

Riparian land use and the relationship between the benthos and litter decomposition in tropical montane streams

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SUMMARY

1. Although stream–catchment interactions have been analysed in some detail in temperate environments, little is known about the effects of land-use changes in the tropics. Here, we analyse differences in benthic communities (macroinvertebrates and fungi) under two contrasting land uses (mature secondary forest and pasture) in montane streams in north-western Ecuador and their influence on the rates of litter processing.

2. Between 2005 and 2006, we used a combination of coarse and fine mesh bags to study the relative contribution of macroinvertebrates and fungi to processing of two types of litter, *Alnus acuminata* and *Inga spectabilis*, in three first-order streams running through mature secondary montane forests and adjacent downstream reaches running through pastures. At the same time, we characterised the assemblages of shredding macroinvertebrates and fungi communities and the litter processing rates in stream reaches under both vegetation types.

3. Litter processing rates attributable to invertebrate feeding (coarse mesh bags) were significantly slower in streams running through pastures. Nevertheless, shredder diversity and richness were similar between pasture and forest sections, while shredder abundance was significantly higher in forest streams (mainly *Phylloicus* sp.: Trichoptera). Fungal reproductive activity and litter processing rates were low (fine mesh bags) and did not differ significantly between pasture and forest stream reaches.

4. *Phylloicus* sp. abundance was the best predictor of the percentage of litter remaining in coarse mesh bags across pasture and forest sites. Neither shredder diversity nor their species richness was a significant predictor of mass loss, as most of the decomposition was performed by a single keystone species. Although litter decomposition by microbial decomposers was low, fungal biomass (but not diversity) was the best variable explaining the percentage of litter remaining in fine mesh bags.

5. Our data suggest that, in these Neotropical montane streams, land use can have a significant impact on the rates of critical ecosystem processes, such as litter decomposition. In this study, this effect was not mediated by a major shift in the structure of the benthos,

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but by a decrease in the abundance and relative representation of a single species whose life history makes it critical to litter processing.

6. This study highlights the significant role that macroinvertebrate fauna can have in the processing of litter in Neotropical streams and the predominant role that single species can have in terms of controlling stream ecosystem-level processes. Understanding the extent to which these patterns affect the long-term and large-scale functioning of stream ecosystems still needs further research and will become increasingly important in terms of managing lotic ecosystems in the context of rapid land-use change.

Keywords: fungal activity, litter processing, macroinvertebrate community, *Phylloicus* sp, riparian vegetation

Introduction

The relationship between biodiversity and ecosystem processes has critical implications for the understanding and management of ecosystems, although, despite several years of intense debate, it remains controversial (Tilman *et al.*, 1997; Cardinale, Nelson & Palmer, 2000). The spatial and temporal scale at which such relationships are relevant, the often predominant role of single species in controlling particular ecosystem processes, and the issue of redundancy within ecological communities are still under intense scrutiny and resist simple generalisations (Jonsson & Malmqvist, 2003; Jonsson, 2006; Taylor, Flecker & Hall, 2006; Boyero, Pearson & Bastian, 2007; Bengtson, Evans-White & Gido, 2008; McKie *et al.*, 2008, 2009). In aquatic environments in general, and particularly in tropical streams, the relationship between biodiversity and ecosystem processes remains poorly understood and is further complicated by the role of flow and by interactions with the terrestrial catchment (e.g. Bärlocher & Graça, 2002; Jonsson & Malmqvist, 2003; Covich *et al.*, 2004; Wright & Covich, 2005). Understanding these relationships becomes increasingly urgent as lotic ecosystems throughout the world undergo rapid changes that affect not only the structure of their biological communities (Stone & Wallace, 1998) but also their ecosystem processes (Freeman, Pringle & Jackson, 2007). In this article, we explore whether conversion of the riparian forest to pasture in tropical montane streams modifies the benthos (including fungi) and thus affects the rate of litter processing.

A growing body of literature concerning the relationship between biodiversity and ecosystem pro-

cesses in aquatic systems has shown great variability in its nature and intensity. While some studies have reported positive responses of the rate of ecosystem processes to high biodiversity (Boyero *et al.*, 2007; Singer & Battin, 2007; Ball *et al.*, 2008), others have found no relationship or a strong dependence of ecosystem processes on the identity of the species involved. This last outcome suggests little redundancy in the roles performed by different members of the ecological communities in streams (Dangles & Malmqvist, 2004; Dang, Chauvet & Gessner, 2005; Jonsson, 2006; Taylor *et al.*, 2006; Vaughn, Spooner & Galbraith, 2007; McKie *et al.*, 2009). Moreover, the relationship between biodiversity and stream processes is complex and varies greatly with spatial and temporal scale, the structure of the food web, species identity and nature of the process being considered (Jonsson & Malmqvist, 2005; Ball *et al.*, 2008; Bastian, Pearson & Boyero, 2008; Bengtson *et al.*, 2008; McKie *et al.*, 2008). In addition, the differences assumed in the relative importance of several functional feeding groups (FFG) in temperate versus tropical regions (Irons *et al.*, 1994; Dobson *et al.*, 2002; Jacobsen *et al.*, 2008) could lead to different patterns in the relationship between ecosystem processes and community structure. These relationships have been studied only rarely in the tropics and are important in assessing the potential effects of ongoing changes in land use in tropical regions (Freeman *et al.*, 2007).

Litter breakdown is an important ecosystem process (Gessner & Chauvet, 2002), particularly in streams in which litter inputs represent a significant source of energy and nutrients (Wallace *et al.*, 1997; Abelho, 2001; Graça, 2001). In such streams, changes in the riparian vegetation (e.g. lower litter inputs,

increased light and temperature fluctuations) could cause changes in the benthos. These altered communities could in turn lead to changes in litter processing rates. Although effects on the benthos resulting from land use change have been studied in temperate systems, their potential effects on litter processing have rarely been assessed (but see McKie & Malmqvist, 2009). This is particularly true for the tropics where riparian areas are undergoing rapid land use changes.

The montane forests of northern South America offer a clear opportunity to assess how changes in land use affect stream benthic communities and, consequently, ecosystem processes. Not only are these forests and their streams extremely important for the provision of water for irrigation, generation of electricity and human consumption throughout most of the northern Andean region, but they are also an extremely diverse and threatened ecosystem (Jokisch & Lair, 2002), and one of the planet's 'biodiversity hotspots' for conservation (*sensu* Myers *et al.*, 2000). They are undergoing rapid change as a result of an increasing human population with growing demands for water and food (Doumenge *et al.*, 1995). The conversion of forests to pasture for cattle rearing is common and probably the most destructive change in land use because of the radical modification of the vegetation and the reduced opportunities for regeneration. This change produces a great increase in light reaching the stream and a reduction in the amounts of allochthonous organic matter (Bojsen & Jacobsen, 2005). However, we know little about the effects on the benthos or on the processes in such systems.

