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Contribution of aquatic shredders to leaf litter decomposition in Atlantic island streams depends on shredder density and litter quality

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Abstract. It has been widely reported that shredders play an important role in leaf decomposition, especially in continental temperate streams. However, the paucity of shredders in many oceanic island streams leads to a greater contribution of microbes to litter decomposition in these streams. In this study, we investigated the importance of shredder presence and density (three levels) and leaf litter identity (*Alnus glutinosa*, *Clethra arborea* and *Acacia melanoxylon*) on leaf litter decomposition in one stream located in the Azores Archipelago. Coarse and fine mesh bags were used to allow natural colonisation of leaf litter by benthic macroinvertebrates or to exclude macroinvertebrates respectively. Treatments with one and three shredders were accomplished by enclosing one or three shredders in the fine mesh bags. Rates of litter decomposition differed significantly among shredder density treatments only for *A. glutinosa* and *C. arborea*. Decomposition rates were significantly faster for the natural within-stream shredder density treatment than for other shredder treatments. Shredder density differed significantly among litter species, being higher in *A. glutinosa* than in *C. arborea* and *A. melanoxylon.* The results indicate that when shredders are present at high densities in oceanic island streams they can substantially contribute to the decomposition of high-quality leaf litter, whereas the decomposition of hard leaf litter is mostly performed by the microbial community.

Additional keywords: Azores Archipelago, *Limnephilus atlanticus*, litter processing, macroinvertebrates, oceanic island streams.

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Introduction

The decomposition of terrestrial plant litter in forest streams is a key process that allows the transfer of energy and matter along the detrital food web (Webster and Benfield 1986; Cummins *et al.* 1989; Wallace *et al.* 1997). The incorporation of plant carbon into secondary production is generally mediated by the actions of microbes and macroinvertebrate shredders (Gessner and Chauvet 2002; Hieber and Gessner 2002; Cornut *et al.* 2010).

It is widely reported that shredders play an important role in leaf decomposition, especially in continental temperate streams (Hieber and Gessner 2002; Graça and Canhoto 2006; Gulis *et al.* 2006; Cornut *et al.* 2010; Woodward *et al.* 2012). However, the relative contribution of shredders to leaf decomposition in streams varies across regions. For example, the paucity of shredders in many oceanic island streams can lead to a greater contribution of microbes to litter decomposition in these streams (Benstead *et al.* 2009; MacKenzie *et al.* 2013; Raposeiro *et al.* 2014; Ferreira *et al.* 2016). But what would happen in the presence of high shredder abundance in oceanic island streams? In many tropical oceanic island streams, shredders are abundant and contribute substantially to litter decomposition (Crowl *et al.* 2001; Larned *et al.* 2003; Wright and Covich 2005).

The variable contribution of shredders to leaf litter decomposition in island streams could be related to several factors. Physical barriers (biogeographical filters) limit the successful colonisation of some stream ecosystems by shredders (Poff 1997; Bilton *et al.* 2001; Covich 2006, 2009; Raposeiro *et al.* 2012, 2013), which can explain the low shredder species richness in many island streams (Malmqvist *et al.* 1993; Hughes 2006; Benstead *et al.* 2009). The characteristics of the allochthonous litter input can also affect shredder abundance and production (Wallace *et al.* 1999; Haapala *et al.* 2001; Graça *et al.* 2002);

litter intrinsic characteristics, such as the concentration of structural and secondary compounds, affect litter palatability to shredders (Canhoto and Graça 1999; Balibrea *et al.* 2017), with streams that receive larger amounts of recalcitrant litter (i.e. tough with low nutrient concentration) having lower shredder abundance (Martínez *et al.* 2013; Ferreira *et al.* 2015). Because the rate of litter decomposition has been shown to be positively related to shredder density (Short and Maslin 1977; Wallace *et al.* 1982; Encalada *et al.* 2010; Rincón and Covich 2014), low shredder density in many island streams may explain the low contribution of benthic macroinvertebrates to litter decomposition in these systems.

The Azores islands are located in the North Atlantic Ocean, more than 1500 km from the nearest mainland, and most of the tree species, especially endemic species, are sclerophyll evergreen (Borges *et al.* 2009) and have many essential oils, which act as a moderate insecticide (Dias *et al.* 2007; Rosa *et al.* 2010). This combination of isolation and recalcitrant litter explains the paucity of shredders in many Azorean streams and the larger contribution of microbes to litter decomposition (Raposeiro *et al.* 2014; Ferreira *et al.* 2016). However, streams at higher elevation may have a high density of shredders (Raposeiro *et al.* 2013), which could play an important role in litter processing.

