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# Aquatic hyphomycetes, benthic macroinvertebrates and leaf litter decomposition in streams naturally differing in riparian vegetation

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**Abstract** Small forest streams and their riparian vegetation are closely linked ecosystems. Stream consumers obtain most of their energy from leaf litter provided by the terrestrial vegetation. Thus, understanding the relationship between riparian vegetation, aquatic communities and litter decomposition may help explaining the variability in aquatic communities and processes among non-impacted streams, and anticipate their responses to anthropogenic-induced changes in the riparian vegetation. We surveyed 10 small non-impacted forest streams in central Portugal for riparian vegetation (species richness), benthic litter (species richness and biomass), aquatic hyphomycete conidia in transport (species richness and conidia concentration) and macroinvertebrates associated with benthic litter (taxon richness, density and biomass), during the litter fall peak. We found significant correlations between (a) aquatic communities and riparian vegetation species richness, (b) aquatic communities and benthic litter species richness and biomass and (c) within aquatic communities. Oak litter decomposition rates (from a previous experiment on the same streams) were also correlated with riparian tree species richness. This survey showed that spatial variability in riparian vegetation, benthic litter, aquatic communities and litter decomposition can be high even within a relatively small area, and allowed the identification of complex interactions between these components of the aquatic detrital food web. The

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positive correlation between aquatic hyphomycete species richness, macroinvertebrate taxon richness, litter decomposition and riparian tree species richness suggests that anthropogenic-induced decreases in riparian species richness may affect aquatic communities and processes. Surveys over streams naturally differing in environmental conditions may allow forecasting the response of aquatic communities and processes to anthropogenic activities.

**Keywords** Deciduous vegetation · Forest streams · Litter breakdown · Litter processing

## Introduction

The relationships between the diversity of resources and consumers and between the diversity of consumers and ecosystem process rates have long been a subject of interest for ecologists (Gessner et al. 2010). In forest streams, aquatic communities depend on the supply of organic matter from the riparian vegetation, mostly in the form of leaf litter (Wallace et al. 1997). Once in the water, leaf litter is colonized and conditioned by microbial decomposers, primarily aquatic hyphomycetes, whose activities (i.e., organic carbon mineralization, conversion of coarse into fine particulate organic matter (FPOM) and production of reproductive propagules) cause litter mass loss (Gulis and Suberkropp 2003; Cornut et al. 2010). Additionally, the maceration of leaf litter by fungal enzymes and the accumulation of fungal biomass increases litter palatability to leaf-shredding detritivores (detritivores henceforth), who convert detritus into secondary production and FPOM though litter fragmentation and feces production, causing further litter mass loss (Cummins et al. 1989; Canhoto and Graça 2008).

In temperate climates, streams flowing through native deciduous mixed forests receive a diverse input of leaf litter, especially during the litter fall peak in autumn/winter (Swan and Palmer 2004; Lecerf et al. 2005). Leaf litter in these multi-species mixtures varies in physical and chemical properties (Ostrofsky 1997), with high-quality leaf litter (i.e., softer leaves with low lignin and/or high nutrient concentration) being generally colonized and decomposed faster than low-quality litter (Gessner and Chauvet 1994; Schindler and Gessner 2009; Frainer et al. 2015). Recalcitrant litter may, however, provide more stable substrates

that allow decomposer activity and support consumers long after the litter fall peak has passed (Ferreira et al. 2015a). Since fungi and detritivores exhibit substrate preferences (Canhoto and Graça 1995, 1996; Gulis 2001; Swan and Palmer 2006) and colonize litter following an ecological succession (Gessner et al. 1993; Gulis and Suberkropp 2003; Gonçalves et al. 2004), more diverse riparian vegetation and benthic litter will likely support more diverse aquatic communities. Indeed, previous studies have found a positive correlation between fungal species richness and riparian tree or benthic leaf litter species richness (Rajashekhar and Kaveriappa 2003; Laitung and Chauvet 2005; Lecerf et al. 2005), although the relationship between detritivore diversity and riparian tree or benthic leaf litter species richness is not clear (Jonsson et al. 2001).

Differences in benthic litter standing stock among streams, which can be driven by differences in riparian plant composition and stream retentive capacity, may also explain differences in aquatic communities. For example, streams with higher benthic litter storage are likely to have higher diversity, abundance and biomass of consumer taxa ('productivity hypothesis'; Srivastava and Lawton 1998 and references therein). Indeed, higher fungal species richness and conidia concentrations have been found in stream sections where litter retention was experimentally enhanced (Laitung et al. 2002). Macroinvertebrate taxon richness and density were also found to increase with benthic litter standing stock in surveys and manipulative studies (Richardson 1991; Dobson and Hildrew 1992; Dudgeon 1994; Negishi and Richardson 2003; Graça et al. 2004).

High leaf litter species richness is likely to stimulate litter decomposition (Lecerf et al. 2011) by sustaining more diverse decomposer communities. Increases in species richness of aquatic hyphomycetes and detritivores may stimulate litter decomposition through complementarity in species characteristics (e.g., enzymatic activities) or increased chance of having a highly efficient species (Jonsson and Malmqvist 2000, 2003; Jonsson et al. 2001; Duarte et al. 2006). High abundance of detritivores generally also promotes litter decomposition (Tiegs et al. 2008).

Unraveling the relationships between riparian vegetation, benthic litter, aquatic communities and processes is of fundamental importance to better understand the natural variability in aquatic communities and process rates among non-disturbed streams.

