

Land-use effects on structural and functional composition of benthic and leaf-associated macroinvertebrates in four Andean streams

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Abstract The replacement of native forests by pastures takes place widely in the Andes. The effects of such land-use change on aquatic assemblages are poorly understood. We conducted a comparative analysis of the effects of forest conversion to pastures on the taxonomic, structural, and functional composition of macroinvertebrates (benthic and leaf-associated) in montane and upper montane streams (ecosystem type) of the south Ecuadorian Andes. Taxonomic composition of benthic and leaf-

associated macroinvertebrates was different between ecosystem type and land use. Also, major differences in the structural and functional composition of benthic and leaf-associated macroinvertebrates were mainly promoted by land use in both ecosystem types. Forested streams showed higher diversity than pasture streams, sustaining more shredder, scraper, and predatory invertebrates. We also observed differences in the macroinvertebrate communities between benthic and leaf-bag samples. Leaf bags had lower diversity and more collector invertebrates than benthic samples. This study highlights the large effect of riparian forest conversion to pasture land on macroinvertebrate communities, and the importance of using appropriate sampling techniques to characterize aquatic assemblages. We also recommend the maintenance and restoration of riparian vegetation to mitigate the effects of deforestation on stream communities and ecosystem processes.

Keywords Riparian conversion · Macroinvertebrate composition · FFG · Benthic · Leaf bags · Montane streams

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Introduction

Stream ecosystems are being affected by land-use change, resulting in significant modifications to

aquatic communities (Allan 2004). One of the most common land-use practices across different regions is the replacement of riparian forests by pastures. Riparian clearance can increase light penetration and water temperature (Cole and Newton 2013). Moreover, the establishment of pastures for livestock can significantly increase the nutrient concentrations in streams (Neill et al. 2001) and reduce the organic matter inputs to them (Hladyz et al. 2011). Tropical montane streams are globally recognized by their ecosystem services and biodiversity (Buytaert et al. 2011). However, streams in tropical montane regions are very susceptible to land-cover change (Astudillo et al. 2016). The rapid deforestation occurring in the tropical Andes since the 1970s (Brandt and Townsend 2006; Rodríguez Eraso et al. 2013; Tapia-Armijos et al. 2015) has offered the opportunity to assess the effects of forest conversion to pasture on their streams. Deforestation has decreased the ecological condition of Andean streams by reducing the water quality and modifying the aquatic assemblages (Iñiguez-Armijos et al. 2014). Also, environmental factors controlling the aquatic assemblages such as light, temperature, and nutrients in Andean streams have been recently altered most likely as an effect riparian-stream disruption because of land-use change and associated anthropogenic activities (Lujan et al. 2013). However, the multiple pathways through which human-related disturbances affect aquatic assemblages as described in temperate regions need further attention in streams of the Andes. For example, anthropogenic stress can affect the organization of stream macroinvertebrates altering key ecosystem processes (e.g., Voß and Schäfer 2017). In this sense, a better understanding of how macroinvertebrates responds to land-use change at different montane ecosystems is crucial in a region where best land-use practices and land planning are underdeveloped.

Macroinvertebrate communities are the most used aquatic biota to assess the response of stream ecosystems to several anthropogenic impact across geographic regions (Barbour et al. 1999; Carter et al. 2006; Buss et al. 2015). In this regard, current biomonitoring programs are also using the macroinvertebrates to assess the effects of land-cover/land-use change on stream ecosystems (Collier and Hamer 2012; European Environment Agency 2012; Environmental Protection Agency 2013), because macroinvertebrate communities can respond in different

pathways. For instance, major differences in the presence or absence of specific taxa have been observed in streams affected by pastures compared to forested streams (Death and Collier 2009; Astudillo et al. 2016). Conversion of riparian forest to pasture can lead to lower macroinvertebrate species richness and higher macroinvertebrate abundance, modifying their structural (diversity patterns) and functional (trophic organization) composition (Lorion and Kennedy 2009; Miserendino and Masi 2010; Fugère et al. 2016). Shifts in the functional organization of benthic macroinvertebrates can affect ecosystem-level processes, such as the leaf-litter breakdown in streams. Lower organic matter inputs due to the conversion of riparian forest to pasture can reduce (Iñiguez-Armijos et al. 2016) or eliminate (Danger and Robson 2004) leaf-shredding invertebrates having consequences on organic matter dynamics. Moreover, the high levels of light, nutrient, and temperature as a consequence of the establishment of pasture can increase the periphyton biomass favoring a higher abundance of scraper invertebrates (Allan 2004).

