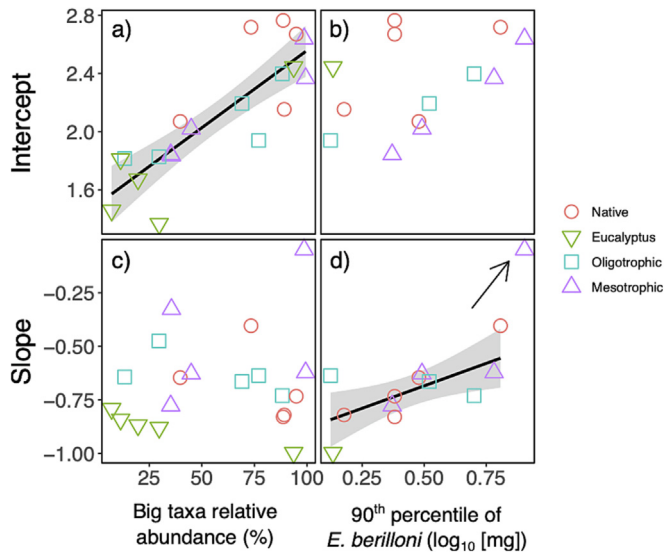
Fig. 3. Relationships between the relative abundance of big taxa (Amphipoda and Trichoptera) (a and c) and 90th percentile of the body mass of *Echinogammarus berilloni* (b and d) with the intercept and the slope of detritivore size spectra. The arrow indicates an outlying site, which was excluded from the regression due to its extremely high leverage (Cook's distance >1). Beware that only 13 sites showed enough *E. berilloni* individuals to be able to compute the 90th percentile.

size for each site (i.e. number of *E. berilloni* individuals) also supported the significant relationship with the slope ($F_{1,10} = 20.73$, $p = 0.001$).

Decomposition rate was lowest in streams from eucalypt plantations compared to the other site types (Fig. 4, Fig. S6). Considering the 20 streams together, litter decomposition rate was positively related to the slope of detritivore size spectra ($F_{1,17} = 15.08$, p = 0.001), but not to the intercept ($F_{1,18} = 1.91$, $p = 0.184$; Fig. 4). Total density or metabolic capacity were not significantly related to litter decomposition (Dens: $F_{1,18} = 0.13$, $p = 0.721$; MC: $F_{1,18} = 2.74$, $p = 0.115$), but biomass nearly was (Biom: $F_{1,18} = 4.35$, $p = 0.051$). A significant relationship was observed between the total biomass and the slope of the size spectra ($F_{1,18} = 7.91$, $p = 0.012$).

4. Discussion

In this study we observed that drops in detritus quality (due to eucalypt plantations or to low water nutrient levels) were reducing the relative abundance of large detritivores, i.e. steeper size spectra, whereas a drop in quantity (due to the lower forest cover) originated an overall reduction of the abundance irrespective of the body size, i.e. lower intercept. Whereas changes of the intercept were related to the relative abundance of large detritivores, changes of the slope were related to their maximum body size. Decomposition rates were related to the relative abundance of large detritivores, i.e. size spectra slope, and not to the abundance, metabolic capacity or the biomass of the assemblage. Although relationships between consumers and their resources are abundant in the literature, we have been able to isolate the effect of quantity from the effect of quality of the resources in this study.

1) Consumer-resource stoichiometric imbalance disrupts size spectra slope.

Here we show that the effects of changes in quality of detritus on food web structure differ from those originated by changes in quantity. A size spectrum slope of $-\frac{3}{4}$ within trophic levels is a pervasive phenomenon in nature (Damuth, 1981; Nee et al., 1991; Perkins et al., 2019; White et al., 2007), but departures of that slope have also been observed in many studies (Ehnes et al., 2014; Perkins et al., 2018; Reuman et al., 2009). Our study shows that variations in detritus quality changed the slope of the size spectra as observed in other studies dealing with stoichiometric constraints on food webs (Ehnes et al., 2014; Martínez et al., 2016; Mulder and Elser, 2009). Specifically, reduction of the detritus quality linked to eucalypt plantations (demonstrated previously by Molinero and Pozo, 2004) increased the slope of the detritivores size spectra, whereas water nutrient enrichment (and the consequent increase of the quality of benthic detritus, Cross et al., 2003) was related to a significantly shallower slope than $-\frac{3}{4}$ (although slopes were not significantly different, and only tended to be shallower in the nutrient rich sites). Both of these observations are linked to detritus-detritivore stoichiometric imbalances, which become more severe with a eucalypt plantations offering a low quality leaf litter and alleviate with moderate nutrient enrichment reducing the stoichiometric gap between resources and consumers. From our study we cannot categorically say that eucalypt plantations are able to more strongly shift the size distribution of the detritivores than water nutrient enrichment. The intensity of both perturbations can vary with more or less eucalypt in the basin and the riparian forest, and, higher or lower nutrient availability in the water. In our particular case, resource quality changes associated to eucalypt have been stronger when shaping size spectra of detritivores. On the other hand, when comparing systems with detritus of similar quality, but differing in quantity, we observed a change in the intercept and not in the slope, which corresponds to an increase on detritivore secondary productivity without altering the size spectrum slope. Our results highlight the significance of detritus quantity for predicting productivity of detritus dependant
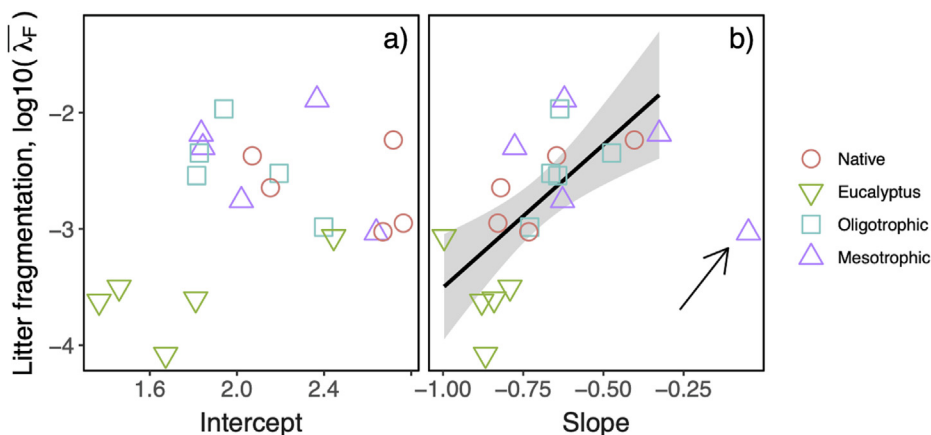
Fig. 4. Relationship between the intercept (a) and slope (b) of detritivore size spectra, and litter decomposition. The arrow points an outlying site which was excluded from the regression due to its extremely high leverage (Cook's distance >1).