If we understand how aquatic communities and litter decomposition correlate with riparian species richness and benthic litter species richness and abundance, we may be able to anticipate, and eventually mitigate, the responses of aquatic communities and processes to anthropogenic-induced changes to the riparian vegetation. However, previous surveys of forest streams have generally focused on the relationship between aquatic communities (either aquatic hyphomycetes or macroinvertebrates) and environmental variables and riparian vegetation, but have not simultaneously considered all the components of the detrital food web (riparian vegetation, benthic litter, microbial decomposers, macroinvertebrates, and litter decomposition). We surveyed 10 non-disturbed forest streams in central Portugal with similar environmental characteristics, but naturally differing in riparian vegetation, for riparian woody species richness, benthic litter species richness and biomass, and aquatic communities (aquatic hyphomycete conidia in transport and benthic macroinvertebrates), to uncover possible correlations among these variables. Based on existing evidence, as explained above, we expected positive correlations between (1) riparian woody and benthic litter species richness, (2) benthic litter species richness and abundance and aquatic hyphomycetes species richness and conidia concentration, (3) benthic litter species richness and abundance and macroinvertebrate/detritivore taxon richness, density and biomass, and (4) aquatic hyphomycetes species richness and conidia concentration and macroinvertebrate/detritivore taxon richness, density and biomass (Fig. 1a). The expected positive correlation between litter decomposition rates and riparian woody species richness was tested using published litter decomposition rates for the same streams.

## Methods

### Streams and riparian vegetation

Ten small (1st–4th order; Strahler 1957) forest streams were sampled in Lousã and Caramulo Mountains (113–814 m a.s.l.), central Portugal, in November 13–16, 2006, during the peak of litter fall (Table 1). The climate was temperate, and both mountain ranges had similar rainfall (Lousã: 91.3 mm; Caramulo: 107.8 mm) and maximum (Lousã: 21.3 °C; Caramulo: 21.0 °C) and minimum (Lousã: 11.1 °C;

Caramulo: 10.8 °C) air temperatures (average values for 2006; IPMA 2007). The streams had little human impact and similar geomorphology and water characteristics and had been used as reference streams in previous litter decomposition experiments (e.g., Gulis et al. 2006; Ferreira et al. 2015b).

A 50-m-long reach was selected in each stream for water characterization and biological sampling (see below). The streams had similar geology (schist bedrock, except for Agadão stream that had granite bedrock), were cool (9.3–13.7 °C), well aerated (>10 mg $O_2$ $L^{-1}$) and circumneutral (pH = 6.3–7.1), and had low conductivity ($\leq$ 46 µS cm$^{-1}$) and low-to-moderate nutrient concentrations (50–408 µg N $L^{-1}$, 5–29 µg SRP $L^{-1}$) (Table 1).

Woody species (trees + shrubs + lianas) and tree richness in the riparian vegetation were determined in a 50-m-long and 10-m-wide area parallel to the stream reach on each margin in July 10–14, 2007. The riparian survey was done in spring, since plant species identification is easier in this season than in autumn when most deciduous species have already shed their leaves. Given that we were interested in woody species only, all species identified in spring were already present in autumn.

### Benthic leaf litter

Ten random leaf litter samples were taken in each of the 10 stream reaches. For each sample, a 20 × 20 cm wood quadrat was placed on top of a leaf patch, and leaves and any attached invertebrates were retrieved by hand from the top 3–4 cm, to avoid anoxic conditions at higher depths and the inorganic substrate below. For small and sparse leaf patches, leaves were collected from several locations or patches within a <2-m radius to get a whole sample with an area of ∼20 × 20 cm. To minimize the loss of macroinvertebrates during the sampling, a net (0.3 × 0.3 m opening, 0.5-mm mesh pore) was placed immediately downstream of the leaf pack during litter retrieval. Litter samples and the material collected in the net were placed in individual plastic bags and transported in ice to the laboratory.

In the laboratory, leaf samples were rinsed through a 0.5-mm mesh sieve to retain macroinvertebrates and litter fragments. Litter fragments >1 cm were sorted and assigned to morphotypes based on their characteristics (e.g., venation, presence/absence of trichomes, shape of leaf margins) to allow estimation
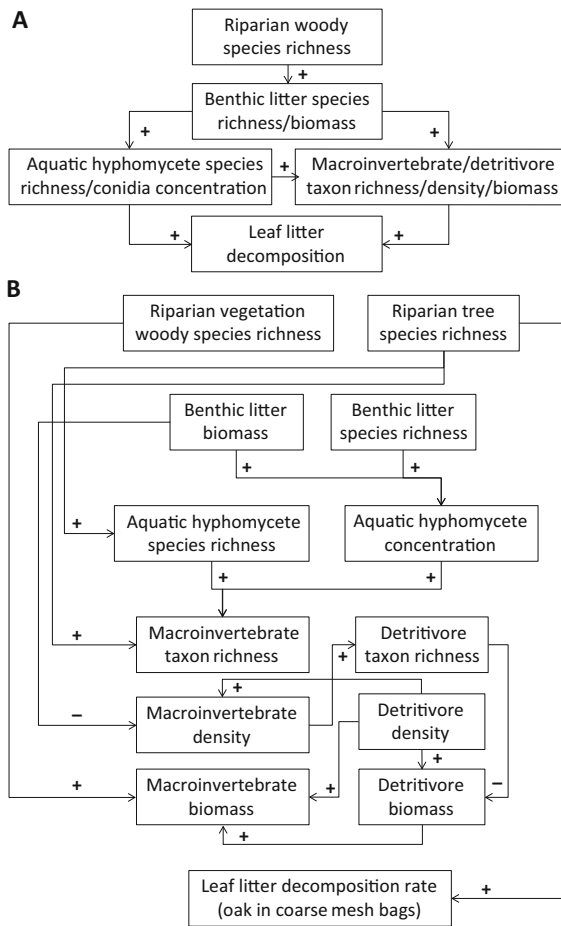
**A**

Riparian woody species richness

+

Benthic litter species richness/biomass

+    +

Aquatic hyphomycete species richness/conidia concentration   +   Macroinvertebrate/detritivore taxon richness/density/biomass

+    Leaf litter decomposition    +

**B**

Riparian vegetation woody species richness          Riparian tree species richness

Benthic litter biomass          Benthic litter species richness

+

+   Aquatic hyphomycete species richness          Aquatic hyphomycete concentration