Benthic macroinvertebrates can be sampled with a variety of techniques. For example, the kick-net device is the most common technique used for bioassessment (Buss et al. 2015) as it is efficient and collects more taxa from a greater variety of habitats than other sampler devices (Hauer and Resh 2006). Also, different types of artificial substrates have been used to sample benthic macroinvertebrates (Flannagan and Rosenberg 1982; Rosenberg and Resh 1982). Leaf packs enclosed in mesh bags, which are mainly used to assess ecosystem functioning (Gessner and Chauvet 2002; Dangles et al. 2004), have been proposed to complement the biomonitoring of streams. However, artificial leaf packs are complementary, and not alternative, of benthic sampling in stream ecosystems because they are less efficient to characterize macroinvertebrate communities (Di Sabatino et al. 2014). The attractiveness of artificial leaf pack for shredders can be low if a high quantity and quality of food is available in the stream (Cortes et al. 1997). Also, artificial leaf packs can favor the colonization of collectors or predators because they can serve as a source of fine particulate organic matter (FPOM) and as refuge of potential preys (Dangles et al. 2001; Fenoglio et al. 2006).

We investigated how ecosystem type (montane vs. upper montane) and land use (forest vs. pasture)

influenced the taxonomic, structural, and functional composition of benthic and leaf-associated macroinvertebrates, hypothesizing that there will be difference between the compositions of contrasting sites and that response of macroinvertebrates to land-use change will be similar both ecosystem types.

Methodology

Study sites

We used data from two field experiments that addressed the effects of land use on litter breakdown in Andean streams located in montane (Mon; Iñiguez-Armijos et al. 2016) and upper montane (UMon; unpublished) ecosystems in the south of Ecuador (Fig. 1). We used a set of two comparable streams per ecosystem, all of them tributaries of the Zamora-Santiago River (Amazon basin). The field experiments were carried out during the dry season, starting on October 2011 at Mon streams and on September 2013 at UMon streams, looking for stable flow conditions to achieve homogeneity in the macroinvertebrate community composition (Ríos-Touma et al. 2011). In each stream, we located an upstream site flowing through native forest and a downstream site in open pastures. The study sites were placed at the downstream end of each land use, and the distance between forest and pasture sites was 3500–4000 m. Each study site consisted of a stream reach of 30 m in length (in total $n = 8$) with a similar slope (3–4%) that was dominated by rifles.