Here, we assess the structure of the benthos (macroinvertebrates and fungi: hyphomycetes) and the mass loss of leaf litter in streams in north-western Ecuador, comparing upstream reaches running through secondary montane forest with adjacent downstream reaches draining areas converted to pasture lands. Our main objective was to assess whether contrasting riparian vegetation (forest versus pasture) was associated with differences in benthic assemblages (shredders and fungi species) and whether such differences could influence the rate of litter processing in the streams. Our focus on macroinvertebrates and hyphomycetes reflects the fact that in this low-order montane forest streams, the benthos ultimately depends on riparian leaf litter

inputs as a primary energy source. We hypothesised that alterations in the riparian vegetation have altered the benthic invertebrate community and microbial activity, thus ultimately affecting leaf decomposition (Graça, 2001).

Methods

Study area

We studied streams located in a Tropical Montane Forest situated in Nanegalito (Pichincha province), in north-western Ecuador (00°06'N, 78°39'W), at an altitude of 1200 m. Precipitation fluctuates between 1500 and 4000 mm annually, with a relatively dry period from June to September. Mean daily temperature ranges from 14 to 24 °C, with little seasonal variation. During the experiment (November 2005 to January 2006), total precipitation was 508 mm and mean air temperature 22 °C.

We studied three headwater (first order) streams, all tributaries of the Alambi River, in which the upstream reaches run through mature secondary forest, while the lower reaches drain areas converted to pasture *c.* 20 years ago. The altitudinal difference between the upstream and downstream reaches was <20 m, and the distance between forest and pasture reaches was 150–200 m. In the forest sections, dominant riparian trees were *Solanum cucullatum* S.Knapp, *Inga* spp. and *Sauraria* sp., while the pastures downstream sections were open grassland with occasional pioneer trees such as *Tesaria* sp., *Alnus acuminata* Kunth, sparse bamboo thickets (*Guadua* sp.) and shrubs (*Acalipha* sp.). *Inga spectabilis* Benth and *A. acuminata* Kunth are common species in the area and were chosen for the decomposition experiment (see our rationale below).

Environmental variables and invertebrate communities

We measured physicochemical factors, characteristics of the riparian vegetation and macroinvertebrate parameters in streams running through forest and pasture sections. Factors included temperature, pH, oxygen concentration, conductivity, alkalinity, NO₃, NH₃, PO₄, discharge, substratum composition, width, depth and current velocity. Most parameters were measured *in situ* using field probes (4-Star Orion pH/conductivity portable meter and a WTW oxygen

meter), while water samples for nutrients and alkalinity were taken to the laboratory for immediate analyses using standard methods (Gruntec Laboratories Cia. Ltda., Quito, Ecuador). Water chemistry was assessed once during the initial survey and again on each sampling date of the experiment.

In both sections of each stream, we estimated canopy cover using a spherical densitometer and vertical litter input along a 100 m reach. Litter-fall traps were constructed from plastic laundry baskets of 0.22 m²; a minimum of six traps were placed in each pasture section and a maximum of 16 in the forest section (the number of baskets in the pasture section varied because some were stolen and were replaced when possible). Litter traps were suspended *c.* 1 m above the water surface, using ropes attached to nearby trees or shrubs. Litter was recovered from the traps every other week and stored in plastic bags for further analysis in the laboratory. Samples of leaves were dried in an oven at 56 °C for 48 h and then weighed to the nearest 0.01 g. We ashed the material at 500 °C for 4 h and then weighed it again. We calculated grams of Ash Free Dry Mass (AFDM) by subtracting the mass of ash from that of the dry matter.

To compare the composition and structure of the invertebrate communities between forest and pasture sections, we took three Surber samples (31 cm × 31 cm; 500- μ m mesh size,) per stream section, 2 weeks before starting the decomposition experiment. All invertebrates were preserved in 70% ethanol and were brought to the laboratory for further analyses. In the laboratory, invertebrates were sorted and identified to the lowest taxonomical level possible using the keys by Fernández & Domínguez (2001), Merrit & Cummins (1996) and Roldán (2003). Invertebrate FFG were assigned according to Merrit & Cummins (1996) and also based on information from gut content analysis (Andrea Encalada unpublished data).

Experimental setup

In representative forest and pasture sections of the three streams, we conducted a leaf bag experiment to estimate litter breakdown rates, in which three factors were tested: vegetation cover (forest versus pasture), tree species (leaves of Aliso: *A. acuminata* versus Guaba: *I. spectabilis*) and mesh size (coarse versus fine).

Each leaf bag was 15 cm × 17 cm in size and was filled with 5 ± 0.20 g of air-dried leaves of *Alnus* (240 bags) or *Inga* (240 bags). These tree species were selected because of their frequent occurrence in the riparian habitat of the study area and their contrasting litter quality characteristics, which could influence the response of the decomposers. Chemical analysis revealed that *A. acuminata* leaves are soft (Lignin: 35%) and N rich (N: 2%) compared with the tougher and rigid leaves of *I. spectabilis* (Lignin: 45% and N: 1.8%). Nitrogen was measured applying a modification of Kjeldahl methods (Flindt & Lillebo, 2005), and lignin was determined gravimetrically using acid-detergent fibre analysis (Gessner, 2005). Freshly abscised leaves were collected in net traps located at the base of the selected trees. Leaves were retrieved daily from the bags and stored dry until needed.

Two mesh sizes were used in the litter breakdown experiment. Half of the bags had a mesh size of 10 mm and allowed the entrance of all macroinvertebrates into the bags, while the other half had a mesh size of 0.5 mm and prevented their access with the exception of very few small chironomids. These mesh sizes had been used in previous experiments to discriminate between the relative contribution of microbial (fine mesh bags) and the combined effects of macroinvertebrates, microbial and physical fragmentation (coarse mesh bags) to litter breakdown.