+          +

+   Macroinvertebrate taxon richness          Detritivore taxon richness

+

–   Macroinvertebrate density          Detritivore density

+

+   Macroinvertebrate biomass   +   Detritivore biomass   –

+

Leaf litter decomposition rate (oak in coarse mesh bags)   +

Fig. 1 Graphical representation of expected correlations between biological variables (**a**) and significant correlations found in our survey (**b**). *Plus* positive correlation; *minus* negative correlation

of litter species richness. Litter was oven dried at 80 °C for 48 h and weighed ($\pm$0.01 g) to determine litter dry mass (DM). Dry mass was ignited at 500 °C for 4 h and ashes were weighed ($\pm$0.01 g). Ash-free dry mass (AFDM) was determined as the difference between DM and ash mass. Benthic leaf litter species richness was expressed as the number of taxa per stream (samples combined), and biomass as g of litter AFDM per sample (average of 10 samples).

### Benthic macroinvertebrates

Macroinvertebrates associated with benthic leaf litter were transferred into scintillation vials and stored in a solution of ethanol/formalin (70 %/10 % volume,

which minimized mass loss; Leuven et al. 1985; von Schiller and Solimini 2005) until later identification (generally genus or species level; Tachet et al. 2000; Vieira-Lanero 2000), counting, and biomass determination. Individuals were generally measured (body length or head width) using an eyepiece reticle in a stereoscopic microscope, and biomass was estimated using published body length–DM or head width–DM relationships (Meyer 1989; Burgherr and Meyer 1997; Benke et al. 1999; Johnston and Cunjak 1999). When relationships for the same taxa were given by multiple publications, the relationship to be used was selected based on the following criteria: (1) it should be derived for European invertebrates, (2) the body length or head width range used should contain the range observed for our individuals, (3) it should have the largest sample size and highest coefficient of determination, and (4) the conservation method should be the same as ours. *Tipula* sp. individuals were weighed wet ($\pm$1 mg) and wet mass was converted into DM following Canhoto (1994). Oligochaeta and *Herpobdella octoculata* individuals were oven dried at 80 °C for 24 h and weighed ($\pm$1 mg). Macroinvertebrates were grouped into two categories: leaf-shredding detritivores and non-detritivores following Tachet et al. (2000). Macroinvertebrate taxon richness was expressed as number of taxa per stream (samples combined), density as number of individuals per g of litter AFDM, and biomass as mg per g of litter AFDM (average of 10 samples).

### Aquatic hyphomycetes conidia in transport

At each stream reach, triplicate 500-mL samples of stream water were filtered through membrane filters (47 mm diameter, 5-μm pore size; SMWP membrane filters, Millipore Corp., Billerica, MA, USA) to retain conidia from aquatic hyphomycetes. The filters were stained with cotton blue in lactic acid (0.05 %) and stored individually in sealed Petri dishes. In the laboratory, the filters were cut by half, mounted on a slide, and conidia were identified and counted under a compound microscope (Leitz Diaplan, Wetzlar, Germany) at 200$\times$ magnification (Graça et al. 2005). Aquatic hyphomycete species richness was expressed as number of species per stream (triplicates combined) and conidia concentration as number of conidia per L (average of triplicates).

**Table 1** Location and physical and chemical characterization of the 10 study streams in central Portugal

| Variables | Tábuas | Sardeira | Candal 1 | Candal 2 | Catarredor 1 | Catarredor 2 | Foz | Tojosa | Agadão | Agueda | Methods |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Mountain range | Lousã | Lousã | Lousã | Lousã | Lousã | Lousã | Caramulo | Caramulo | Caramulo | Caramulo | |
| Latitude, N | 40°03'49" | 40°05'21'' | 40°04'44" | 40°04'44" | 40°04'10" | 40°04'07" | 40°30'57" | 40°31'29" | 40°31'59" | 40°35'44" | GPS (Garmin, Barcelona, Spain) |
| Longitude, W | 8°17'59" | 8°12'06" | 8°12'10" | 8°12'30" | 8°12'39" | 8°13'18" | 8°13'23" | 8°11'08" | 8°13'53" | 8°10'30" | Idem |
| Elevation (m a.s.l.) | 545 | 683 | 592 | 592 | 741 | 814 | 113 | 255 | 570 | 796 | Idem |
| Slope (%) | 17 | 13 | 43 | 38 | 59 | 35 | 11 | 20 | 23 | 11 | Military maps 1: 250000 |
| Catchment area (km²) | 2.1 | 2.9 | 0.8 | 0.3 | 0.5 | 0.2 | 3.8 | 3.2 | 2.4 | 0.8 | Idem |
| Substrate | Schist | Schist | Schist | Schist | Schist | Schist | Schist | Schist | Granite | Schist | Field observation |
| Temperature (°C) | 11.9 | 11.6 | 10.5 | 10.0 | 10.4 | 9.3 | 13.7 | 12.8 | 11.5 | 11.2 | Field probe LF 330 (WTW, Weilheim, Germany) |
| Conductivity ($\mu S\ cm^{-1}$) | 37 | 32 | 25 | 22 | 31 | 26 | 46 | 35 | 39 | 31 | Idem |
| Dissolved oxygen ($mg\ L^{-1}$) | 11.0 | 10.8 | 11.2 | 11.2 | 11.2 | 11.2 | 10.1 | 10.0 | 10.1 | 10.3 | Field probe Oxi 92 (WTW, Weilheim, Germany) |
| pH | 6.8 | 6.8 | 7.1 | 6.4 | 6.5 | 6.9 | 6.7 | 6.7 | 6.7 | 6.3 | Field probe Jenway 3310 (Bibby Scientific Ltd., Staffordshire, UK) |
| $NO_3^- + NO_2^-$–N ($\mu g\ L^{-1}$) | 137 | 50 | 56 | 65 | 295 | 101 | 117 | 53 | 408 | 369 | Ion chromatography (Dionex DX-120, Sunnyvale, CA, USA) |
| SRP ($\mu g\ L^{-1}$) | 10 | 7 | 8 | 8 | 7 | 5 | 7 | 29 | 25 | 5 | Ascorbic acid method (APHA 1995) |