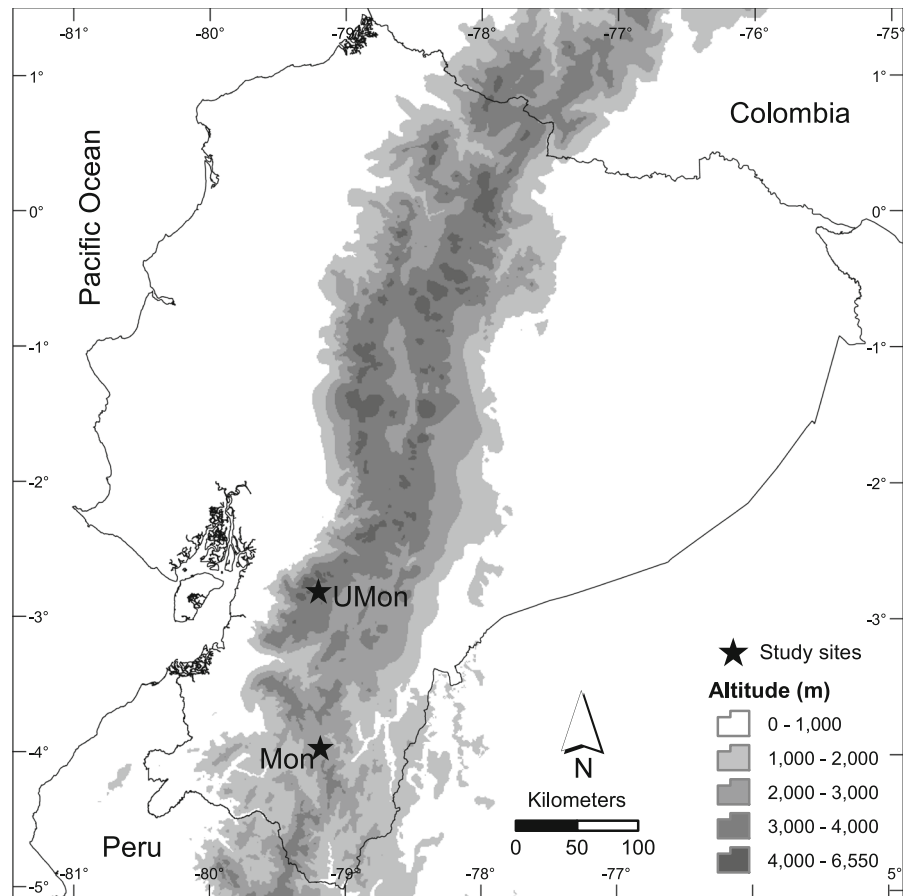
In both ecosystems, forests are evergreen, and the diversity of plant species along the riparian buffers supplies an organic matter of different litter quality across the year. In contrast, pasture areas are used for cattle ranching and can extend to stream margins resulting in reduced riparian vegetation and canopy clearing. Streams (2nd order) of the Mon ecosystem are located at 2200 m above sea level (a.s.l.) at the Zamora upstream catchment, east of the city of Loja (Loja Province). Mean annual precipitation is around 2200 mm, and mean daily temperature is around 16 °C. In the forest sites, riparian sections were dominated by trees of the genera *Croton*, *Hedyosmum*, *Clusia*, *Morella* and *Juglans*; while the pasture sites present commonly trees of *Alnus acuminata* Kunth and occasionally *Eucalyptus* spp. and *Inga* spp. along

the riparian margins. Streams (1st order) of the UMon ecosystem are located at 3200 m a.s.l. within the Zhurucay experimental catchment, approximately 85 km west of the city of Cuenca (Azuay province). Mean annual precipitation and temperature are around 1460 mm and 5.9 °C, respectively. Trees of the genera *Polylepis* are common in the riparian margins of forest sites, while trees of *A. acuminata* and *Eucalyptus* spp. occasionally grow along the riparian margins of the pasture sites.

Sampling methods

Macroinvertebrate communities were sampled using benthic sampling and leaf bags. Leaf bags were periodically collected during an experiment of 56 days (see details below), and benthic samples were collected on the last day of such experiment. Benthic sampling differed slightly regarding the sampler device because the Mon streams are deeper and wider than UMon streams. In Mon streams, we used a D-frame net (0.30 m wide, 0.5 mm mesh) to collect four benthic samples per study site. Sampling was standardized by time (40 s kicking) and by area (0.30×1.5 m). It was not possible to place the D-frame net in UMon streams due to channel characteristics (width and depth). Hence, we used a Surber sampler (0.30×0.30 m, 0.5 mesh), which is more suitable for stream depths < 0.15 m (Barbour et al. 1999; Hauer and Resh 2006). We collected five benthic samples per study site by removing the substrate during 40 s. Macroinvertebrates were preserved in ethanol, taken to the laboratory identified mostly to genus level (Fernández and Domínguez 2001; Roldán Pérez 2003), and assigned to functional feeding groups (FFG) (Cummins et al. 2005; Tomanova et al. 2006; Ramirez and Guitiérrez 2014). Each benthic sample was used as a replicate for each land use in data analysis. To determine the macroinvertebrate communities in leaf bags, alder (*A. acuminata*) leaves enclosed in mesh bags were used as the artificial substrate. Leaves were gathered after abscission from the ground and were air-dried, and approximately 4–5 g of leaf-litter was enclosed within coarse mesh bags (10 mm mesh size) of approximately 16×17 cm. Twenty leaf bags were deployed at each study site and tied in groups of five to iron bars separated one from another. Four leaf bags were retrieved on each of five dates of incubation (3, 14, 28,

Fig. 1 Location of the study sites in streams at different Andean ecosystems of Ecuador, *Mon* montane, *UMon* upper montane



42, 56 days) from each study site, were placed in plastic bags, and taken to the laboratory. Leaf litter was carefully rinsed to remove associated macroinvertebrates, which were processed as described above. For data analysis, all individuals recovered during the sampling dates were considered as subsamples and were accumulated in four samples for each land use.