In the present study, we investigated the importance of shredder presence and density, as well as leaf litter identity on leaf litter decomposition in one oceanic island stream, located at high elevation, where the density of shredders is high. We anticipated a higher contribution of shredders to litter decomposition when they are present at higher densities compared with lower densities or when they are absent (Fazi and Rossi 2000; Rincón and Covich 2014) and a stronger effect of shredder presence and density on high- than low-quality leaf litter species (Hieber and Gessner 2002; Rincón and Covich 2014).

Materials and methods

Study region

The leaf litter decomposition experiment was conducted in the Ribeira do Folhado Stream (37°48′51″N, 25°14′36″W, 729 m above sea level, ASL), located in the north-east part of São Miguel Island (Azores Archipelago). This is an oceanic island located in the North Atlantic Ocean, ~1500 km and 2700 km off the European and American mainland respectively. The climate is temperate oceanic, with mild temperatures (mean annual temperature ~17°C at sea level, decreasing 0.6°C per 100 m of elevation) and moderate to high precipitation (mean annual precipitation 740 mm in coastal areas, increasing with elevation to 2500 mm above 600 m), with most of the precipitation (65–70%) falling between October and March (Agostinho 1938; Hernández *et al.* 2016).

Ribeira do Folhado is a perennial first-order stream, narrow (1 m wide), short (~7 km long) and <20 cm deep, with circumneutral pH (7), low conductivity (54 $\mu S\ cm^{-1}$) and low nutrient concentration (190 $\mu g\ L^{-1}$ N, 14 $\mu g\ L^{-1}$ P). Predominant substrates comprise mixed gravel or cobbles with occasional large, submerged boulders (Balibrea *et al.* 2017). The riparian forest is dominated by *Cryptomeria japonica* (L.f.) D. Don and *Clethra arborea* Aiton, both exotic species.

The surveys performed herein comply with the current laws of Portugal.

Shredders

Limnephilus atlanticus Nybom (Trichoptera, Limnephilidae) is a stream caddis fly endemic to the Azores Archipelago and common in the upstream sections of some Azorean streams (Raposeiro *et al.* 2012, 2013). Individuals were collected with a kick net (30 × 30-cm opening; 500-μm mesh size) on depositional areas in Ribeira do Folhado, downstream of the experiment location, 1 day before the decomposition experiment started (Day −1) and transported to the laboratory in a cooler. Individuals were maintained in plastic containers with aerated stream water and sediment, at 10°C, and weighted within 24 h after collection. A large range of sizes of *L. atlanticus* was collected, but larvae with similar wet weight (mean ± s.e., 30.0 ± 1.9 mg) were selected for use in the experiment (see below). The remaining individuals were returned to the stream.

Leaves

Leaves of *Clethra arborea* Aiton, *Acacia melanoxylon* R. Br. and *Alnus glutinosa* (L.) Gaertn. were selected to provide a range of litter characteristics, namely toughness, lignin and nitrogen (N) concentrations (Ferreira *et al.* 2016, 2017; Balibrea *et al.* 2017). According to several authors, these leaf characteristics are highly correlated with litter decomposition (Lecerf and Chauvet 2008; Ferreira *et al.* 2012; Frainer *et al.* 2016). *C. arborea* and *A. melanoxylon* are two broadleaf evergreen tree species commonly present in the riparian area of Azorean streams. *C. arborea* has high concentrations of polyphenols and low concentrations of lignin, whereas *A. melanoxylon* is tough and has high concentrations of lignin and N (Ferreira *et al.* 2016). *A. glutinosa* is a broadleaf deciduous tree species that is rare in the Azores Archipelago, but it was used here to provide a high-quality resource (soft with high nutrient concentrations) for the biological communities. This species has been used in decomposition experiments worldwide for comparative purposes (e.g. among regions; Boyero *et al.* 2012; Ferreira *et al.* 2012; Woodward *et al.* 2012) because it is a highly palatable leaf species to shredders (Friberg and Jacobsen 1994; Graça and Cressa 2010).