Leaf litter decomposition

Leaf litter decomposition experiments were carried out in winter 2002/2003 at the 10 streams surveyed in the present study (see Gulis et al. 2006; Ferreira et al. 2015b). Briefly, senescent, air-dried oak (*Quercus robur*) leaf litter was enclosed in coarse (10-mm mesh pore) and fine (0.5-mm mesh pore) mesh bags (10 × 15 cm) and incubated in the 10 streams in January 2003. Litter bags ($n = 6$) were retrieved from the streams after 57 days, and remaining AFDM was determined. Litter decomposition rates ($k$, day$^{-1}$) were estimated by fitting a negative exponential model to the fraction of AFDM remaining over time (see Gulis et al. 2006; Ferreira et al. 2015b for a full description of the methods).

Data analyses

Correlations among variables were assessed by Pearson correlation; variables that were not normally distributed (checked with Shapiro–Wilk test) were log($x$)-transformed. Pearson correlation coefficients (r) were obtained by permutation with 'corPerm' function (developed by P. Legendre; http://adn.biol. umontreal.ca/∼numericalecology/Rcode/), using R software (R Core Team 2013). Water temperature was negatively correlated with elevation ($r = -0.84$, $p = 0.002$), but since temperature was recorded on a single date, elevation was selected for further analyses instead. Dissolved oxygen was above saturation in all streams, conductivity was low, and pH varied by <1 unit, and therefore these

variables were not considered in further analyses. Nitrogen and soluble reactive phosphorus (SRP) concentration varied by one order of magnitude across streams, but no significant correlations with aquatic communities were obtained ($p > 0.055$), and thus results are not shown. Published decomposition rates ($k$, day$^{-1}$) for oak leaf litter incubated in the same streams 4 years earlier (see Gulis et al. 2006; Ferreira et al. 2015b) were contrasted against riparian woody species richness and riparian tree species richness since these were unlikely to change much in our non-impacted streams between the previous studies and the present survey.

Results

Riparian vegetation and benthic leaf litter

Streams were surrounded by dense vegetation, generally dominated by *Q. robur*, *Castanea sativa* or *Salix atrocinerea* trees. Although a total of 58 woody species were identified across streams (including 35 tree species; Online resource ESM 1), woody species richness per stream varied between 10 and 23 species (6–14 tree species) (Table 2). Species richness in the benthic litter standing stock per stream varied between 6 and 16 species (with *Q. robur* and *C. sativa* as dominant species), and benthic litter biomass between 7.1 and 76.4 g AFDM sample$^{-1}$ (Table 2). The correlations between benthic litter species richness or biomass and riparian tree or woody species richness were not significant (Table 3; Fig. 1b).

**Table 2** Riparian woody species richness and benthic leaf litter species richness and biomass in the 10 study streams in central Portugal

| Riparian species and benthic litter | Tábuas | Sardeira | Candal 1 | Candal 2 | Catarredor 1 | Catarredor 2 | Foz | Tojosa | Agadão | Agueda |
|---|---|---|---|---|---|---|---|---|---|---|
| *Riparian woody species richness (no. taxa stream$^{-1}$)* | | | | | | | | | | |
| Woody species | 13 | 23 | 18 | 10 | 14 | 14 | 15 | 21 | 19 | 18 |
| Trees | 8 | 14 | 13 | 6 | 10 | 8 | 6 | 10 | 10 | 7 |
| *Benthic litter* | | | | | | | | | | |
| Species richness (no. taxa stream$^{-1}$) | 8 | 8 | 13 | 8 | 15 | 16 | 13 | 7 | 6 | 11 |
| Biomass (g AFDM sample$^{-1}$) | 25.00 | 8.56 | 16.77 | 8.13 | 76.40 | 14.62 | 14.31 | 7.38 | 7.12 | 8.80 |

Woody species, trees + shrubs + lianas; AFDM, ash-free dry mass

**Table 3** Pearson correlations for riparian vegetation, benthic leaf litter, aquatic hyphomycetes in transport, macroinvertebrates associated with benthic litter and litter decomposition rates ($n = 10$ streams in central Portugal)

| Variables | | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Riparian tree species richness | 1 | | *0.023* | *0.757* | *0.931* | *0.022* | *0.082* | *0.026* | *0.504* | *0.383* | *0.354* | *0.377* | *0.380* | *0.019* | *0.389* |
| Riparian woody species richness | 2 | **0.71** | | *0.348* | *0.233* | *0.211* | *0.937* | *0.121* | *0.869* | *0.123* | *0.288* | *0.021* | *0.055* | *0.276* | *0.552* |
| Benthic litter species richness | 3 | −0.11 | −0.33 | | *0.043* | *0.807* | *0.045* | *0.571* | *0.649* | *0.376* | *0.528* | *0.534* | *0.531* | | |
| Benthic litter biomass* | 4 | 0.03 | −0.42 | 0.62 | | *0.663* | *0.033* | *0.417* | *0.238* | *0.026* | *0.126* | *0.077* | *0.112* | | |
| Hyphomycete species richness | 5 | **0.71** | 0.43 | −0.10 | 0.15 | | *0.107* | *<0.001* | *0.669* | *0.552* | *0.709* | *0.632* | *0.323* | | |
| Hyphomycete concentration | 6 | 0.57 | 0.03 | **0.65** | **0.66** | 0.53 | | *0.043* | *0.358* | *0.659* | *0.676* | *0.494* | *0.635* | | |
| Macroinvertebrate taxon richness | 7 | **0.69** | 0.53 | 0.20 | 0.29 | **0.89** | **0.65** | | *0.962* | *0.585* | *0.861* | *0.557* | *0.366* | | |
| Detritivore taxon richness | 8 | 0.24 | 0.07 | 0.18 | 0.42 | −0.16 | 0.32 | 0.03 | | *0.894* | *0.382* | *0.170* | ***0.040*** | | |
| Macroinvertebrate density | 9 | 0.31 | 0.52 | −0.31 | **−0.68** | 0.22 | −0.16 | 0.20 | −0.05 | | ***0.023*** | *0.213* | *0.232* | | |
| Detritivore density | 10 | 0.33 | 0.38 | −0.25 | −0.52 | 0.12 | −0.16 | 0.06 | −0.31 | **0.68** | | ***0.035*** | ***0.045*** | | |
| Macroinvertebrate biomass | 11 | 0.31 | **0.71** | −0.23 | −0.58 | 0.17 | −0.25 | 0.21 | −0.48 | 0.43 | **0.67** | | *<0.001* | | |
| Detritivore biomass | 12 | 0.31 | 0.63 | −0.23 | −0.54 | 0.34 | −0.18 | 0.32 | **−0.65** | 0.42 | **0.67** | **0.96** | | | |
| k oak in coarse mesh | 13 | **0.70** | 0.39 | | | | | | | | | | | | *0.240* |
| k oak in fine mesh | 14 | 0.31 | 0.21 | | | | | | | | | | | 0.42 | |