When leaf bags were retrieved on each of five collection dates, we determined hydraulic (channel width, depth, current velocity) and physicochemical variables (water temperature, conductivity, pH, dissolved oxygen) using portable probes (GW FP311 Flow Probe and WTW Multi 3430 in Mon streams; Hydromate CMC3 and Horiba U-50 in UMon streams). All measurements were taken at four transects placed across the 30 m stream reach during daylight between 9 a.m. and 4 p.m., and values were averaged per date. In general, Mon streams were about two times wider and deeper than UMon streams, but the studied stream reaches had a similar slope and

streamflow characteristics providing comparable morphological conditions. More information about macroinvertebrates and stream variables datasets in Mon streams can be found in Iñiguez-Armijos et al. (2016).

Data analysis

Before analysis, we created a matrix using the total abundance data of each genus as columns found at each benthic or leaf-bag replicate as rows. Additionally, abundance data were log-transformed to reduce the effect of large numbers in single data. Taxa represented by three or fewer individuals were excluded to avoid the influence of rare taxa on analysis. Data analysis was performed in the R environment (R Development Core Team 2017) applying different packages as described below.

For both benthic and leaf-associated macroinvertebrates, a separate permutational multivariate analysis

of variance (perMANOVA; Anderson 2001) was used to test differences in macroinvertebrate taxonomic composition between land use (forest and pasture) and ecosystem type (montane and upper montane). Using the ‘adonis’ function in ‘vegan’ package (Oksanen et al. 2014), the perMANOVA was applied on a Bray–Curtis similarity matrix calculated from the relative abundance data (Bray and Curtis 1957) of macroinvertebrates. Thus, the resulting resemblance matrix was analyzed in a hierarchical design of two factors, and the tested sources of variation were ecosystem type (E: 2 levels), land use (Lu: 2 levels), and their interaction. The statistic tests were computed using 999 permutations. Additionally, non-metric multidimensional scaling (nMDS) was used to explore the taxonomic composition between land uses and ecosystem types. The nMDS was performed using the ‘metaMDS’ function in ‘vegan’ package.

To assess the differences in the structural composition of benthic and leaf-associated macroinvertebrates, we calculated macroinvertebrate richness and abundance, evenness (Pielou’s index), and Shannon’s diversity by using the ‘vegan’ package (Oksanen et al. 2014). These diversity metrics were compared between ecosystem types and land uses by generalized linear mixed models (GLMMs) using the ‘glmer’ function in ‘lme4’ package (Bates et al. 2017). Ecosystem type and land use (nested within the stream) were treated as fixed factors, while the stream was treated as a random factor. GLMMs were fitted assuming a Poisson (count data) and gamma (continuous data) error distribution, and parameters were estimated using the Laplace approximation (Bolker et al. 2008). To examine significant differences between ecosystem types and land uses, we performed post hoc tests using the ‘mcposthoc.fnc’ function in ‘LMERConvenienceFunctions’ package (Tremblay and Ransijn 2015). To assess the differences in the functional composition of benthic and leaf-associated macroinvertebrates, the percentages of FFG were analyzed by using GLMMs similarly parameterized, assuming a binomial (proportion data) error distribution and considering the same fixed and random factors.

Results

Stream variables

At both ecosystems, stream water was well oxygenated and had circumneutral pH and low conductivity. Stream water was warmer in Mon than UMon streams. Stream hydraulic and physicochemical variables showed little variation between forest and pasture sites within each ecosystem type. However, water temperature was higher in pasture sites in both ecosystem types. Also, conductivity was higher in pasture sites, while dissolved oxygen was higher in forest sites (Table 1).