C. arborea and *A. melanoxylon* leaves were collected directly from the trees because, in these evergreen species, it is difficult to collect sufficient naturally abscised leaves in a short period (to avoid large variations in leaf characteristics). Leaves of *A. glutinosa* were collected after natural senescence in autumn. All leaves were transported to the laboratory where they were air dried at ambient conditions and stored in the dark until use. The use of air-dried leaves is ecologically relevant because a substantial fraction of the leaf litter entering the streams consists of air dried leaves that arrive from lateral inputs (Molinero and Pozo 2004).

Leaf litter decomposition

Air-dried leaves were weighed (2.95–3.05 g), sprayed with distilled water to render them soft and less susceptible to breakage due to handling and enclosed individually in experimental bags (10 × 12 cm). Leaves were exposed to three different shredder densities in fine (0.5-mm) mesh bags: no shredders, one shredder and three shredders. Coarse mesh bags (5 mm) were used to allow natural colonisation of leaf litter by benthic macroinvertebrates (natural shredder density treatment).

On 29 July 2015, 20 litter bags for each shredder density treatment and leaf species were incubated in Ribeira do Folhado (20 bags × 4 shredder density treatment × 3 litter species = 240 bags in total). After 7, 14, 21 and 28 days, five randomly chosen bags from each shredder density treatment and litter species were collected (60 bags per date). In the laboratory, leaves were gently rinsed with tap water into a 500-μm mesh sieve to retain small leaf fragments. The remaining litter was oven dried at 60°C for 48 h and weighed for determination of dry mass (DM). DM was ignited at 500°C for 8 h and the ash was weighed for determination of ash mass. The remaining ash-free dry mass (AFDM) was estimated as the difference between DM and ash mass, and the fraction of the remaining AFDM was estimated as the ratio between the remaining AFDM and the post-leaching AFDM. *L. atlanticus* individuals were collected from bags from the natural density treatment for counting (density is expressed as the number of individuals per gram leaf litter AFDM).

Leaves lost substantial mass over the first week in the stream (30–63% of total mass remaining for *A. glutinosa*, 44–81% for *C. arborea* and 41–99% for *A. melanoxylon*), mostly due to leaching because no visible loss in area (e.g. from invertebrate feeding) was observed. This fast initial mass loss would affect the fitting of a decay model for estimation of decomposition rates. Thus, a conversion factor between air-dried mass at Day 0 and AFDM after leaching (Day 7) was estimated and results are shown considering Day 7 as the new Day 0 (post-leaching AFDM).

Benthic macroinvertebrates

Benthic macroinvertebrates were sampled on three occasions: before (Day −7), during (Day 7) and at the end of the experiment (Day 28). Samples were collected following the Portuguese macroinvertebrate sampling method (Instituto Nacional da Água 2008). Briefly, each sample was consisted of six substrate kicks (1 m each), taken with a kick net (30 × 30-cm opening; 500-μm mesh size), along a 10-m reach to cover local spatial heterogeneity. Samples were preserved in the field with 96% ethanol. In the laboratory, macroinvertebrates were sorted and identified under a stereomicroscope (Zeiss Stemi, Gottingen, Germany) to the lowest possible taxonomic level.

Data analysis

Decomposition rates (k; day^{-1}) for each leaf species exposed to the four shredder density treatments (0, 1 and 3 shredders or natural shredder density) were estimated by linear regression of the ln-transformed fraction of AFDM remaining (negative exponential model) over time considering the intercept at $\ln(1) = 0$. Litter decomposition (ln-transformed fraction of AFDM remaining) was compared among the four shredder density treatments for each litter species by analysis of covariance (ANCOVA; with time as a covariable) followed by Tukey's unequal honestly significant difference (HSD) test when significant effects were detected in the ANCOVAs.

Natural shredder density associated with decomposing litter was compared among time and leaf species by a two-way analysis of variance (ANOVA), followed by Tukey's unequal HSD test. Because heteroscedasticity persisted on natural shredder density even after transformation, analyses were run on the untransformed data using a more conservative level of significance ($\alpha = 0.01$; Underwood 1997). Data were checked for