Pearson r and p values (italics) are shown; significant correlations ($p < 0.050$) are shown in bold. The fraction of the variance in the dependent variable that is explained by the independent variable in a linear regression ($R^2$) can be estimated as $r \times r$ and varied between 0.42 and 0.92 for the significant correlations. Decomposition rates ($k$, day$^{-1}$) are contrasted only against riparian tree and woody species richness because the litter decomposition experiment was performed 4 years before the stream survey (see Methods for details)

* log(x)-transformed

**Table 4** Aquatic hyphomycete conidia in transport and macroinvertebrate taxon richness, density and biomass associated with benthic leaf litter in the 10 study streams in central Portugal

| Stream name | Tábuas | Sardeira | Candal 1 | Candal 2 | Catarredor 1 | Catarredor 2 | Foz | Tojosa | Agadão | Agueda |
|---|---|---|---|---|---|---|---|---|---|---|
| *Aquatic hyphomycete conidia in transport* | | | | | | | | | | |
| Species richness (no. species stream$^{-1}$) | 11 | 16 | 14 | 8 | 12 | 9 | 13 | 12 | 12 | 4 |
| Conidia concentration (no. conidia L$^{-1}$) | 1905 | 5015 | 9191 | 1370 | 9453 | 5899 | 3332 | 2420 | 2050 | 84 |
| *Macroinvertebrate taxon richness (no. taxa stream$^{-1}$)* | | | | | | | | | | |
| Total macroinvertebrates | 21 | 26 | 24 | 16 | 24 | 22 | 24 | 23 | 22 | 17 |
| Detritivores | 9 | 8 | 9 | 8 | 10 | 9 | 7 | 10 | 8 | 9 |
| *Macroinvertebrate density (no. ind. g$^{-1}$ AFDM)* | | | | | | | | | | |
| Total macroinvertebrates | 3 | 9 | 4 | 6 | 1 | 8 | 4 | 9 | 5 | 4 |
| Detritivores | 2 | 6 | 2 | 3 | 1 | 3 | 1 | 2 | 2 | 3 |
| *Macroinvertebrate biomass (mg g$^{-1}$ AFDM)* | | | | | | | | | | |
| Total macroinvertebrates | 1.25 | 6.21 | 2.63 | 1.82 | 0.85 | 2.15 | 3.91 | 2.66 | 3.04 | 4.62 |
| Detritivores | 1.10 | 4.46 | 2.01 | 1.58 | 0.71 | 1.59 | 3.23 | 1.66 | 2.36 | 2.58 |

Aquatic hyphomycete conidia in transport

Twenty-five aquatic hyphomycete species were found across streams, with *Articulospora tetracladia* and *Flagellospora curvula* being the most common, present in all 10 streams (Online resource ESM 2). Species richness per stream varied between 4 and 16 species (Table 4). Aquatic hyphomycete species richness was positively correlated with riparian tree species richness (Fig. 2a) and macroinvertebrate taxon richness (Table 3; Fig. 1b).

Conidia concentration in the water column varied among streams by two orders of magnitude: 84–9453 conidia L$^{-1}$ (Table 4). *Anguillospora filiformis*, *A. tetracladia*, *F. curvula*, *Lunulospora curvula*, and *Tetrachaetum elegans* were the species contributing the most to conidial production (Online resource ESM 2). Conidia concentration was positively correlated with benthic litter species richness, benthic litter biomass and macroinvertebrate taxon richness (Table 3; Fig. 1b).

Benthic macroinvertebrates

Benthic leaf litter across streams was colonized by 47 macroinvertebrate taxa, 14 of which were detritivores (Online resource ESM 3). Macroinvertebrate taxon richness per stream varied between 16 and 26 taxa, and detritivore taxon richness between 7 and 10 taxa (29–53 % of total taxa) (Table 4). Among non-detritivores, Orthocladiinae midges, Simuliini blackflies, and the beetle *Hydraena* sp. were the most common taxa, present in all 10 streams. The most common detritivores were the caddisfly *Lepidostoma hirtum*, the stoneflies *Nemoura* sp., *Protonemoura* sp. and *Leutra* sp., and the beetle *Elodes* sp., which were found in all 10 streams (Online resource ESM 3). Macroinvertebrate taxon richness was positively correlated with riparian tree species richness (Table 3; Figs. 1b, 2b).