Macroinvertebrate taxonomic composition

We collected a total of 14,070 macroinvertebrate individuals. In Mon streams, 2648 individuals were collected with benthic samples, and 2805 individuals were found in leaf bags (see Iñiguez-Armijos et al. 2016). In UMon streams, 5707 individuals were collected with benthic samples, and 2874 individuals were found in leaf bags. We observed significant differences in the macroinvertebrate composition between ecosystem types and land uses (Table 2; Fig. 2). In Mon streams, benthic and leaf-associated macroinvertebrates were mostly dominated by aquatic insects (> 98% of total abundance) than by non-insects. Here, Chironomidae taxon-2 (Diptera; 27%) and *Thraulodes* (Ephemeroptera; 19%) were the most common macroinvertebrates in benthic samples, while Chironomidae taxon-2 (45%) and *Simulium* (Diptera; 37%) were in leaf bags (Table 3). In UMon streams, aquatic insects (98%) largely dominated the leaf-associated macroinvertebrates compared to the non-insects. However, the benthic macroinvertebrates here were almost equally distributed between aquatic insects (49%) and non-insects (51%). Chironomidae taxon-2 (29%) and the non-insects taxa *Dugesia* (Tricladida; 24%) and *Tubifex* (Haplotaxida; 19%) were the most abundant macroinvertebrates in benthic samples, while Chironomidae taxon-2 (64%) and *Tubifex* (34%) were in leaf bags (Table 3). In the case of land use, both benthic and leaf-associated macroinvertebrates were largely dominated by aquatic insects (> 96%) than by non-insects in forest and

Table 1 Hydraulic and physicochemical variables (mean $\pm$ SE) of the montane and upper montane (Ecosystem type) streams at forest and pasture (land-use) sites in the Ecuadorian Andes

Stream variable	Montane (Mon) ^a		Upper Montane (UMon)	
	Forest	Pasture	Forest	Pasture
Width (m)	4.4 $\pm$ 0.3	4.5 $\pm$ 0.2	1.5 $\pm$ 0.0	1.5 $\pm$ 0.0
Depth (cm)	16.8 $\pm$ 1.2	15.1 $\pm$ 1.8	8.1 $\pm$ 0.5	6.7 $\pm$ 0.4
Velocity (cm s ⁻¹)	54.3 $\pm$ 0.5	53.9 $\pm$ 0.4	42.5 $\pm$ 12.2	48.2 $\pm$ 24.1
Temperature (°C)	13.5 $\pm$ 0.2	17.0 $\pm$ 0.3	7.1 $\pm$ 0.3	9.9 $\pm$ 1.1
pH	6.9 $\pm$ 0.1	6.9 $\pm$ 0.1	6.5 $\pm$ 0.3	6.2 $\pm$ 0.3
Conductivity (μ S cm ⁻¹)	26.9 $\pm$ 2.4	45.3 $\pm$ 0.9	47.9 $\pm$ 1.8	93.6 $\pm$ 3.4
Dissolved oxygen (mg L ⁻¹)	7.9 $\pm$ 0.1	7.3 $\pm$ 0.1	8.8 $\pm$ 0.5	8.4 $\pm$ 1.1

^aData for the montane stream variables were taken from Iñiguez-Armijos et al. (2016)

Table 2 Summary of the perMANOVA analysis on taxonomic composition of benthic (A) and leaf-associated (B) macroinvertebrates of montane and upper montane (ecosystem type) streams at forest and pasture (land use) sites in the Ecuadorian Andes

Source of variation	df	SS	MS	F	p
A					
Ecosystem type, E	1	3.6122	3.6122	21.5	0.001
Land use, Lu	1	1.3760	1.3760	8.2	0.001
E $\times$ Lu	1	1.2161	1.2161	7.2	0.001
Residuals	32	5.3803	0.1681		
Total	35	11.5846			
B					
Ecosystem type, E	1	2.2707	2.2707	16.8	0.001
Land use, Lu	1	1.3184	1.3184	9.8	0.001
E $\times$ Lu	1	0.4675	0.4675	3.5	0.019
Residuals	28	3.7790	0.1350		
Total	31	7.8356			