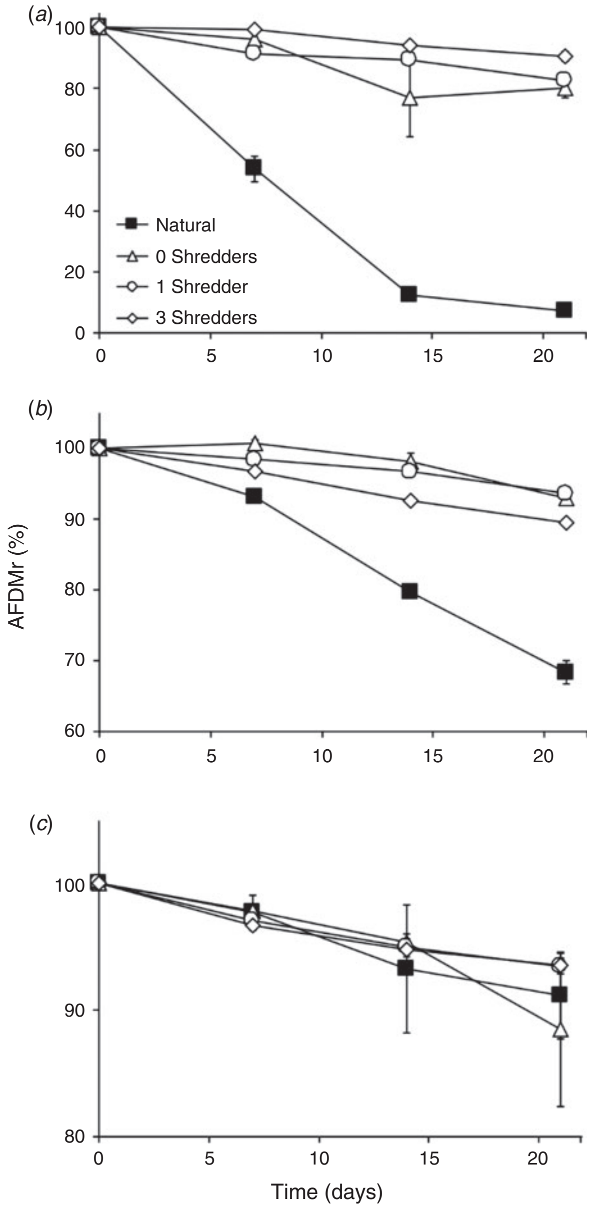

Fig. 1. Ash-free dry mass remaining (AFDMr) of three leaf litter species, (*a*) *Alnus glutinosa*, (*b*) *Clethra arborea* and (*c*) *Acacia melanoxylon*, exposed to different shredder densities in Ribeira do Folhado over 21 days after the leaching phase (1 week). Note the different *y*-axis scales. Natural shredder density refers to coarse (5-mm) mesh bags in which natural colonisation of leaf litter by benthic macroinvertebrates was allowed. Data are the mean ± s.e.m.

homoscedasticity (Cochran's test) and normality (Shapiro–Wilk test) before analysis. Data analyses were performed using STATISTICA (ver. 7, StatSoft, Tulsa, OK, USA).

Results

Litter decomposition

After correcting for leaching, litter mass remaining decreased exponentially over the incubation period and, after 21 days, ranged between 7 and 90% of post-leaching mass for *A. glutinosa*, between 68 and 93% for *C. arborea* and between 88 and 93% for *A. melanoxylon* across shredder density treatments (Fig. 1). The exponential mass loss dynamics translated into decomposition rates of 0.0044–0.1297 day^{-1} for *A. glutinosa*, 0.0026–0.0171 day^{-1} for *C. arborea* and 0.0034–0.0053 day^{-1} for *A. melanoxylon* across shredder density treatments (Table 1).

Litter decomposition rates differed significantly among shredder density treatments for *A. glutinosa* and *C. arborea* (ANCOVA, $P < 0.001$ for both species; Table 1). Decomposition rates were significantly faster for the natural shredder density treatment than for the other shredder treatments: 14- to 29-fold for *A. glutinosa* and 3- to 7-fold for *C. arborea* (Tukey's test, $P < 0.05$). No significant differences were found in leaf decomposition rates among shredder density treatments for *A. melanoxylon* (ANCOVA, $P = 0.837$; Fig. 1; Table 1).