At the start of the experiment (22 November 2005), a total of 480 leaf bags were placed in the three streams representing four replicates of each combination of tree species × mesh size × land use (forest versus pasture), for five sampling dates. Leaf bags replicates were anchored to the stream substratum using tie rods and were dispersed *c.* 5 m from each other along the stream channel under similar conditions of water velocity and depth. Four replicate bags of each treatment were collected on day 2 to assess mass loss because of leaching and then after 15, 21, 34 and 63 days to assess litter breakdown (% of mass remaining) as affected by each treatment. On collection, leaf bags were placed in individual plastic bags containing stream water and transported to the laboratory in an icebox.

In the laboratory, the leaves were rinsed to remove invertebrates and sediment, dried in an oven at 70 °C

for 24 h and ash-free dry mass estimated as described earlier. Mass loss from each leaf bag (corrected for the leaf discs mass used for fungal determinations) was estimated as the difference between the initial and final mass after recovery from the stream. All our estimates of mass loss were additionally corrected for handling effects, using the average of litter loss of eight bags that were taken to the field, placed on the streams, brought back to the laboratory in the same day and treated in the same way as the rest of the experimental samples. In addition, 20 bags (10 for each tree species) were dried and weighed to evaluate any change in mass because of humidity. The final AFDM was corrected for both handling and humidity.

Fungal activity and communities associated with fine mesh bags. We analysed fungal reproductive activity (sporulation), biomass and diversity in the fine mesh bags from one of the three streams (four samples on each date). From each fine mesh bag, we cut 20 leaf discs (diameter, 1 cm) using a cork borer. Fungal sporulation was stimulated by incubating 10 leaf discs in 250-mL Erlenmeyer flasks containing 150 mL of distilled water, under constant aeration by aquarium pumps for 48 h at 25 °C. After incubation, the conidial suspension was filtered through membrane filters (47 mm, 8 µm MF-Millipore, Ireland), and the discs were oven dried for 24 h at 70 °C, weighed, ashed for 4 h at 550 °C and reweighed to determine disc AFDM. Each filter was stained with 0.1% Trypan blue solution and examined microscopically (200× magnification) to allow species identification and estimation of the sporulation rate (number of conidia per milligram of AFDM per day).

Ergosterol was used as a surrogate of fungal biomass (Gessner & Chauvet, 1993). Ergosterol was extracted by the Solid Phase Extraction (SPE) method (Gessner & Schmitt, 1996) from the remaining 10 leaf discs from each sample. These leaf discs were preserved in 10 mL KOH/methanol (8 g L⁻¹) and placed in the dark in a freezer until analysis. Ergosterol was extracted in a water bath at 80 °C for 30 min, purified by solid-phase extraction and quantified by high-pressure liquid chromatography (Gessner & Schmitt, 1996). Leaf discs were assumed to weigh the same as those used to induce sporulation. Values were expressed as µg ergosterol g⁻¹ leaf litter AFDM.

Invertebrate communities associated with coarse mesh bags. We counted and identified all the invertebrates associated with the coarse mesh litter bags, having gently rinsing them from the leaves with tap water. Invertebrates obtained from the coarse leaf bags were treated similarly as those from the Surber samples.

Data analysis

Differences in physicochemical variables between forest and pasture stream sections were analysed with t-tests performed on Ln-transformed data. Percent canopy cover was arcsine transformed (Sokal & Rolf, 1995). Measurements of litter input between forest and pasture sections were compared by a two-way ANOVA, with month and land use as independent variables in the model.

To assess overall differences in invertebrate community composition between forest and pasture sections, we used richness and abundance data to perform an analysis of similarity ANOSIM (based on Bray–Curtis similarity matrix) (Clarke & Gorley, 2006). Additionally, we compared taxon richness with rarefied taxon richness (1000 iterations of sampled-based rarefaction scaled to individuals) using 95% confidence intervals at different abundances levels (Gotelli & Colwell, 2001; Gotelli & Entsminger, 2001). The evenness of the macroinvertebrate community and of the shredder assemblages in forest and pasture stream sections was estimated through the probability of interspecific encounter (PIE; Hurlbert, 1971) and compared with GLM procedures. Finally, differences in the abundance of invertebrates and in FFG between pasture and forest sections were analysed using GLM procedures.

For the litter processing experiment, decomposition rate was measured using an exponential decay model: $M_t = M_0 e^{-kt}$ where M_t is the mass at time t , M_0 is the mass at time 0, k is the exponential decay coefficient and t is the time in days (Graça, Barlocher & Gessner, 2005). To analyse the effects of land use (forest versus pasture), mesh size and tree species on the rate of decomposition, we used a split-plot design in which sampling date and stream identity were used as 'between-subject' factors, and land use, mesh size and tree species were considered to be 'within-subject' factors. In each relevant case, the F -values and corresponding P -values were calculated using error terms and degrees of freedom that incorporated

information from the between-subject factors as described by Quinn & Keough (2002).

Differences in fungal sporulation and ergosterol content were analysed with an analysis of covariance (ANCOVA model), in which time was used as covariate, the response variables were sporulation (conidia mg AFDM⁻¹ day⁻¹; log ($x + 1$) transformed) or ergosterol content ($\mu\text{g g}^{-1}$), and the factors were land use (forest versus pasture) and tree species (*Alnus* versus *Inga*) and their two-way interactions. In this case, we did not have a stream effect since this analysis was performed in one stream only. Differences in the invertebrate assemblages (invertebrate density, family richness, shredder diversity and shredders abundance) found in the mesh bags were also analysed with ANCOVA, with time as covariate and land use (forest versus pasture), tree species (*Alnus* versus *Inga*) and streams as main factors.

Relationships between diversity and leaf breakdown

To evaluate the relationships between shredder diversity and ecosystem processes (i.e. decomposition of organic matter), we performed two multiple regressions with backward model selection criteria to analyse which factors contributed most to the pattern of decomposition. Plant species was included as a parameter in the model since the percentage of litter remaining differed between the two. At each step, we removed the least significant variable and re-evaluated the reduced model until it contained only significant variables. In the first regression, we used mean litter mass remaining in the coarse mesh bags as the response variable and mean abundances of *Phylloicus* sp. (Trichoptera), *Anchytersus* sp. (Coleoptera) and the richness of shredders as explanatory factors in the model. Shredder abundance was discarded because of high autocorrelation with other parameters, while the remaining variables were not overly autocorrelated (Tabachnick & Fidell, 2001). In the second regression, we used the mean percentage of litter remaining in the fine mesh bags as the response variable and fungal biomass (measured as ergosterol), fungal activity (sporulation) and hyphomycete species richness as independent variables. In this case, we used data of just one stream in which we used the four different samples of each date as replicates.