ecosystems, but also reinforces the idea of the quality of detritus as the driver for the relative abundance of large organisms.

2) Intra- and interspecific changes defined size spectra slope and intercept, respectively.

The changes of size spectra slope and intercept happened without large taxonomic compositional changes. Although eucalypt and native sites showed the largest compositional discrepancies, detritivore composition did not differ strongly among the four site type studied. Our study suggests that variations in the slope and the intercept of size spectra are likely to be related to two different mechanisms, but both include large detritivores as central players. Firstly, intraspecific changes in maximum body mass of large detritivore taxa were tilting the relationship between body mass and abundance, and thus, changing the slope of size spectra. The Growth Rate Hypothesis (Elser et al., 2003, 2000) might help explain our observations as the higher nutrient availability could either originate a faster individual growth or at least make it easier for larger individuals to find resources, which both can contribute to the changes of the size spectra we observe in our study. Other field studies corroborate changes in body size of detritivores due larger detritus quantity (Estévez et al., 2020) and quality (Danger et al., 2013; Evans-White and Halvorson, 2017). Nevertheless, growth stimulus had to be biased towards big size taxa to observe changes in the slope size spectra, as an overall increase of the size of all body mass categories would have conserved the slope. The second mechanism that can help explain the changes of size spectra parameters is the variation of the relative abundance of big taxa in contrast to smaller taxa, which were linked to the changes of the intercept. For this interspecific response to have an effect on the intercept, but not on the slope, the taxa changing abundances had to add or remove individuals across the body size categories, which it was the case for the two groups considered, Amphipoda and Trichoptera. When becoming abundant, these two taxa had no significant effect on the average body mass, what explains the lack of effect on the slope of size spectra. Thus, from our data, it seems larger detritivores are more responsive to detritus than smaller ones and attain larger body masses (intraspecific response) when resource quality rises and increase their numerical dominance (interspecific response) when quantity is higher.

3) Fluctuating environments and size spectra.

If this intra- and interspecific forces are constantly responding to the detritus quantity and quality, their fluctuations should create biases from equilibrium that should manifest as departures from linearity of size spectra. A linear relationship is the most common model to build size spectra (Edwards et al., 2020) and it was a successful approach in our study. Nevertheless, the goodness of fit varied markedly among the four site types studied. It was highest for native forests, with only 8 % of the variation left for residuals when considering body size, stream and their interaction in the model. For eucalypt sites the amount left unexplained by the model jumped to 20 %, whereas for oligotrophic and mesotrophic sites it reached to nearly 30 %. This lack of linearity, has often been associated to dynamics among trophic levels (Arranz et al., 2019; Chang et al., 2014; Perkins et al., 2021; Rossberg et al., 2019). In our study we only have information about detritivores and we miss data on fish to discard their involvement on creating departures from linearity of size spectra. Nevertheless, we suggest that the temporal instability of detritus and nutrient supply can also explain the lack of linearity of size spectra. Fluctuations of the supply rate and quality of resources will modulate the edge that individuals of certain body sizes get and thus, departures from linearity are likely to appear. In our study, the residuals seemed to show that native sites were the most stable streams, with eucalypt sites less stable and the oligotrophic and mesotrophic sites the least stable from the lot. Although streams below deciduous forests receive the bulk of organic matter in autumn, natural watercourses have retaining structures that buffer the seasonality of the inputs to extend the availability of organic matter along the year (Diez et al., 2000; Wohl et al., 2012). These retentive structures are highly reduced in plantations

(Diez et al., 2001) and together with the much smaller inputs of high quality leaf litter, such as alder (Pozo et al., 1997), can make availability and quality of detritus to show much larger seasonal fluctuations, with periods with an extremely low overall resource quality (Basaguren et al., 2022; Martínez et al., 2016). Instability of the detrital conditions can also apply to the oligotrophic and mesotrophic sites in our work. They display a lower stock of organic matter, which can already make consumer's body and population growth in these sites to be less stable, as small oscillations on the stock can originate large relative modifications in terms of resource opportunities to individuals of different size. On the other hand, nutrients in the water are naturally, or artificially, highly fluctuating (Bowes et al., 2018; Jarvie et al., 1998), which can cause changes in the quality of the resource. Moreover, nutrients inputs can create a faster resource use (Greenwood et al., 2007), which create the risk of depleting its availability in certain periods of the year. Thus, both land use change and moderate nutrient enrichment can create oscillations in the quality and quantity of detritus, and, can therefore, be included in the same mechanism responsible for departures from linearity to appear in detritivore size spectra. Interestingly, our study also suggests that departures from linearity can be used to assess the level of naturalness of headwater forested streams, as the most preserved site types in our study showed the most linear size spectra.