Table 1. Exponential decomposition rates (*k*) of three leaf litter species exposed to different shredder densities in Ribeira do Folhado over 21 days after the leaching phase (1 week), standard error and coefficient of determination of the regression

Natural shredder density refers to coarse (5-mm) mesh bags in which natural colonisation of leaf litter by benthic macroinvertebrates was allowed. Treatments with the same letter do not significantly differ (ANCOVA followed by Tukey's unequal HSD test, $P > 0.050$)

Litter species	Shredder density	k (day^{-1})	s.e.	R^2	Tukey's test
Alnus glutinosa	Natural	0.1297	0.0046	0.90	a
	0 Shredders	0.0094	0.0012	0.56	b
	1 Shredders	0.0091	0.0006	0.58	b
	3 Shredders	0.0044	0.0006	0.51	b
Clethra arborea	Natural	0.0171	0.0011	0.79	a
	0 Shredders	0.0026	0.0005	0.48	b
	1 Shredders	0.0029	0.0004	0.50	b
	3 Shredders	0.0053	0.0002	0.86	b
Acacia melanoxylon	Natural	0.0047	0.0014	0.11	a
	0 Shredders	0.0053	0.0016	0.17	a
	1 Shredders	0.0034	0.0002	0.73	a
	3 Shredders	0.0036	0.0002	0.58	a

Benthic macroinvertebrates and litter-associated shredders

In all, 838 macroinvertebrates were collected from the benthos in Ribeira do Folhado. Macroinvertebrates were represented by 19 taxa (Table 2), with the community being dominated by filter feeder taxa (60% relative abundance), especially the endemic black fly *Simulium azorense* (60%). Gatherer or collector taxa were also well represented (22%), mainly by Orthocladiinae midges (11%). Shredders were represented by three taxa only: the caddis fly *L. atlanticus* (7%), Limoniidae crane flies (0.7%) and the isopod *Jaera insulana* (0.1%).

Colonisation of leaf litter in coarse mesh bags (natural shredder density treatment) by *L. atlanticus* was faster for *A. glutinosa*, followed by *C. arborea*, whereas for *A. melanoxylon* colonisation remained low throughout (Fig. 2). Maximum *L. atlanticus* density in coarse mesh bags was in the order

Table 2. Relative abundance of benthic macroinvertebrate taxa and total taxa richness in Ribeira do Folhado before (Day −7), during (Day 7) and at the end of the experiment (Day 28)

The functional feeding group (FFG) for each taxon (according to Schmidt-Kloiber and Hering 2015) is also shown

	Phylum	Family	Lower taxonomic level	FFG	Day −7	Day 7	Day 28
Relative abundance (%)	Platyhelminthes	Dugesiidae	*Dugesia* sp.	Predator	1.1	0.9	0.7
	Annelida	Lumbricidae		Gatherer or collector	–	–	4
		Naididae	*Nais* sp.	Gatherer or collector	2.6	9.5	32.7
		Lumbriculidae		Gatherer or collector	0.3	0.3	2.0
		Serpulidae		Filter feeder	0.3	–	–
	Arthropoda	Hydracnidae		Gatherer or collector	–	0.3	0.7
		Sperchonidae	*Sperchon brevirostris*	Gatherer or collector	0.9	0.6	1.3
		Malaconothridae	*Trimalaconothrus* sp.	Gatherer or collector	–	2.7	8.7
		Hydrozetidae	*Hydrozetes* sp.	Gatherer or collector	–	0.0	1.3
		Janiridae	*Jaera insulana*	Shredder	–	0.3	0.0
		Isotomidae		Gatherer or collector	–	0.0	0.7
		Dytiscidae	*Agabus* sp.	Predator	0.6	3.0	2.0
		Chironomidae	Orthocladiinae	Gatherer or collector	7.4	12.76	17.33
		Chironomidae	Tanypodinae	Predator	0.3	0.6	6.7
		Empididae	Clinocerinae	Gatherer or collector	–	1.2	0.7
		Hydroptilidae	*Oxyethira falcata*	Grazer or scraper	–	0.3	–
		Limnephilidae	*Limnephilus atlanticus*	Shredder	6.8	2.7	13.3
		Limoniidae		Shredder	0.6	0.9	0.7
		Simulidae	*Simulium azorense*	Filter feeder	79.2	64.1	7.3
Total taxa richness (total number of taxa)					11	15	16