Results

Environmental variables and invertebrate communities

Most stream physicochemical variables were similar between forest and pasture sections (Table 1), but there were some important exceptions: not surprisingly, canopy cover was higher in forest than in pasture stream sections and, accordingly, water temperature was significantly higher in the pasture streams (Table 1). Similarly, stream substratum was more heterogeneous in the pasture sections, with a higher percentage of clay (22%), cobbles (19%) and pebbles (17%) than the forest stream sections (gravel, 27%; cobbles, 26%).

As expected, litter fell throughout the year but there were two main peaks in input, one in April (coinciding with the highest precipitation) and another in September (the driest month). Litter inputs to streams were significantly higher in forest sections (500 g year⁻¹; ANOVA: $F_{1,11} = 16.77$; $P = 0.002$) than in pasture sections (208 g year⁻¹), with significant variation between months (ANOVA: $F_{1,11} = 6.72$, $P = 0.002$).

Overall, the macroinvertebrate assemblage was significantly different between forest and pasture sections (ANOSIM: $R = 0.63$, $P < 0.001$). Family richness was significantly higher for pasture (31) than forest (28) sections, even after adjusting for sampling differences through rarefaction methods. Mean rarefied richness for pasture section was 30.98 (95% C.I. 31.00–31.02) and for forest sections was 23.36 (95%

Table 1 Main characteristics of riparian vegetation and streams running through forest and pasture sections in Nanegalito, Ecuador

Parameter	Forest Mean \pm SE	Pastures Mean \pm SE
Canopy cover (%)	70 \pm 1.6*	32 \pm 1.7*
Width (m)	1.33 \pm 0.43	1.27 \pm 0.27
Depth (cm)	14.04 \pm 3.60	10.83 \pm 1.44
Discharge (L s ⁻¹)	52.47 \pm 10.62	58.20 \pm 12.1
Temperature (°C)	17.80 \pm 0.03*	18.61 \pm 0.06*
Dissolved oxygen (mg L ⁻¹)	7.25 \pm 0.06	7.68 \pm 0.16
pH	8.2 \pm 0.03	8.0 \pm 0.21
Conductivity ($\mu\text{S cm}^{-2}$)	112.5 \pm 0.92	112.2 [†]
Alkalinity (CaCO ₃) (mg L ⁻¹)	110.7 \pm 6.89	129.77 \pm 10.19
NH ₃ (mg L ⁻¹)	0.31 \pm 0.02	0.31 \pm 0.03
PO ₄ ⁻ (mg L ⁻¹)	0.47 \pm 0.05	0.40 \pm 0.04

*When significantly different at $P = 0.05$.

[†]parameter measured only once during the survey.

C.I. 22.00 -24.00). The PIE showed that pasture stream communities had higher evenness (PIE: 0.92 ± 0.01 ; $F_{1,12} = 11.75$; $P = 0.001$) than forest communities (0.85 ± 0.02). Nevertheless, shredder community evenness was similar ($F_{1,14} = 2.09$; $P = 0.174$) between forest (0.55 ± 0.04) and pasture (0.35 ± 0.11) stream sections. Shredder PIE values were low for both communities.

Invertebrate density was similar between forest ($1590.9 \pm 331 \text{ m}^{-2}$) and pasture ($1596.7 \pm 283.9 \text{ m}^{-2}$; $F_{1,14} = 0.18$; $P = 0.676$) stream sections. However, the relative contribution of different FFG was significantly different between forest and pasture stream reaches ($F_{1,20} = 8.26$; $P < 0.001$; Fig. 1). Most importantly, shredder abundance was significantly higher in forest ($380 \pm 122 \text{ m}^{-2}$) than in pasture streams ($111 \pm 41 \text{ m}^{-2}$), especially as a result of the higher abundance of the genera *Phylloicus* (Calamoceratidae: Trichoptera) (Appendix S.I.). In contrast, the abundances of predators and scrapers in pasture streams (260 ± 67 , and $304 \pm 78 \text{ m}^{-2}$, respectively) were significantly higher than that in forest streams (158 ± 60 and $34 \pm 15 \text{ m}^{-2}$, respectively). In terms of dominance, the most abundant macroinvertebrate families in forest streams were Elmidae (collector), Hydropsychidae (collector), Calamoceratidae (shredder) and Ptilodactylidae (shredder), while in pasture streams, the dominant families were Elmidae, Hydropsychidae, Leptohiphidae (collector), Helicopsychidae (scraper) and Perlidae (predator).

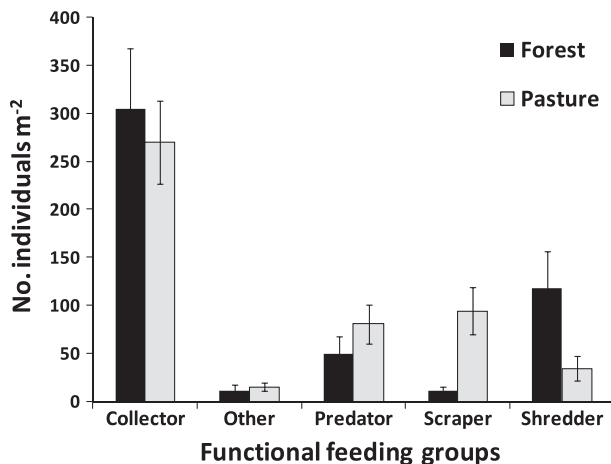


Fig. 1 Mean abundances of Functional Feeding Groups (FFG) of invertebrates found in streams running through forest and pasture sites in a montane tropical area in north-western Ecuador.

Litter breakdown experiment

During the first 2 days in the streams, leaves lost *c.* 11% of their mass because of leaching. From day 15 onwards, differences between treatments were observed which increased towards the end of the experiment. Litter decomposed significantly faster in forest stream reaches, than in pasture reaches (Fig. 2; Table 2). Decomposition rates of *Alnus* leaves were significantly faster than that of *Inga* leaves and also significantly higher in the coarse mesh bags than that in the fine mesh bags. Leaves in coarse mesh bags lost significantly more mass in forest than in pastures, but this did not occur in fine mesh bags (Table 2).