Degrees of freedom (df), sums of squares (SS), means of squares (MS), *F*-statistic, and *p* values are shown (significant difference at $p < 0.05$ level is indicated in bold)

pasture sites of Mon streams. In forest sites, *Thraulodes* (27%) and *Atanatolica* (Trichoptera; 20%) were the most common taxa in benthic samples, while *Simulium* (62%) was in leaf bags (Table 3). In pasture sites, Chironomidae taxon-2 was the most common taxon in both benthic (64%) and leaf-bag (69%) samples (Table 3). In UMon streams, both benthic and leaf-bag macroinvertebrates in forest sites were slightly dominated by aquatic insects (53%–62%)

than by non-insects, while in pasture sites the benthic macroinvertebrates were dominated by non-insects (54%) and the leaf-bag macroinvertebrates by aquatic insects (66%). In forest sites, Chironomidae taxon-2 (29%), *Dugesia* (15%), *Tubifex* (14%), and *Hyalella* (Amphipoda; 12%) were the most common taxa in benthic samples, while Chironomidae taxon-2 (60%) and *Tubifex* (36%) were in leaf bags (Table 3). In pasture sites, Chironomidae taxon-2 (29%), *Dugesia* (28%), and *Tubifex* (22%) were the most common taxa in benthic samples, while Chironomidae taxon-2 (65%) and *Tubifex* (34%) were in leaf bags (Table 3).

Macroinvertebrate structural composition

In benthic samples, no significant differences were found in the four structural macroinvertebrate metrics between ecosystem types (post hoc test $p > 0.1$) as opposed to land uses (Fig. 3). Forest sites had significantly higher evenness (post hoc test $p < 0.02$) and Shannon's diversity (post hoc test $p < 0.03$) than pasture sites, while pasture sites had higher total macroinvertebrate abundance (post hoc test $p < 0.03$). Macroinvertebrate richness (post hoc test $p = 0.15$) did not differ between land uses (Fig. 3). The two-factor interaction ecosystem type $\times$ land use was only significant for total abundance (post hoc test $p < 0.01$). In leaf-bag samples, Mon streams had significantly lower total macroinvertebrate abundance (post hoc test $p < 0.01$), although higher richness (post hoc test $p < 0.01$) and Shannon's diversity (post hoc test $p < 0.01$) than UMon streams. Macroinvertebrate evenness (post hoc test $p = 0.37$) did not differ

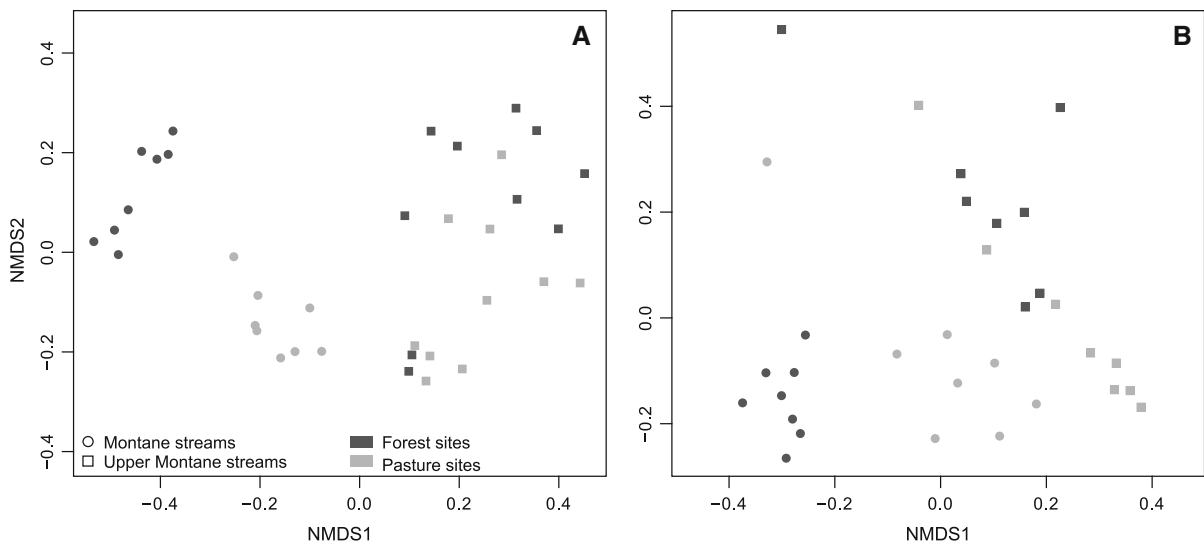


Fig. 2 nMDS biplot ordination of benthic (a) and leaf-associated (b) macroinvertebrates collected in montane and upper montane streams at forest and pasture sites in the Ecuadorian Andes