4) Decomposition is controlled by the relative abundance of big consumers.

Both eucalypt plantations and nutrient enrichment have been reported to inhibit and stimulate decomposition, respectively (Ferreira et al., 2016, 2014), but in our case decomposition of alder, particularly the part that is carried out by macroinvertebrates, was significantly slowed down when incubated in streams surrounded by eucalypt plantations, whereas nutrient enrichment only showed a non-significant increase of the rates. The stronger functional consequences of eucalypt plantations compared to nutrient enrichment cannot be generalized as the effect of both stressors highly depends on their intensity (cover of eucalypt plantation or amount of nutrients added). When modelling organic matter decomposition, previous studies have successfully used abundance or biomass of detritivores as explanatory variables (Martínez et al., 2013; Pozo et al., 2011). In our study, abundance did not explain processing rates of organic matter in the field and although biomass was a stronger, but still not significant, predictor of processing rates, the slope of size spectra was a much better descriptor. Bear in mind that the slope of the size spectra is a proxy for the relative abundance of large individuals. Thus, this result highlights the relevance of larger organisms on organic matter consumption, which is in line with previous studies (Handa et al., 2014; Tonin et al., 2018; Woodward et al., 2012). Larger detritivores are able to more easily fragment detritus, which can increase the abundance of other feeding groups, such as filterers, as they feed on the processed organic matter (Lecerf and Richardson, 2011). As energetic demands scale with body mass, it is expected that metabolic capacity is a better predictor of resource use than the slope of the size spectra. In this regard, total metabolic capacity of the studied assemblage has also been successfully used to model decomposition in microscosm experiments (Perkins et al., 2010). Nevertheless, detritivores can consume small amounts of other resources beside coarse detritus, such as fine detritus, biofilm and other animals, but the larger they become the more their preference for coarse detritus (Basaguren et al., 2002). Amphipods tend to become predators as they grow (Rewicz et al., 2014), but for the amphipod in our study, *Echinogammarus berilloni*, there is no sign that other materials beside coarse organic matter become relevant (Piscart et al., 2011). With the higher preference for coarse detritus by big detritivores we can anticipate intraguild competition between detritivores of different sizes feeding on coarse detritus. Being body size a determinant factor for competition, we would expect big individuals to exploit more successfully their preferred resource, coarse detritus, which would displace the smaller individuals to the consumption of smaller bits or other materials. This smaller bits can be washed away from the leaf litter bags anyway, so the feeding activity of the smallest individuals can go partly undetected when using leaf litter bags to estimate decomposition. Thus, we expect the

functional consequence of the metabolism of the larger detritivores to be reflected on our decomposition rates, but the consequence of the metabolism of the smaller detritivores to be partly neglected. This argumentation is in line with the observed better fit of decomposition with the slope of the size spectra, which is basically a surrogate of the relative abundance of large vs small individuals, than with the metabolic capacity or the abundance of the entire assemblage. In field studies, size spectra obtained from very detailed communities, including prokaryotes, protists. Meiofauna and macroinvertebrates, has successfully predicted decomposition rates of artificial substrates (Peralta-Maraver et al., 2021). In that study multiple trophic levels were included and trophic transfer efficiency was key to determine the slope of size spectra. That study reiterates the very well-known relevance of organic matter for ecosystem productivity (see Wallace et al., 1997), but links it with the transfer of energy among trophic levels. Our study is, as far as we are aware, the first one that predicts decomposition from the body size distribution of detritivores, which only depends on the allocation of energy on individuals of different sizes in the same feeding guild. This approach can set a precedent when linking resource consumption, organic matter in this case, with consumers, detritivores in this case, going beyond the more standard procedure of using abundance or biomass values. A possible line that can be developed from here is the use of large bodied macroinvertebrates (e.g. those collected with a 1 mm or 2 mm mesh; see Gruenert et al., 2007) to estimate ecosystem functioning rates. With molecular techniques gaining ground, combining them with more classical morphological identifications of the largest individuals could more cost-effectively address both biodiversity and ecosystem functioning issues in the future.

5. Conclusion

We have demonstrated that the quantity and quality of the detritus can control the allocation of energy into detritivores modulating their size distribution. Quantity of detritus relates positively to the size corrected abundance, or the carrying capacity, and the quality of detritus (reduced by eucalypt plantations or increased by water nutrient enrichment) with the slope the size spectra, or the efficiency of allocation of energy to big size detritivores. We have also shown that the relative contribution of big animals to the assemblage, or the slope of the size spectra, can control decomposition rates of detritus, improving the predictive power of abundance, biomass or assemblage metabolic capacity. Thus, body size distribution, which is backed by metabolic theory in ecology, hinges between environmental drivers that modify the quantity and quality of available detritus, and the rate at which that detritus is processed by the consumers. Studying body size distribution, or at least abundance of the biggest individuals, is then paramount to understand energy transfer in ecosystems facing environmental change.