In forest streams, *Alnus* leaves in coarse bags showed an average mass loss of 75% of the AFDM while *Inga* leaves in coarse bags only lost 40% (Fig. 2). This difference between tree species was much smaller in the fine mesh bags, in which *Alnus* and *Inga* bags lost 39% and 30%, respectively. In pasture, *Alnus* leaves showed the highest mass loss in coarse bags with 51% of the original AFDM remaining, while *Inga* leaves only lost 29% in coarse mesh bags (Fig. 2). Finally, *Alnus* in fine mesh bags lost 40% of the original AFDM, while *Inga* lost 29% (Fig. 2). Overall, the stronger effect on litter decomposition was evidenced for *Alnus acuminata* leaves in coarse mesh bags (when invertebrates were present) in the forest sites (Fig. 2); therefore, *Alnus* showed the faster decomposition rate (*k*) in forest in coarse mesh bag, while the slowest decomposition rate was for *Inga* in pastures in fine mesh bags (Table 2).

Fungal activity and communities associated with fine mesh bags. In contrast to the patterns that we found in macroinvertebrate assemblages, the main differences in fungal activity and community structure did not occur between forest and pasture samples, but rather between tree species (*Inga* versus *Alnus*). The total number of species of aquatic hyphomycetes found in *Alnus* leaves (20 species in pasture bags and 14 in forest bags; Table 3) was almost twice the number of species found in *Inga* leaves (nine and six species in pasture and forest bags, respectively). Similarly, sporulation rates were significantly higher in fungi colonising *Alnus* than that in *Inga* leaves ($F_{1,52} = 10.94$; $P = 0.002$; ANCOVA), but no significant differences were observed between forest and pasture ($F_{1,52} = 2.13$; $P = 0.151$; Fig. 3). In the case of *Alnus*,

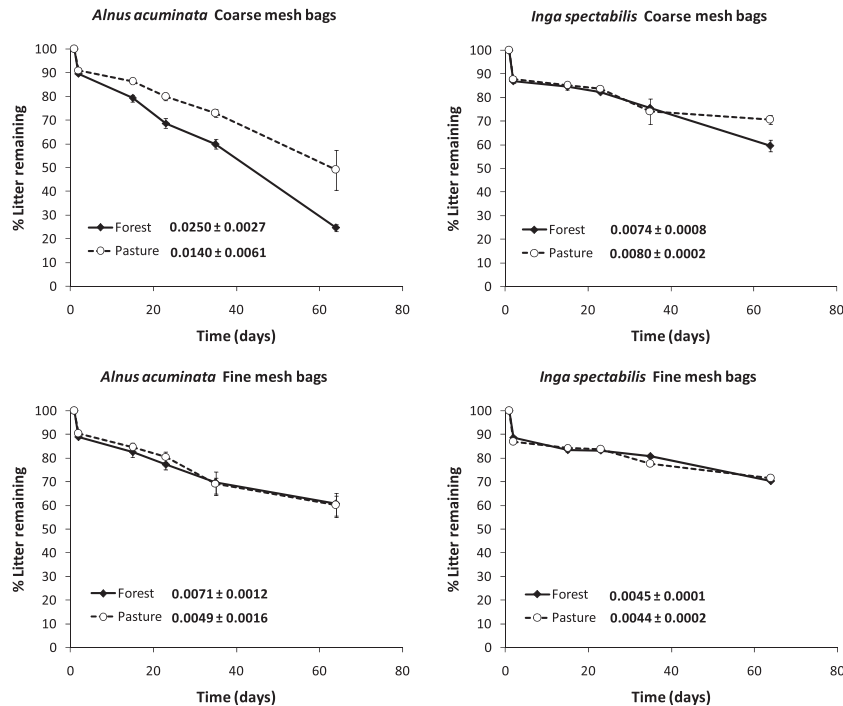


Fig. 2 Percentage of litter remaining through time (five different dates) from a litter breakdown experiment assessing the relative importance of macroinvertebrates and microbes (coarse mesh bags) and microbes alone (fine mesh bags) in the processing of two contrasting litter types (*Alnus acuminata* and *Inga spectabilis*) in forest and pasture streams in a montane tropical area in north-western Ecuador. Main decomposition rates ($-k \text{ d}^{-1} \pm \text{SE}$ values) for $n = 3$ streams, are next to the main labels.

the peak of conidial production was reached at day 21 in forest (181 conidia mg AFDM day^{-1}) and at day 15 in pasture (65 conidia mg AFDM day^{-1}) followed by a constant decrease of conidial production until the end of the experiment (Fig. 3). In the case of *Inga* leaves, conidial production was low until day 21 and peaked on both land uses towards the end of the experiment (Fig. 3), but never reached the values found on *Alnus*. Conidia of *Filospora versimorpha* were the most common in both leaf types and on both land uses (Table 3).

Ergosterol content of leaves did not differ between *Alnus* and *Inga* leaves ($F_{1,54} = 0.00$, $P = 0.996$) or between land uses ($F_{1,54} = 1.30$; $P = 0.260$; Fig. 4). Ergosterol content increased continuously during the experiment and reached a peak at the end in both forest and pasture samples (Fig. 4).

Invertebrates associated with coarse mesh bags. The structure of the macroinvertebrate assemblage associated with coarse mesh bags resembles some patterns found in the Surber samples, particularly in terms of

the higher family richness (families bag^{-1}) in the pasture stream reaches compared to the forest reaches ($F_{1,55} = 15.26$; $P < 0.001$; Table 4a). In the bags, invertebrate abundance (number bag^{-1}) was significantly higher in pasture than in forest sections ($F_{1,55} = 42.58$; $P < 0.001$), while in the Surber samples, abundance was similar. The PIE for macroinvertebrates was similar between coarse mesh bags placed in forest and pasture reaches and also between bags filled with *Alnus* or *Inga* leaves ($F_{1,55} = 2.73$; $P = 0.104$).

The biggest difference between the coarse mesh bags in forest and pasture streams was the much higher density of the shredder *Phylloicus* sp. (Calamoceratidae) that was significantly more abundant in forest than in pasture sections ($F_{1,55} = 6.27$; $P = 0.015$; Appendix S.I.). The structure and composition of the macroinvertebrate assemblages associated with the coarse mesh litter bags were similar for both leaf types (Table 4).