A. glutinosa (30 individuals g^{-1} AFDM by Day 14) > *C. arborea* (9 individuals g^{-1} AFDM by Day 14) > *A. melanoxylon* (1 individuals g^{-1} AFDM by Day 21; Fig. 2). Shredder density differed significantly among litter species (ANOVA, $P < 0.0001$), but not over time ($P > 0.1$). Indeed, shredder density was significantly higher in *A. glutinosa* than in *C. arborea* and *A. melanoxylon* (Tukey's test, $P < 0.0001$), with no significant differences between the two latter species ($P > 0.01$). When results are expressed per metre squared, the natural density of *L. atlanticus* was significantly higher in coarse mesh bags compared with the stream bed (86 individuals m^{-2} for *A. glutinosa*, 9-fold difference; 124 individuals m^{-2} for *C. arborea*, 29-fold difference; and 22 individuals m^{-2} for *A. melanoxylon*, 19-fold difference) (Table 3). The difference in the number of shredders on Days 14 and 21 between litter species when the results are expressed as individuals per gram AFDM (Fig. 2; *A. glutinosa* > *C. arborea* > *A. melanoxylon*) and as individuals per metre squared (Table 3; *C. arborea* > *A. glutinosa* > *A. melanoxylon*) results from lower mass remaining for *A. glutinosa* after 21 days, which translates into a higher number of individuals per gram of AFDM but a lower number of individuals per metre squared.

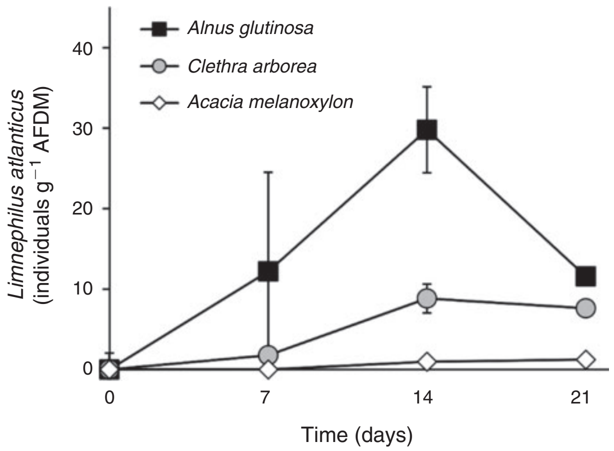

Fig. 2. Total *Limnephilus atlanticus* density associated with three leaf litter species incubated in coarse mesh bags in Ribeira do Folhado over 21 days after the leaching phase (1 week). Values are the mean ± s.e.m. AFDM, ash-free dry mass.

Discussion

In the present study we show that when shredders are present at high densities in North Atlantic oceanic island streams they can contribute substantially to the decomposition of high-quality leaf litter (i.e. soft with high nutrient concentrations), whereas the decomposition of hard leaf litter is mostly performed by the microbial community.

Effect of L. atlanticus *presence on litter decomposition*

Litter decomposition rates were faster when *L. atlanticus* larvae were present at high densities (natural treatment, coarse mesh bags) than when they were at low densities or absent (0, 1 and 3 shredders treatment, fine mesh bags) for *A. glutinosa* (14- to 30-fold faster) and *C. arborea* (3- to 7-fold faster). These findings agree with previous studies on tropical island streams in which shredder density is high that reported faster leaf litter decomposition in the presence of shredders than in their absence (i.e. when shredders were experimentally excluded; March *et al.* 2001; Wright and Covich 2005; Rincón and Covich 2014). Similarly, studies in oceanic island streams where shredders are rare or absent have reported a negligible contribution of stream macroinvertebrates to litter decomposition (Benstead *et al.* 2009; MacKenzie *et al.* 2013; Raposeiro *et al.* 2014; Ferreira *et al.* 2016). In addition, several studies in island and continental streams have reported litter decomposition to be positively correlated with shredder density in mesh bags (Encalada *et al.* 2010; Rincón and Covich 2014).

In the Azores, as in many other oceanic islands, shredder taxa are rare due to strong biogeographic filters, and they are restricted to high-elevation forested sites mostly by land use constraints (Malmqvist *et al.* 1993; Hughes 2006; Benstead *et al.* 2009; Raposeiro *et al.* 2012). In fact, Ribeira do Folhado (729 m ASL) had greater than eightfold higher mean shredder densities than the streams used in previous studies (310–632 m ASL; Raposeiro *et al.* 2014; Ferreira *et al.* 2016). This difference in shredder density between the stream used in the present and previous (Raposeiro *et al.* 2014; Ferreira *et al.* 2016) studies may have contributed to the higher contribution of macroinvertebrates to litter decomposition in the present study. In high-elevation streams, shredders may play a key role in litter decomposition.