CRediT authorship contribution statement

Aitor Larrañaga: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Daniel M. Perkins:** Data curation, Formal analysis, Writing – review & editing. **Ana Basaguren:** Methodology, Supervision, Writing – review & editing. **Santiago Larrañaga:** Data curation, Writing – review & editing. **Jesús Pozo:** Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing. **Jose M. Montoya:** Conceptualization, Methodology, Writing – review & editing.

Data availability

Data and code are provided as private-for-peer review via the following link: https://figshare.com/s/fe6ce002cf154d871e9c.

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.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2023.164552.

References

Allen, S., Grimshaw, H., Parkinson, J., Quarmby, J., 1974. Chemical Analysis of Ecological Materials. Blackwell Scientific, Oxford, UK.

Arranz, I., Hsieh, C. hao, Mehner, T., Brucet, S., 2019. Systematic deviations from linear size spectra of lake fish communities are correlated with predator–prey interactions and lake-use intensity. Oikos 128, 33–44. https://doi.org/10.1111/oik.05355.

Barton, K., 2023. MuMIn: Multi-Model Inference. R package version 1.47.5, < https://CRAN.R-project.org/package=MuMIn>.

Basaguren, A., Riano, P., Pozo, J., 2002. Life history patterns and dietary changes of several caddisfly (Trichoptera) species in a northern Spain stream. Arch. Hydrobiol. 155, 23–41.

Basaguren, A., Larrañaga, A., Otermin, A., Molinero, J., Larrañaga, S., Pozo, J., 2022. Resource preference of two stream detritivores in the laboratory largely differs from the supply of detritus below eucalypt plantations. Hydrobiologia 849, 2983–2997. https://doi.org/10.1007/s10750-022-04908-7.

Bates, D., Mächler, M., Bolker, B.M., Walker, S.C., 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67. https://doi.org/10.18637/jss.v067.i01.

Baumgartner, D., Rothhaupt, K.O., 2003. Predictive length-dry mass regressions for freshwater invertebrates in a pre-alpine lake littoral. Int. Rev. Hydrobiol. 88, 453–463.

Benke, A.C., Huryn, A.D., Smock, L.A., Wallace, J.B., 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. J. North Am. Benthol. Soc. 18, 308–343.

Blanchard, J.L., Jennings, S., Law, R., Castle, M.D., McCloghrie, P., Rochet, M.-J., Benoît, E., 2009. How does abundance scale with body size in coupled size-structured food webs? J. Anim. Ecol. 78, 270–280. https://doi.org/10.1111/j.1365-2656.2008.01466.x.

Borenstein, M., Hedges, L.V., Higgins, J.P.T., Rothstein, H.R., 2009. Introduction to Meta-analysis. John Wiley & Sons, Ltd, Chichester, UK https://doi.org/10.1002/9780470743386.

Bowes, M.J., Armstrong, L.K., Harman, S.A., Wickham, H.D., Nicholls, D.J.E., Scarlett, P.M., Roberts, C., Jarvie, H.P., Old, G.H., Gozzard, E., Bachiller-Jareno, N., Read, D.S., 2018. Weekly water quality monitoring data for the river Thames (UK) and its major tributaries (2009-2013): the Thames initiative research platform. Earth Syst. Sci. Data 10, 1637–1653. https://doi.org/10.5194/essd-10-1637-2018.

Brose, U., Jonsson, T., Berlow, E.L., Warren, P., Banasek-Richter, C., Bersier, L.F., Blanchard, J.L., Brey, T., Carpenter, S.R., Blandenier, M.F.C., Cushing, L., Dawah, H.a., Dell, T., Edwards, F., Harper-Smith, S., Jacob, U., Ledger, M.E., Martinez, N.D., Memmott, J., Mintenbeck, K., Pinnegar, J.K., Rall, B.C., Rayner, T.S., Reuman, D.C., Ruess, L., Ulrich, W., Williams, R.J., Woodward, G., Cohen, J.E., 2006. Consumer-resource body-size relationships in natural food webs. Ecology 87, 2411–2417. https://doi.org/10.1890/0012-9658(2006)87[2411:CBRINF]2.0.CO;2.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. Ecology 85, 1771–1789. https://doi.org/10.1890/03-9000.

Burgherr, P., Meyer, E.I., 1997. Regression analysis of linear body dimensions vs. dry mass in stream macroinvertebrates. Arch. Hydrobiol. 139, 101–112.

Canhoto, C., Graca, M.A.S., 1999. Leaf barriers to fungal colonization and shredders (Tipula lateralis) consumption of decomposing Eucalyptus globulus. Microb. Ecol. 37, 163–172.

Cebrian, J., 2004. Role of first-order consumers in ecosystem carbon flow. Ecol. Lett. 7, 232–240. https://doi.org/10.1111/j.1461-0248.2004.00574.x.

Chang, C.W., Miki, T., Shiah, F.K., Kao, S.J., Wu, J.T., Sastri, A.R., Hsieh, C.H., 2014. Linking secondary structure of individual size distribution with nonlinear size-trophic level relationship in food webs. Ecology 95, 897–909. https://doi.org/10.1890/13-0742.1.