During the leaf decomposition experiment, invertebrates rapidly colonised the coarse mesh bags. The highest number of invertebrates (24 bag^{-1}) and taxa

Table 2 Results of partly nested analyses of variance model comparing the effects of land use (forest and pasture), bag mesh size (fine and coarse) and tree species (*Alnus acuminata* and *Inga spectabilis*) on the rates of litter processing (percentage of litter remaining) in three streams running through mature secondary montane forest and adjacent downstream pastures in north-western Ecuador. Sampling date and stream identity were used as 'between-subject' factors, and land use, mesh size and tree species were considered 'within-subject' factors. $n = 4$ for each treatment combination. Within-subject main factors were tested against the error terms of the interactions (main factors*stream). Within-subject interactions (each main factor*date) were tested against the error terms of the three way interactions (date*stream*mesh size)

	d.f.	MS	F	P
Between subjects				
Date	1	22699.7	179.87	0.0055
Stream	2	129.9	–	–
Date*stream	2	126.2	–	–
Within subjects				
Land use	1	392.6	22.83	0.0411
Land use*Date	1	251.1	10.13	0.0862
Land use *stream	2	17.2	–	–
Land use *date*stream	2	24.8	–	–
Mesh size	1	451.7	107.04	0.0092
Mesh size*date	1	877.9	72.55	0.0135
Mesh size*stream	2	4.22	–	–
Mesh size*date*stream	2	12.1	–	–
Species	1	1049.3	15.97	0.0573
Species*date	1	1884.8	38.78	0.0248
Species*stream	2	65.7	–	–
Species*date*stream	2	48.6	–	–

(23) in forest bags was reached on day 34. The highest number of invertebrates in grassland was reached on day 34 (42 bag⁻¹) and the highest number of taxa (32) on day 63.

Relationships between diversity and leaf breakdown

The abundance of *Phylloicus* sp. was the only parameter in the multiple regression model that explained the percentage of litter remaining at the end of the experiment ($F_{1,9} = 15.66$; $P = 0.041$), after controlling for tree species ($F_{1,9} = 19.87$, $P = 0.002$). A higher mean abundance of *Phylloicus* sp. was associated with a lower percentage of litter remaining (Fig. 5). Shredder species richness and the abundance of the other shredder species (*Anchytarsus* sp.) were not significant predictors in the model.

In terms of the aquatic fungal assemblages in the fine mesh litter bags, the percentage of litter remaining was best explained by ergosterol concen-

tration ($T = -6.67$; $P = 0.001$; adjusted $r^2 = 0.84$); a higher fungal biomass was associated with a lower percentage of litter remaining. Fungal reproductive activity and hyphomycete richness were not significant predictors in the model.

Discussion

The main objective of this study was to assess if two contrasting land uses (forest versus pasture) had significant effects on the benthos of tropical montane streams, consequently affecting the rate of litter decomposition. Our data suggest that the transformation of forest to pastures has resulted in a modification of the macroinvertebrate community of forest and pasture stream reaches in terms of their structure and composition. More specifically, we found a difference in the relative abundance of one particular shredder species in forest and pasture streams, which was accompanied by a significant reduction in the rates of litter processing in the pasture streams. We attribute these differences mainly to the lower abundance of *Phylloicus* sp. in the disturbed sites, when compared to the forested sites. In contrast, aquatic hyphomycete communities and microbial decomposition were not different between forest and pasture sites. In fact, microbial decomposition was very low in general (Fig. 2), suggesting that microbes have a minor role in litter processing in these tropical montane streams.

In general terms, changes in litter processing rates because of the conversion of forest to pasture could be produced by: (i) some environmental factor that changed with the forest conversion and/or (ii) specific differences in the community composition, such as the change in the abundance of key taxa with strong influence on litter processing. Here, we explore these alternatives and analyse their implications in terms of the relationship between biodiversity and ecosystem processes in these montane tropical streams.

Among the environmental variables that affect the rate of litter processing and could be expected to change as result of the conversion of forest to pastures, water temperature is a crucial factor because of its effect on metabolic rate (Irons *et al.*, 1994). In general terms, a temperature increase resulting from the elimination of forest canopy in the pasture areas could be expected to increase microbial and invertebrate activity relative to that in the forest streams, enhancing the rates of litter processing (Bärlocher &

Species	Alnus		Inga	
	Forest	Pasture	Forest	Pasture
<i>Alatospora acuminata</i>	–	0.07	–	–
<i>Alatospora pulchella</i>	1.41	0.65	–	–
<i>Campylospora chaetocladia</i>	13.92	23.39	10.70	33.43
<i>Filosporella versimorpha</i>	54.59	43.00	52.73	43.22
<i>Heliscus tentaculus</i>	1.20	2.61	–	–
<i>Heliscus submersus</i>	–	0.05	–	–
? <i>Lemonniera aquatica</i>	–	–	–	3.43
? <i>Lemonniera terrestris</i>	–	0.29	–	3.43
<i>Lunulospora curvula</i>	1.15	0.39	–	–
<i>Phalangispora constricta</i>	2.20	6.20	9.53	–
<i>Tetracladium marchalianum</i>	0.41	2.19	6.45	–
<i>Tricladium chaetocladium</i>	0.31	2.25	–	3.24
? <i>Trinacrium</i> sp.	15.96	10.21	–	3.24
<i>Tripaspermum</i> sp.	1.10	5.74	20.00	5.71
<i>Triscelophorus acuminatus</i>	1.50	0.12	–	–
Unidentified lunate	2.90	0.33	0.59	0.88
Unidentified oval	2.40	1.15	–	–
Unidentified pentaradiate	0.95	0.29	–	–
Unidentified tetraradiate 1	–	0.26	–	–
Unidentified tetraradiate 2	–	0.26	–	–
Unidentified tetraradiate 3	–	0.55	–	3.43
Total number species	14	20	6	9

Table 3 Aquatic hyphomycetes (relative contribution of each species to the total conidial production) associated with *Alnus acuminata* and *Inga spectabilis* incubated in fine mesh bags, in three streams running through mature secondary montane forest and adjacent downstream pastures in north-western Ecuador. Unidentified conidia contributed with <10% for the total conidia production. (?) Denotes species whose identification is tentative

Graça, 2002). Our data showed that water temperature was higher in the pasture stream reaches, although this was accompanied by slower litter processing in coarse mesh bags, contrary of the finding of McKie & Malmqvist (2009). Final mean differences in litter remaining in the fine mesh bags between forest and grassland were <1%, compared to a mean difference of almost 30% in the coarse mesh bags, suggesting that variation in fungal activity did not contribute significantly to the slower litter processing in the pasture stream sections. In fact, neither fungal activity nor fungal biomass was different between pasture and forest sections (Figs 3 & 4), regardless of the increase in temperature in the pasture sites, as was expected by the findings of others (Irons *et al.*, 1994; McKie & Malmqvist, 2009).