A total of 6059 individuals was collected across streams, but densities of macroinvertebrates (1–9 individuals g$^{-1}$ AFDM) and detritivores (1–6 individuals g$^{-1}$ AFDM; 22–70 % of total macroinvertebrate density) were low and varied among streams (Table 4). Among non-detritivores, Orthocladiinae was the most abundant taxon, which dominated macroinvertebrate communities in Catarredor 1, Catarredor 2, Candal 1, Tojosa, and Agadão streams (43–64 % relative contribution to total density). The most abundant detritivores were the stoneflies

*Protonemoura* sp. (up to 42 % relative contribution to total density), *Nemoura* sp. (up to 28 %), and *Leuctra* sp. (up to 16 %), and the caddisfly *L. hirtum* (up to 19 %) (Online resource ESM 3). Macroinvertebrate density was negatively correlated with benthic leaf litter biomass and positively correlated with detritivore density (Table 3; Fig. 1b).
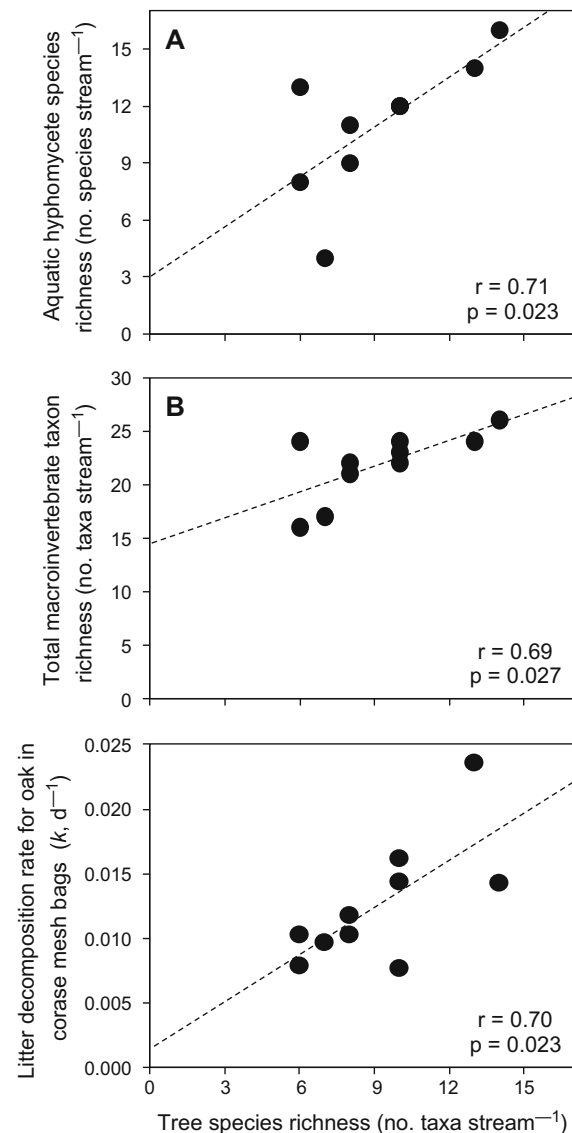


**Fig. 2** Correlations between tree species richness and aquatic hyphomycete species richness (**a**), total macroinvertebrate taxon richness (**b**), and litter decomposition rate for oak in coarse mesh bags (**c**). Pearson r and p values are shown ($n = 10$ streams in central Portugal)

Biomass of macroinvertebrates (0.85–6.21 mg g$^{-1}$ AFDM) and detritivores (0.71–4.46 mg g$^{-1}$ AFDM) on benthic litter also varied among streams (Table 4). Detritivores contributed the most to total macroinvertebrate biomass (56–88 % relative contribution to total biomass), mainly the caddisfly *Alogamus laureatus* (10–75 %), Tipulidae craneflies (18–51 %), and the stoneflies *Protonemura* sp (5–20 %) and *Nemoura* sp. (up to 24 %) (data not shown). Macroinvertebrate biomass was positively correlated with riparian woody species richness and detritivore density (Table 3; Fig. 1b). Detritivore biomass was negatively correlated with detritivore taxon richness and positively correlated with detritivore density and macroinvertebrate biomass (Table 3; Fig. 1b).

Leaf litter decomposition

Oak leaf litter decomposition rates varied among streams, being 0.0077–0.0236 day$^{-1}$ in coarse mesh bags and 0.0043–0.0099 day$^{-1}$ in fine mesh bags (Gulis et al. 2006; Ferreira et al. 2015b). Decomposition rates in coarse mesh bags were positively correlated with riparian tree species richness (Figs. 1b, 2c) and decomposition rates in fine mesh bags were negatively correlated with elevation (Table 3).

**Discussion**

Our results reveal important relationships between riparian vegetation, benthic litter, aquatic communities and litter decomposition in streams that derive most of their energy from litter of terrestrial origin, which are described below.

Benthic leaf litter standing stock

Benthic leaf litter species richness varied up to 2.7 fold among our study streams, but values were similar to those of other streams flowing through similar broadleaf mixed deciduous forests (Gönczöl and Révay 2004; Laitung and Chauvet 2005; Lecerf et al. 2005). Unexpectedly, benthic leaf litter species richness was not correlated with riparian woody or tree species richness, which may have several, non-exclusive explanations. Firstly, leaf litter in a given stream reach can also arrive from upstream reaches (Molinero and Pozo 2003), which may explain the higher benthic

litter species richness than riparian woody species richness found in some streams. Secondly, the composition of the benthic litter standing stock is likely to depend on the identity, abundance and characteristics of the riparian species. Dominant tree species that produce high amounts of leaves will likely contribute high amounts of leaf litter to the stream bed, while less abundant riparian species that have low leaf production may be less represented in the benthic standing stock; some rare riparian species may not even contribute to the benthic litter standing stock in a noticeable way (Gonçalves et al. 2014). In fact, although the riparian woody species richness varied between 10 and 23 species, *Q. robur* and *C. sativa* were the species contributing the most to benthic litter standing stock in all streams. Leaves of different species may also be retained in the stream bed with different efficiency, depending on the leaf litter characteristics and their interaction with stream retentive structures (Canhoto and Graça 1998; Larrañaga et al. 2003). Lastly, benthic sampling was done on a single date, which might have been insufficient to capture the maximum benthic leaf litter diversity in these streams, even if the sampling was done during the litter fall peak.