Chauvet, E., Ferreira, V., Giller, P.S., McKie, B.G., Tiegs, S.D., Woodward, G., Elosegi, A., Dobson, M., Fleituch, T., Graça, M.A.S., Gulis, V., Hladyz, S., Lacoursière, J.O., Lecerf, A., Pozo, J., Preda, E., Riipinen, M., Rîşnoveanu, G., Vadineanu, A., Vought, L.B.M., Gessner, M.O., 2016. Litter decomposition as an indicator of stream ecosystem functioning at local-to-continental scales: insights from the European RivFunction project. Adv. Ecol. Res. 55, 99–182. https://doi.org/10.1016/bs.aecr.2016.08.006.

Cook, R.D., 1979. Influential observations in linear regression. J. Am. Stat. Assoc. 74, 169. https://doi.org/10.2307/2286747.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K., Dorrepaal, E., Eviner, V.T., Godoy, O., Hobbie, S.E., Hoorens, B., Kurokawa, H., Pérez-Harguindeguy, N., Quested, H.M., Santiago, L.S., Wardle, D.A., Wright, I.J., Aerts, R., Allison, S.D., Van Bodegom, P., Brovkin, V., Chatain, A., Callaghan, T.V., Díaz, S., Garnier, E., Gurvich, D.E., Kazakou, E., Klein, J.A., Read, J., Reich, P.B., Soudzilovskaia, N.A., Vaieretti, M.V., Westoby, M., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol. Lett. 11, 1065–1071. https://doi.org/10.1111/j.1461-0248.2008.01219.x.

Cox, P.M., Betts, R.A., Jones, C.D., Spall, S.A., Totterdell, I.J., 2000. Acceleration of global warming due to carbon-cycle feedbacks in a coupled climate model. Nature 408, 184–187. https://doi.org/10.1038/35041539.

Cross, W.F., Benstead, J.P.J.P., Rosemond, A.D.A.D., Wallace, J.B., 2003. Consumer-resource stoichiometry in detritus-based streams. Ecol. Lett. 6, 721–732. https://doi.org/10.1046/j.1461-0248.2003.00481.x.

Cross, W.F., Benstead, J.P., Frost, P.C., Thomas, S.A., 2005. Ecological stoichiometry in freshwater benthic systems: recent progress and perspectives. Freshw. Biol. 50, 1895–1912. https://doi.org/10.1111/j.1365-2427.2005.01458.x.

Cummins, K.W., Petersen, R.C., Howard, F.O., Wuycheck, J.C., Holt, V.I., 1973. The utilization of leaf litter by stream detritivores. Ecology 54, 336–345. https://doi.org/10.2307/1934341.

Damuth, J., 1981. Population density and body size in mammals. Nature 290, 1980–1981.

Danger, M., Funck, J.A., Devin, S., Heberle, J., Felten, V., Laboratoire, L., Continentaux, E., Cnrs, U.M.R., Bernard, C., 2013. Phosphorus Content in Detritus Controls Life-History Traits of a Detritivore 807–815. https://doi.org/10.1111/1365-2435.12079.

Davis, J.M., Rosemond, A.D., Eggert, S.L., Cross, W.F., Wallace, J.B., 2010. Nutrient enrichment differentially affects body sizes of primary consumers and predators in a detritus-based stream. Limnol. Oceanogr. 55, 2305–2316. https://doi.org/10.4319/lo.2010.55.6.2305.

de la Riva, E.G., Prieto, I., Villar, R., 2019. The leaf economic spectrum drives leaf litter decomposition in Mediterranean forests. Plant Soil 435, 353–366. https://doi.org/10.1007/s11104-018-3883-3.

Diez, J.R., Larrañaga, S., Elosegi, A., Pozo, J., 2000. Effect of removal of wood on streambed stability and retention of organic matter. J. North Am. Benthol. Soc. 19, 621–632.

Diez, J.R., Elosegi, A., Pozo, J., 2001. Woody debris in north Iberian streams: influence of geomorphology, vegetation, and management. Environ. Manag. 28, 687–698.

Dinmore, T.A., Jennings, S., 2004. Predicting abundance-body mass relationships in benthic infaunal communities. Mar. Ecol. Ser. 276, 289–292.

Edwards, A., Robinson, J., Blanchard, J., Baum, J., Plank, M., 2020. Accounting for the bin structure of data removes bias when fitting size spectra. Mar. Ecol. Prog. Ser. 636, 19–33. https://doi.org/10.3354/meps13230.

Ehnes, R.B., Pollierer, M.M., Erdmann, G., Klarner, B., Eitzinger, B., Digel, C., Ott, D., Maraun, M., Scheu, S., Brose, U., 2014. Lack of energetic equivalence in forest soil invertebrates. Ecology 95, 527–537. https://doi.org/10.1890/13-0620.1.

Elser, J.J., Brien, W.J.O., Dobberfuhl, D.R., Dowling, T.E., 2000. The evolution of ecosystem processes : growth rate and elemental stoichiometry of a key herbivore in temperate and arctic habitats 13, 845–853.

Elser, J.J., Acharya, K., Kyle, M., Cotner, J., Makino, W., Markow, T., Watts, T., Hobbie, S., Fagan, W., Schade, J., Hood, J., Sterner, R.W., 2003. Growth rate-stoichiometry couplings in diverse biota. Ecol. Lett. 6, 936–943. https://doi.org/10.1046/j.1461-0248.2003.00518.x.