Although higher temperature in pasture streams probably increase microbial activity, this was not reflected in litter loss in the fine mesh bags. However, higher temperature and solar radiation in the pasture sites could promote the growth of primary producers and invertebrates that depend on autotrophic resources (Noel, Martin & Federer, 1986). This shift from a heterotrophic to an autotrophic community was evident in our data, since we found more invertebrate scrapers and fewer shredders in the

pasture sites. Hence, some of the reduction of litter processing that we found in the pasture sites might be related to this shift in the composition of invertebrate communities.

A second ecological factor that differed dramatically between the forest and pasture stream reaches was the amount and type of allochthonous organic matter entering the stream channel. Litter inputs to the forest reaches were 2.4 times higher than those to pasture reaches, a difference that probably affected benthic organisms that depend directly on litter for their feeding or habitat, inducing changes in the benthic community. In fact, our data showed significant differences in species richness, biodiversity and representation of shredders between pasture and forest streams (Appendix S.I.). To what extent these differences in structure of the shredder community can explain the large change in ecosystem processes in terms of litter processing?

The multiple regression analyses between litter processing rates and the mean abundance of different shredder species suggested that only one species (*Phylloicus* sp.) was a significant predictor of the percentage of litter remaining in the coarse mesh bags (Fig. 5). Thus, although the forest and pasture streams both had at least four species of shredders, the overall

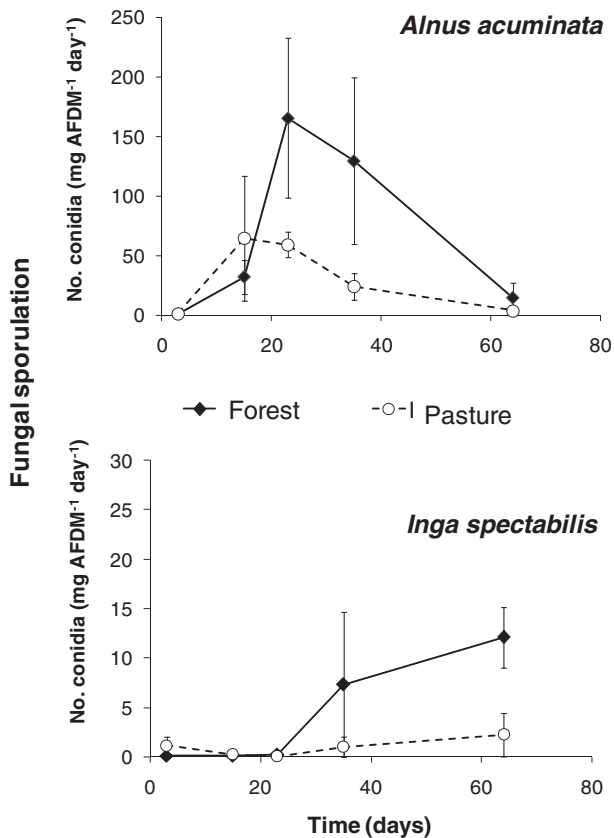


Fig. 3 Fungal sporulation (conidia mg^{-1} AFMD day^{-1}) on *Alnus acuminata* (Kunth) and *Inga spectabilis* (Benth) leaves incubated in a forest and in a pasture reach in a tropical montane area in north-western Ecuador. Each point represents the mean values (± 1 SE). Note the difference in scale on the y-axis.

magnitude of the litter processing rates was better explained by the mean abundance of *Phylloicus* sp. This observation suggests that in these tropical montane streams, the rate of litter processing was not related to the overall diversity of the shredder community, but to the presence and abundance of a single species, whose feeding behaviour makes it a predominant driver of this ecosystem process. Interestingly, the lower abundance of *Phylloicus* sp. in the litter bags of the pasture stream reaches (Table 4) was accompanied by a higher overall density of benthic fauna compared to that of the forest stream reaches, which suggest that litter in pasture sites is used largely as a refuge or substratum for other non-shredding invertebrates. Although this pattern deserves additional study and cannot be directly tested with our data, we hypothesised that the lower abundance of *Phylloicus* sp. in the pasture stream

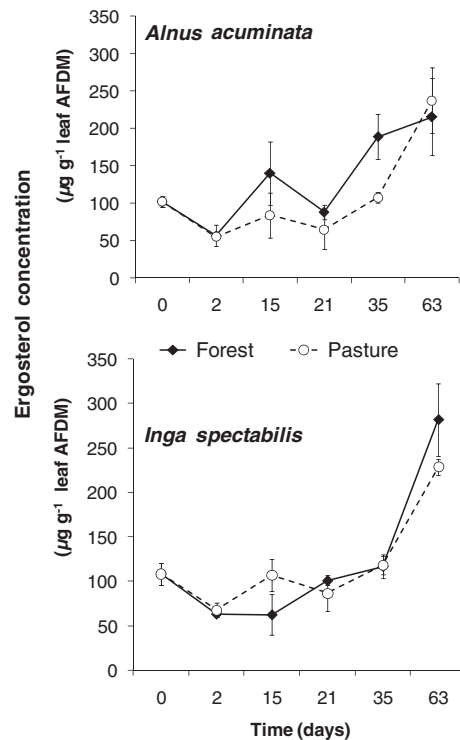


Fig. 4 Mean ergosterol concentration (μg of ergosterol g^{-1} leaf AFDM) in *Alnus acuminata* (Kunth) and *Inga spectabilis* (Benth) leaves incubated in a forest and a pasture reach in a tropical montane area in north-western Ecuador. Each point represents the mean values (± 1 SE).

samples could result not only from a reduction in the amount of litter in these stream reaches but also from a potential increase in competition for space or from predation. This speculation is supported by the higher abundances of scrapers and predators that we found in the pasture stream samples. Moreover, our results show no evidence of a density compensation process by the remaining shredders in the pasture sites, as has been showed by McKie & Malmqvist (2009), as the litter processing rates were significantly lower in pasture streams.