Aquatic hyphomycete conidia in transport

Aquatic hyphomycete species richness in stream water was low (4–16 species per stream; 25 species in total) when compared with other surveys of non-impacted streams that found 27–77 aquatic hyphomycete species per stream (Gönczöl and Révay 1999; Bärlocher 2000; Bärlocher and Graça 2002; Gulis and Suberkropp 2004; Laitung and Chauvet 2005). However, we note that our survey took place on a single sampling date, while previous surveys were generally based on monthly–bimonthly sampling of stream water over longer time periods (10 months in Laitung and Chauvet (2005) to 5 years in Bärlocher (2000)). The number of aquatic hyphomycete species in stream water is generally highly variable over the year, and 8–81 % of the total number of species can be identified from in a single sampling date (Gönczöl and Révay 1999; Bärlocher 2000; Bärlocher and Graça 2002; Gulis and Suberkropp 2004; Laitung and Chauvet 2005), suggesting that multiple sampling dates are needed to more acurate determinations of aquatic hyphomycete species richness in a stream. In

fact, previous studies have allowed the identification of 26 aquatic hyphomycete species associated with decomposing leaf litter in one of our study streams (Candal 1) and 20 species in another (Candal 2) (Ferreira et al. 2006a, 2012, 2015a; Domingos et al. 2015), in contrast with the 14 and 8 species found in the present survey, respectively.

Aquatic hyphomycete species richness was positively correlated with riparian tree species richness, as expected and previously found in a survey of 21 stream sites in India (Rajashekhar and Kaveriappa 2003). Surveys of 8–10 streams in France also found a positive correlation between aquatic hyphomycete species richness and benthic leaf litter species richness (Laitung and Chauvet 2005; Lecerf et al. 2005), which was not observed in our study (see discussion above on the relationship between riparian and benthic litter species richness). Nevertheless, it is possible that the correlation between aquatic hyphomycete and riparian tree species richness is mediated by changes in benthic leaf litter species composition among streams. Fungi species have distinct enzymatic capabilities (Arsuffi and Suberkropp 1984, 1988), which may translate into distinct colonization patterns and performance on different litter species (Canhoto and Graça 1996; Gulis 2001; Ferreira et al. 2006b). Thus, higher substrate richness may allow the coexistence of more aquatic hyphomycete species (Laitung and Chauvet 2005).

Conidia concentration in stream water varied by two orders of magnitude across streams, and the recorded concentrations included values (>5000 conidia L$^{-1}$ in four streams) that were much higher than those found in other surveys of non-disturbed streams (Bärlocher 2000; Bärlocher and Graça 2002; Gulis and Suberkropp 2004; Laitung and Chauvet 2005). Our highest conidia concentrations resembled those found by Gulis and Suberkropp (2004) in a stream experimentally enriched with nitrogen and phosphorus (383 µg N L$^{-1}$ and 46 µg SRP L$^{-1}$). However, in our case, conidia concentrations in stream water were not correlated with dissolved nutrients, despite the eightfold variation in nitrogen (50–408 µg N L$^{-1}$) and sixfold variation in SRP concentrations (5–29 µg L$^{-1}$) across streams, and the previously reported stimulation of fungal reproductive activity with increases in dissolved nutrient availability (Suberkropp and Chauvet 1995; Gulis and Suberkropp 2003; Ferreira et al. 2006b; Gulis et al. 2006). Our highest conidia concentrations resembled those found

by Gönczöl and Révay (1999, 2004) during autumn. A peak in conidia concentration in stream water is generally found during litter fall (Gönczöl and Révay 1999; Bärlocher 2000), which can help explaining the high conidia concentrations found in our survey.

Conidia concentration was positively correlated with benthic litter species richness and biomass, as expected and in agreement with a previous study (Laitung et al. 2002). Our results suggest that aquatic hyphomycete reproductive output at the stream level may depend more on the availability of organic resources than on dissolved inorganic nutrients. This may be due to the high needs for carbon during conidial production and to nutrient demands by fungi being met at relatively low concentrations of dissolved inorganic nutrients (Rosemond et al. 2002; Ferreira et al. 2006b; Gulis et al. 2006; Fernandes et al. 2014).

Benthic macroinvertebrates

Benthic macroinvertebrates associated with leaf litter were diverse, and detritivores were well represented (29–53 % of total taxon richness), as was also found 4 years earlier in the same streams (Gulis et al. 2006; Ferreira et al. 2015b). Macroinvertebrate taxon richness was positively correlated with aquatic hyphomycete species richness and conidia concentration, as expected. Macroinvertebrates associated with leaf litter may take advantage of aquatic hyphomycetes in multiple ways. Filter feeders may feed on the conidia produced by aquatic hyphomycetes and feeding may be selective toward certain fungal species (Bärlocher and Brendelberger 2004). Even though feeding on conidia may have a negligible contribution to the energetic requirements of filter feeders, they may supply macroinvertebrates with important nutrients and fatty acids as suggested by Bärlocher and Brendelberger (2004). Detritivores may also be favored by increases in aquatic hyphomycete species richness (Lecerf et al. 2005), which may enhance leaf litter palatability due to complementary characteristics among fungal species (e.g., distinct enzymatic activities, distinct concentration of nutrients, distinct identity and concentration of fatty acids; Suberkropp and Arsuffi 1984; Chung and Suberkropp 2009; Funck et al. 2015; Danger et al. 2016). Laboratory experiments have shown that different detritivore species have preferences for distinct fungal species (Arsuffi and Suberkropp 1984, 1986). Thus, an increase in aquatic hyphomycete species richness and conidia concentration may favor a more diverse macroinvertebrate community.