Estévez, E., Larrañaga, A., Alonso, C., Barquín, J., 2020. Effects of changes in food resources due to variations in forest cover on stream macroinvertebrate community size structure. Aquat. Sci. 82, 1–13. https://doi.org/10.1007/s00027-020-0713-5.

Evans-White, M.A., Halvorson, H.M., 2017. Comparing the ecological stoichiometry in green and brown food webs - a review and meta-analysis of freshwater food webs. Front. Microbiol. 8, 1–14. https://doi.org/10.3389/fmicb.2017.01184.

Ferreira, V., Castagneyrol, B., Koricheva, J., Gulis, V., Chauvet, E., Graça, M.A.S., 2014. A meta-analysis of the effects of nutrient enrichment on litter decomposition in streams. Biol. Rev. 90, 669–688. https://doi.org/10.1111/brv.12125.

Ferreira, V., Koricheva, J., Pozo, J., Graça, M.A.S., 2016. A meta-analysis on the effects of changes in the composition of native forests on litter decomposition in streams. For. Ecol. Manag. 364, 27–38. https://doi.org/10.1016/j.foreco.2016.01.002.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N., Snyder, P.K., 2005. Global consequences of land use. Science 309, 570–574. https://doi.org/10.1126/science.1111772.

Frost, P.C., Benstead, J.P., Cross, W.F., Hillebrand, H., Larson, J.H., Xenopoulos, M.A., Yoshida, T., 2006. Threshold elemental ratios of carbon and phosphorus in aquatic consumers. Ecol. Lett. 9, 774–779. https://doi.org/10.1111/j.1461-0248.2006.00919.x.

Greenwood, J.L., Rosemond, A.D., Wallace, J.B., Cross, W.F., Weyers, H.S., 2007. Nutrients stimulate leaf breakdown rates and detritivore biomass: bottom-up effects via heterotrophic pathways. Oecologia 151, 637–649. https://doi.org/10.1007/s00442-006-0609-7.

Gruenert, U., Carr, G., Morin, A., 2007. Reducing the cost of benthic sample processing by using sieve retention probability models. Hydrobiologia 589, 79–90. https://doi.org/10.1007/s10750-007-0722-6.

Handa, I.T., Aerts, R., Berendse, F., Berg, M.P., Bruder, A., Butenschoen, O., Chauvet, E., Gessner, M.O., Jabiol, J., Makkonen, M., McKie, B.G., Malmqvist, B., Peeters, E.T.H.M., Scheu, S., Schmid, B., Van Ruijven, J., Vos, V.C.A., Hättenschwiler, S., 2014. Consequences of biodiversity loss for litter decomposition across biomes. Nature 509, 218–221. https://doi.org/10.1038/nature13247.

Hatton, I.A., Heneghan, R.F., Bar-On, Y.M., Galbraith, E.D., 2021. The global ocean size spectrum from bacteria to whales. Sci. Adv. 7, 1–13. https://doi.org/10.1126/sciadv.abh3732.

Jarvie, H., Whitton, B., Neal, C., 1998. Nitrogen and phosphorus in east coast British rivers: speciation, sources and biological significance. Sci. Total Environ. 210–211, 79–109. https://doi.org/10.1016/S0048-9697(98)00109-0.

Jennings, S., Blanchard, J.L., 2004. Fish abundance with no fishing: predictions based on macroecological theory. J. Anim. Ecol. 73, 632–642. https://doi.org/10.1111/j.0021-8790.2004.00839.x.

Johnston, A.S.A., Sibly, R.M., 2020. Multiple environmental controls explain global patterns in soil animal communities. Oecologia 192, 1047–1056. https://doi.org/10.1007/s00442-020-04640-w.

Kerr, S.R., Dickie, L.M., 2001. The Biomass Spectrum : A Predator-Prey Theory of Aquatic Production. Columbia University Press.

Larrañaga, A., Basaguren, A., Elosegi, A., Pozo, J., 2009. Impacts of *Eucalyptus globulus* plantations on Atlantic streams: changes in invertebrate density and shredder traits. Fundam.

Appl. Limnol. / Arch. für Hydrobiol. 175, 151–160. https://doi.org/10.1127/1863-9135/2009/0175-0151.

Larrañaga, A., Perkins, D.M., Basaguren, A., Larrañaga, S., Pozo, J., Montoya, J.M., 2022. Dataset: land use change alters detritivore size structure and decomposition through shifts in resource quality and quantity. [WWW document]. URL https://doi.org/10.6084/m9.figshare.21431205

Lecerf, A., 2017. Methods for estimating the effect of litterbag mesh size on decomposition. Ecol. Model. 362, 65–68. https://doi.org/10.1016/j.ecolmodel.2017.08.011.

Lecerf, A., Richardson, J.S., 2011. Assessing the functional importance of large-bodied invertebrates in experimental headwater streams. Oikos 120, 950–960. https://doi.org/10.1111/j.1600-0706.2010.18942.x.

Martínez, A., Larrañaga, A., Basaguren, A., Pérez, J., Mendoza-Lera, C., Pozo, J., 2013. Stream regulation by small dams affects benthic macroinvertebrate communities: from structural changes to functional implications. Hydrobiologia 711, 31–42. https://doi.org/10.1007/s10750-013-1459-z.