Table 3. Mean (±s.e.m.) number of *Limnephilus atlanticus* associated with three leaf litter species incubated in coarse mesh bags in Ribeira do Folhado over 21 days after the leaching phase (1 week) and total number of *L. atlanticus* on the stream bed

	L. atlanticus (individuals m^{-2})				
	Day −7	Day 0	Day 7	Day 14	Day 21
Natural shredder density on coarse mesh bags					
Alnus glutinosa	–	–	850.0 ± 147.9	550.0 ± 232.9	83.3 ± 39.3
Clethra arborea	–	–	283.3 ± 69.1	1216.7 ± 142.6	900.0 ± 212.7
Acacia melanoxylon	–	–	0.0 ± 0.0	183.3 ± 72.3	216.7 ± 29.8
Total number of *L. atlanticus* on the stream bed	13.3	5.0	–	–	11.1

Effects of litter characteristics on shredder contribution to litter decomposition

The effect of shredder density on litter decomposition depended on litter species, which is consistent with previous studies in tropical island streams (Rincón and Covich 2014). The leaves of *A. glutinosa* are known to be highly palatable for shredders due to their high N concentration and low toughness (Graça 2001; Graça and Cressa 2010; Balibrea *et al.* 2017), which results in their faster colonisation and higher shredder density compared with other less-palatable leaf species (Hieber and Gessner 2002; Ferreira *et al.* 2012). In fact, on Day 7, *A. glutinosa* leaves had higher shredder density than *C. arborea* and *A. melanoxylon* leaves in the natural shredder density treatment. This initial high shredder density on *A. glutinosa* leaves contributed to the strong difference in litter decomposition rates between the natural shredder density treatment and the treatments where shredders were present at low density or absent. This is in agreement with findings reported in previous studies, where shredders contributed between ~50 and >60% of *A. glutinosa* leaves mass loss (Hieber and Gessner 2002; Cornut *et al.* 2010). *C. arborea* leaves had intermediate litter palatability that resulted in intermediate shredder density in the natural shredder density treatment on Day 7. This intermediate litter palatability resulted in faster decomposition rates in this treatment compared with treatments where shredders were present at low density or absent, but the magnitude of this difference was lower than that found for *A. glutinosa* leaves. *A. melanoxylon* leaves were the toughest and had the lowest shredder density in the natural treatment, which resulted in the absence of significant differences in litter decomposition among shredder density treatments. Therefore, intrinsic leaf characteristics are of major importance in determining the relative contribution of shredders to leaf litter decomposition, with this contribution being higher for high-quality leaf litter.

Azorean native forests are dominated by evergreen trees (e.g. Lauraceae) with glossy leaves (Kondraskov *et al.* 2015) that are of relatively low quality compared with *A. glutinosa* (Balibrea *et al.* 2017), and thus the relative contribution of shredders to leaf litter decomposition in Azorean streams should be low even when they are present. It is also interesting to note that the number of *L. atlanticus* individuals in litter bags was disproportionately higher compared with the benthos. This disproportion was especially true for *A. glutinosa* and *C. arborea* bags, which may have acted as islands of soft litter (with a low concentration of structural compounds) in a stream bed dominated by recalcitrant litter species (e.g. *Laurus azorica* (Seub.) Franco, *Ilex perado* Aiton, *Cryptomeria japonica* (L.f.) D. Don; Raposeiro *et al.* 2014, 2017; Ferreira *et al.* 2016). Moreover, oceanic island streams are characterised by steep systems, where rapid run-off and torrential and highly erosive flow regimes occur almost immediately after episodes of rainfall, washing the litter present in the stream bed downstream, leading to food limitation for invertebrate shredders.

Conclusions

The role of benthic macroinvertebrates in litter decomposition in remote oceanic islands streams depends on litter quality and likely on shredder density. In streams that receive recalcitrant leaves from the riparian vegetation or where shredder density is low, litter decomposition is mostly mediated by microbes (Benstead *et al.* 2009; MacKenzie *et al.* 2013; Raposeiro *et al.* 2014; Ferreira *et al.* 2016). Conversely, in streams that receive high-quality litter and where shredders are abundant, litter decomposition is performed with a substantial contribution of macroinvertebrates (March *et al.* 2001; Rincón and Covich 2014; present study). However, stream and island replication is required to better understand litter decomposition in remote oceanic islands streams.

Conflicts of interest

The authors declare that they have no conflicts of interest.

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