Benthic macroinvertebrate taxon richness and biomass were positively correlated with riparian tree and woody species richness, respectively, but not with benthic litter species richness, suggesting that riparian richness is a better predictor of macroinvertebrate taxon richness than a single measure of benthic litter richness, possibly because the former is a more integrative measure. The increase in the number of riparian species could increase resource availability to benthic macroinvertebrates (although no correlation was found between riparian and benthic litter species richness; but see above), allowing the coexistence of more consumer species, e.g., through niche complementarity (Jonsson and Malmqvist 2000, 2003, 2005). Most detritivores prefer feeding on softer leaves with higher nutrient concentration, while the use of recalcitrant leaves may require specific adaptations (Canhoto and Graça 1995; Azevedo-Pereira et al. 2006). For instance, eucalypt leaves, which are tough and rich in tannins and essential oils, are rarely preferred as food resources by detritivores, in part because tannins bind to proteins (enzymes) and prevent leaf litter digestion, but craneflies (Tipulidae) are able to feed on these leaves because their alkaline guts prevent the formation of tannin–protein complexes (Canhoto and Graça 2006). Leaf litter species with higher concentration of secondary compounds may be preferred by some caddisflies for case building (Moretti et al. 2009). Tough leaf litter may provide grazers with biofilm, and soft leaf litter may provide fine particulate organic matter to benthic collectors and filter feeders. Tough leaf litter may also offer shelter and protection from predators (Boyero 2011).

Benthic macroinvertebrate density was negatively correlated with benthic litter biomass, which was unexpected and contradicts previous observations for streams in our study region (Graça et al. 2004) and elsewhere (Dudgeon 1994), where positive correlations were found. Manipulative studies in streams have also found higher macroinvertebrate density with increases in litter retention (Richardson 1991; Dobson and Hildrew 1992; Negishi and Richardson 2003; but see Tiegs et al. 2008). However, our results could be explained by higher concentration of macroinvertebrates in litter packs in streams with lower benthic litter biomass, and/or higher dispersion of

macroinvertebrates in streams with higher benthic litter biomass (Tiegs et al. 2008). Benthic macroinvertebrate density was positively correlated with detritivore density and macroinvertebrate biomass was positively correlated with detritivore density and biomass. Detritivores contributed largely to macroinvertebrate density (22–70 %) and biomass (56–88 %), with large numbers of small Leuctridae and Nemouridae stoneflies (2065 individuals found in this study) and with large taxa (e.g., the caddisflies *L. hirtum* and *A. laureatus*, and Tipulidae craneflies). Detritivore biomass was positively correlated with detritivore density and negatively correlated with detritivore taxon richness, suggesting that richer detritivore communities are dominated by small taxa.

Leaf litter decomposition

As expected, decomposition rates of oak leaf litter in coarse mesh bags were positively correlated with riparian tree species richness (Lecerf et al. 2011), which was possibly mediated by changes in aquatic communities. Although we could not test the correlation between litter decomposition rates and aquatic communities, since both were assessed at different times, we found positive correlations between riparian tree, aquatic hyphomycete species richness and macroinvertebrate taxon richness (see above). Increases in aquatic hyphomycete and macroinvertebrate taxon richness may stimulate litter decomposition due to complementarity or facilitation in resource use, or to the higher chance of having a particularly efficient species (Jonsson and Malmqvist 2000; Jonsson et al. 2001; Bärlocher and Corkum 2003; Duarte et al. 2006).

Decomposition rates of oak litter in fine mesh bags were negatively correlated with elevation, as observed previously in a survey of 14 stream sites over an elevation gradient in France (Fabre and Chauvet 1998). Elevation can be taken as a surrogate of temperature, which suggests a limitation of decomposer activity at higher elevations (lower temperature). In fact, fungal biomass on leaf litter decreased with increasing elevation in France (Fabre and Chauvet 1998). In our case, however, no correlation was found between aquatic hyphomycetes and elevation, but we recall that litter decomposition rates were assessed 4 years earlier. Nevertheless, in an experiment manipulating stream water temperature in

Candal 1 stream (Lousã Mountain), oak leaf litter decomposed faster when temperature was increased by ∼3 °C in winter, although no strong effect of temperature was found on decomposers associated to litter (Ferreira and Canhoto 2015; Ferreira et al. 2015a).

## Conclusion

This survey of non-impacted forest streams in central Portugal showed that spatial variability in riparian vegetation, benthic litter, aquatic communities and litter decomposition can be high even within a relatively small area, and allowed the identification of complex interactions between these variables. Aquatic hyphomycete species richness, macroinvertebrate taxon richness, and oak litter decomposition were positively correlated with riparian tree species richness in these non-impacted streams, suggesting that anthropogenic-induced decreases in riparian species richness may affect aquatic communities and ecosystem processes. Decreases in riparian species richness could result from forestry practices (e.g., commercial monocultures), invasion by exotic plant species, plant disease outbreaks and climate change (Kominoski et al. 2013; Ferreira et al. 2016). In fact, extensive areas of the Lousã Mountain are becoming invaded by *Acacia* species (Costa 2014), which are exotic fast-growing nitrogen fixers that rapidly establish pure stands, generally expanding from stream banks and road sides into the forest. Similarly, large areas of the Caramulo Mountain are covered by *Eucalyptus globulus* monocultures, which often replace native mixed deciduous riparian forests (Abelho and Graça 1996; Bärlocher and Graça 2002). These changes in the riparian vegetation, with a consequent decrease in tree species richness, will probably lead to the environmental and biological homogenization of streams, in contrast to the high heterogeneity found in this study, and could increase the susceptibility of aquatic communities to additional stressors (McKinney and Lockwood 1999; Olden et al. 2004; Correa-Araneda et al. 2015). Our results suggest that surveys of non-impacted streams that naturally differ in environmental conditions can be useful in forecasting the response of aquatic communities and processes to anthropogenic activities.

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