Martínez, A., Larrañaga, A., Miguélez, A., Yvon-Durocher, G., Pozo, J., 2016. Land use change affects macroinvertebrate community size spectrum in streams: the case of Pinus radiata plantations. Freshw. Biol. 61, 69–79. https://doi.org/10.1111/fwb.12680.

Maxwell, T.A.D., Jennings, S., 2006. Predicting abundance-body size relationships in functional and taxonomic subsets of food webs. Oecologia 150, 282–290.

Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L.F., Backeljau, T., Bonte, D., Brans, K.I., Cours, M., Dahirel, M., Debortoli, N., De Wolf, K., Engelen, J.M.T., Fontaneto, D., Gianuca, A.T., Govaert, L., Hendrickx, F., Higuti, J., Lens, L., Martens, K., Matheve, H., Matthysen, E., Piano, E., Sablon, R., Schön, I., Van Doninck, K., De Meester, L., Van Dyck, H., 2018. Body-size shifts in aquatic and terrestrial urban communities. Nature 558, 113–116. https://doi.org/10.1038/s41586-018-0140-0.

Meyer, E., 1989. The relationship between body length parameters and dry mass in running water invertebrates. Arch. Hydrobiol. 117, 191–203.

Molinero, J., Pozo, J., 2004. Impact of a eucalyptus (*Eucalyptus globulus* Labill.) plantation on the nutrient content and dynamics of coarse particulate organic matter (CPOM) in a small stream. Hydrobiologia 528, 143–165. https://doi.org/10.1007/s10750-004-2338-4.

Mor, J.R., Muñoz, I., Sabater, S., Zamora, L., Ruhi, A., 2022. Energy limitation or sensitive predators? Trophic and non-trophic impacts of wastewater pollution on stream food webs. Ecology 103, 1–13. https://doi.org/10.1002/ecy.3587.

Mulder, C., Elser, J.J., 2009. Soil acidity, ecological stoichiometry and allometric scaling in grassland food webs. Glob. Chang. Biol. 15, 2730–2738. https://doi.org/10.1111/j.1365-2486.2009.01899.x.

Nakagawa, S., Schielzeth, H., 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods Ecol. Evol. 4, 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x.

Nee, S., Read, A.F., Greenwood, J.J.D., Harvey, P.H., 1991. The relationship between abundance and body size in British birds. Nature 351, 312–313. https://doi.org/10.1038/351312a0.

Oksanen, J., Simpson, G.L., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., Evangelista, H.B.A., FitzJohn, R., Friendly, M., Furneaux, B., Hannigan, G., Hill, M.O., Lahti, L., McGlinn, D., Ouellette, M.-H., Cunha, E.R., Smith, T., Stier, A., Ter Braak, C.J.F., Weedon, J., 2022. vegan: community ecology package. R package version 2.6-2, https://CRAN.R-project.org/package=vegan.

Ott, D., Digel, C., Rall, B.C., Maraun, M., Scheu, S., Brose, U., 2014. Unifying elemental stoichiometry and metabolic theory in predicting species abundances. Ecol. Lett. 17, 1247–1256. https://doi.org/10.1111/ele.12330.

Pawar, S., Dell, A.I., Savage, V.M., 2012. Dimensionality of consumer search space drives trophic interaction strengths. Nature 486, 485–489. https://doi.org/10.1038/nature11131.

Peralta-Maraver, I., Stubbington, R., Arnon, S., Kratina, P., Krause, S., de Mello Cionek, V., Leite, N.K., da Silva, A.L.L., Thomaz, S.M., Posselt, M., Milner, V.S., Momblanch, A., Moretti, M.S., Nóbrega, R.L.B., Perkins, D.M., Petrucio, M.M., Reche, I., Saito, V., Sarmento, H., Strange, E., Taniwaki, R.H., White, J., Alves, G.H.Z., Robertson, A.L., 2021. The riverine bioreactor: an integrative perspective on biological decomposition of organic matter across riverine habitats. Sci. Total Environ. 772, 145494. https://doi.org/10.1016/j.scitotenv.2021.145494.

Perkins, D.M., McKie, B.G., Malmqvist, B., Gilmour, S.G., Reiss, J., Woodward, G., 2010. Environmental warming and biodiversity–ecosystem functioning in freshwater microcosms. Adv. Ecol. Res., 177–209 https://doi.org/10.1016/B978-0-12-385005-8.00005-8.

Perkins, D.M., Durance, I., Edwards, F.K., Grey, J., Hildrew, A.G., Jackson, M., Jones, J.I., Lauridsen, R.B., Layer-Dobra, K., Thompson, M.S.A., Woodward, G., 2018. Bending the rules: exploitation of allochthonous resources by a top-predator modifies size-abundance scaling in stream food webs. Ecol. Lett. 21, 1771–1780. https://doi.org/10.1111/ele.13147.

Perkins, D.M., Perna, A., Adrian, R., Cermeño, P., Gaedke, U., Huete-Ortega, M., White, E.P., Yvon-Durocher, G., 2019. Energetic equivalence underpins the size structure of tree and phytoplankton communities. Nat. Commun. 10, 255. https://doi.org/10.1038/s41467-018-08039-3.