Regarding the relationship between diversity and ecosystem processes, our results agree with previous studies that suggest that the rates particular species can have a strong impact in aquatic ecosystems. For example, while studying the temporal and spatial patterns of leaf litter processing and shredder communities, Dangles & Malmqvist (2004) showed that sites strongly dominated by a single shredder species exhibited higher rates of processing than streams in which the shredder abundance was more

Table 4 Mean invertebrate (a) and shredder (b) community parameters (± 1 SE) calculated for invertebrates found in coarse mesh bags during the litter processing experiment in three streams running through mature secondary montane forest and adjacent downstream pastures in north-western Ecuador. Different upper case letters within each column denote significantly different responses as determined through ANCOVA analyses for benthic fauna associated with litter bags. *Family richness was compared with rarified family richness at different abundance values

a.				
	Invertebrate abundance (no. bag ⁻¹)	Family* richness (families bag ⁻¹)	Probability of interspecific encounter	
Pastures				
<i>Alnus</i>	72.2 (± 9.0) ^A	15.9 (± 1.5) ^A	0.751 (± 0.058) ^A	
<i>Inga</i>	63.3 (± 9.9) ^A	14.9 (± 1.8) ^A	0.711 (± 0.074) ^A	
Forest				
<i>Alnus</i>	20.6 (± 2.2) ^B	10.6 (± 0.8) ^B	0.858 (± 0.009) ^A	
<i>Inga</i>	20.7 (± 2.8) ^B	9.7 (± 0.9) ^B	0.790 (± 0.055) ^A	
b.				
	Shredder abundance (no. bag ⁻¹)	Shredder richness (families bag ⁻¹)	Shredders probability of interspecific encounter	<i>Phylloicus</i> sp. abundance (no. bag ⁻¹)
Pastures				
<i>Alnus</i>	2.96 (± 0.8) ^A	1.73 (± 0.2) ^A	0.371 (± 0.057) ^A	1.23 (± 0.17) ^A
<i>Inga</i>	1.66 (± 0.4) ^A	1.26 (± 0.3) ^A	0.285 (± 0.075) ^A	0.86 (± 0.22) ^A
Forest				
<i>Alnus</i>	3.5 (± 0.6) ^A	1.6 (± 0.2) ^A	0.314 (± 0.053) ^A	2.23 (± 0.34) ^B
<i>Inga</i>	2.8 (± 0.5) ^A	1.3 (± 0.2) ^A	0.180 (± 0.054) ^A	2.30 (± 0.49) ^B

evenly distributed among several species. An additional example has been described by Boyero *et al.* (2007), in which the experimental manipulation of

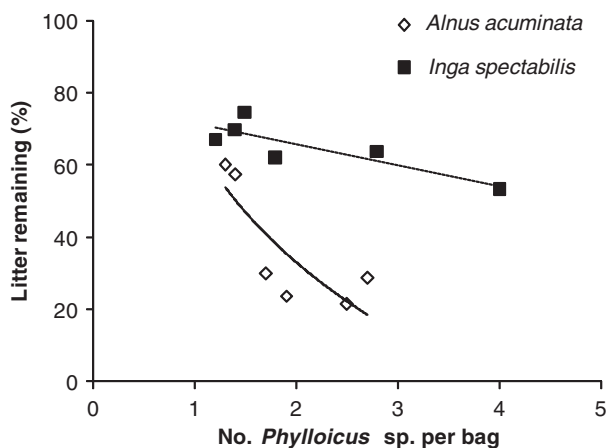


Fig. 5 Relationship between the mean number of *Phylloicus* sp. found in coarse mesh bags and the percentage of *Alnus acuminata* (Kunth) and *Inga spectabilis* (Benth) litter remaining in each litter bag after 63 days in a montane tropical area in north-western Ecuador.

benthic shredder assemblages (three caddisflies and one mayfly) showed that higher species richness tended to increase leaf breakdown rates, but only for the three caddisflies. In the presence of the mayfly, leaf-processing rates by the caddisflies were significantly reduced, suppressing the relationship between the ecosystem process and species richness. Altogether these examples support the notion that, in many cases, the rates of ecosystem processes in aquatic ecosystems are strongly driven by the activity of individual species (Wardle *et al.*, 2002), both through their direct influence on a particular ecosystem process (Taylor *et al.*, 2006) or through interspecific relationships that can overwhelm the influence of the structure and diversity of the ecological community at large (Jonsson & Malmqvist, 2003; Dangles & Malmqvist, 2004). However, it is also important to recall that the nature and magnitude of these relationships could be modified by the interactions between the dominant species with other species from the same or from a different functional group (Jonsson & Malmqvist, 2003), or by the occurrence of functionally dominant

species whose abundance can change over small spatial and temporal scales (McKie *et al.*, 2008).

Regarding the aquatic hyphomycete assemblage, more species and faster rates of decomposition were recorded in bags filled with *Alnus* than with *Inga* leaves; however, decomposition rates were virtually the same in both forest and pasture reaches. Consistently, Lecerf *et al.* (2007) has suggested that microbial decomposers respond to quality of the resource, by processing higher quality leaves faster than poor quality ones. Regardless of the fact that the contribution of hyphomycetes to litter decomposition in these streams was rather minor (difference between fine and coarse mesh bags), we found a strong correlation between litter remaining and fungal biomass (within fine mesh bags), which suggest that fungal biomass (but not diversity) is an important community parameter in explaining microbial litter breakdown in these streams.

In terms of the effects of land-use change on the functioning and structure of these montane stream ecosystems, our study suggests that forest conversion reduced the rates of litter processing, possibly affecting nutrient cycling and productivity. Apparently, the mechanism behind this ecosystem level change was not the overall modification of the shredder or hyphomycete communities, but the reduction of litter inputs into pasture stream reaches, which might have affected the abundance and relative representation of one single species (*Phylloicus* sp.), whose feeding and behaviour have a disproportionate impact on the rates of litter processing. Hence, our results support the notion that the non-random removal of particular species as a result of human intervention can have significant impacts on ecosystem processes (Singer & Battin, 2007; Ball *et al.*, 2008).

The results of this study represent an interesting example of interactions across different scales in which changes at the population level result in modifications of the rates of ecosystem processes. Although these differences between forest and pastures were very clear, we cannot assess to which extent they imply a large-scale or long-term impact on the nutrient cycling and productivity of these montane streams (Stone & Wallace, 1998; Benfield *et al.*, 2001). As suggested by Freeman *et al.* (2007), this topic deserves further attention, especially in Neotropical montane regions that are subject to rapid rates of

change and have a critical role in the hydrological cycle of the Andean region.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Aquatic invertebrate taxa (Ind. m⁻² ± SE) from three streams running through forest and pasture sections in Nanegalito montane forest, Ecuador. Functional Feeding Group (FFG): Scraper (Scr), Predator (Pr), Collectors (Coll), Shredders (Shr), Filtrators (Fil).

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