Perkins, D.M., Durance, I., Jackson, M., Jones, J.I., Lauridsen, R.B., Layer-Dobra, K., Reiss, J., Thompson, M.S.A., Woodward, G., 2021. Systematic variation in food web body-size structure linked to external subsidies. Biol. Lett. 17. https://doi.org/10.1098/rsbl.2020.0798.

Petchey, O.L., Belgrano, A., 2010. Body-size distributions and size-spectra: universal indicators of ecological status? Biol. Lett. 6, 434–437. https://doi.org/10.1098/rsbl.2010.0240.

Piscart, C., Roussel, J.M., Dick, J.T.A., Grosbois, G., Marmonier, P., 2011. Effects of coexistence on habitat use and trophic ecology of interacting native and invasive amphipods. Freshw. Biol. 56, 325–334. https://doi.org/10.1111/j.1365-2427.2010.02500.x.

Pomeranz, J.P.F., Warburton, H.J., Harding, J.S., 2019. Anthropogenic mining alters macroinvertebrate size spectra in streams. Freshw. Biol. 64, 81–92. https://doi.org/10.1111/fwb.13196.

Potapov, A.M., Klarner, B., Sandmann, D., Widyastuti, R., Scheu, S., 2019. Linking size spectrum, energy flux and trophic multifunctionality in soil food webs of tropical land-use systems. J. Anim. Ecol. 88, 1845–1859. https://doi.org/10.1111/1365-2656.13027.

Pozo, J., González, E., Díez, J.R., Molinero, J., Elósegui, A., 1997. Inputs of particulate organic matter to streams with different riparian vegetation. J. North Am. Benthol. Soc. 16, 602–611. https://doi.org/10.2307/1468147.

Pozo, J., Casas, J., Menéndez, M., Mollá, S., Arostegui, I., Basaguren, A., Casado, C., Descals, E., García-Avilés, J., González, J.M., Larrañaga, A., López, E., Lusi, M., Moya, O., Pérez, J., Riera, T., Roblas, N., Salinas, M.J., 2011. Leaf-litter decomposition in headwater streams: a comparison of the process among four climatic regions. J. North Am. Benthol. Soc. 30, 935–950. https://doi.org/10.1899/10-153.1.

R Core Team, 2019. R: a language and environment for statistical computing.

Reuman, D.C., Mulder, C., Banasek-Richter, C., Blandenier, M.F.C., Breure, A.M., Den Hollander, H., Kneitel, J.M., Raffaelli, D., Woodward, G., Cohen, J.E., 2009. Allometry of body dize and abundance in 166 food webs. Adv. Ecol. Res. 41, 1–44. https://doi.org/10.1016/s0065-2504(09)00401-2.

Rewicz, T., Grabowski, M., MacNeil, C., Bącela-Spychalska, K., 2014. The profile of a 'perfect' invader – the case of killer shrimp. Dikerogammarus villosus. Aquat. Invasions 9, 267–288. https://doi.org/10.3391/ai.2014.9.3.04.

Robinson, J.P.W., Williams, I.D., Edwards, A.M., McPherson, J., Yeager, L., Vigliola, L., Brainard, R.E., Baum, J.K., 2017. Fishing degrades size structure of coral reef fish communities. Glob. Chang. Biol. 23, 1009–1022. https://doi.org/10.1111/gcb.13482.

Rossberg, A.G., Gaedke, U., Kratina, P., 2019. Dome patterns in pelagic size spectra reveal strong trophic cascades. Nat. Commun. 10, 1–11. https://doi.org/10.1038/s41467-019-12289-0.

Tachet, H., Richoux, P., Bournaud, M., Usseglio-Polatera, P., 2002. Invertébrés d'eau douce: systématique, biologie et écologie. CNRS Editions, Paris.

Tonin, A.M., Pozo, J., Monroy, S., Basaguren, A., Pérez, J., Gonçalves, J.F., Pearson, R., Cardinale, B.J., Boyero, L., 2018. Interactions between large and small detritivores influence how biodiversity impacts litter decomposition. J. Anim. Ecol. 87, 1465–1474. https://doi.org/10.1111/1365-2656.12876.

Wallace, J.B., Eggert, S.L., Meyer, J.L., Webster, J.R., 1997. Multiple trophic levels of a forest stream linked to terrestrial litter inputs. Science 277, 102–104. https://doi.org/10.1126/science.277.5322.102.

White, E.P., Ernest, S.K.M., Kerkhoff, A.J., Enquist, B.J., 2007. Relationships between body size and abundance in ecology. Trends Ecol. Evol. 22, 323–330. https://doi.org/10.1016/j.tree.2007.03.007.

Wohl, E., Dwire, K., Sutfin, N., Polvi, L., Bazan, R., 2012. Mechanisms of carbon storage in mountainous headwater rivers. Nat. Commun. 3, 1–8. https://doi.org/10.1038/ncomms2274.

Woodward, G., Gessner, M.O., Giller, P.S., Gulis, V., Hladyz, S., Lecerf, A., Malmqvist, B., McKie, B.G., Tiegs, S.D., Cariss, H., Dobson, M., Elosegi, A., Ferreira, V., Graca, M.A.S., Fleituch, T., Lacoursiere, J.O., Nistorescu, M., Pozo, J., Risnoveanu, G., Schindler, M., Vadineanu, A., Vought, L.B.-M., Chauvet, E., 2012. Continental-scale effects of nutrient pollution on stream ecosystem functioning. Science 336, 1438–1440. https://doi.org/10.1126/science.1219534.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403.