between ecosystem types (Fig. 4). No significant differences were found in the four structural macroinvertebrate metrics between forest and pasture sites. The two-factor interaction ecosystem type $\times$ land use was only significant for total abundance (post hoc test $p < 0.01$).

Macroinvertebrate functional composition

In benthic samples, Mon streams had a significantly higher relative abundance of scrapers (post hoc test $p < 0.01$) and lower abundance of shredders (post hoc test $p < 0.02$) than UMon streams. No significant differences in the abundance of collectors and predators (post hoc test $p > 0.19$) were detected between ecosystem types (Fig. 5). In terms of land use, the abundance of scrapers (post hoc test $p < 0.01$) and predators (post hoc test $p < 0.01$) was significantly higher in forest than in pasture sites, while the abundance of collectors (post hoc test $p < 0.01$) was significantly higher in pasture than in forest sites (Fig. 5). No significant differences were detected in the shredder abundance between land uses. The two-factor interaction ecosystem type $\times$ land use was significant for the abundance of collectors, scrapers, and predators (post hoc tests $p < 0.01$).

In leaf-bag samples, the abundance of collectors (post hoc tests $p < 0.01$) was significantly higher in UMon than in Mon streams, while the abundance of

scrapers (post hoc tests $p = 0.01$) and shredders (post hoc tests $p = 0.05$) was significantly higher in Mon than in UMon streams (Fig. 6). No significant differences were detected in the abundance of predators between ecosystem types. On the other hand, pasture sites had a significantly higher abundance of collectors (post hoc tests $p < 0.01$) than forest sites, while forest sites had a significantly higher abundance of predators (post hoc tests $p < 0.01$) and shredders (post hoc tests $p = 0.03$) than pasture sites (Fig. 6). The scraper abundance did not differ between land uses. A significant effect of the two factors interaction ecosystem type $\times$ land use was only detected for shredder abundance (post hoc tests $p = 0.04$).

Discussion

In this study, we assessed how the taxonomic, structural, and functional composition of benthic and leaf-associated macroinvertebrates is affected by riparian conversion (forest vs. pasture) at different stream ecosystem types (montane vs. upper montane) in four Andean streams. Our data suggest that there were differences in the macroinvertebrate communities between stream ecosystem types and that land-use change along riparian buffers is a major factor altering the macroinvertebrate composition of Andean streams.

Table 3 Overview of the taxonomic composition of benthic and leaf-associated macroinvertebrates of montane and upper montane (ecosystem type) streams at forest and pasture (land use) sites in the Ecuadorian Andes

Order	Family	Genus	Upper montane				Montane				FFG	
			Forest		Pasture		Forest		Pasture			
			Benthos	Leaf bags	Benthos	Leaf bags	Benthos	Leaf bags	Benthos	Leaf bags		
Amphipoda	Hyalellidae	<i>Hyalella</i>	205	2	75	0	0	0	0	0	Shr	
Coleoptera	Elmidae	<i>Austrelmis</i>	89	0	0	0	0	0	0	0	Col	
		<i>Austrolimnius</i>	61	0	193	0	0	0	0	0	Col	
		<i>Cylloepus</i>	0	0	0	0	14	2	0	1	Col	
		<i>Heterelmis</i>	47	0	60	0	3	0	12	2	Col	
		<i>Macrelmis</i>	0	0	2	0	3	0	12	0	Col	
		<i>Microcylloepus</i>	0	0	2	0	0	0	0	0	Col	
		<i>Phanocerus</i>	0	0	0	0	2	0	0	0	Col	
		<i>Anchytarsus</i>	0	0	0	0	3	5	4	2	Shr	
	Philodactylidae	<i>Scirtes</i>	0	0	0	0	0	1	0	1	Scr	
	Scirtidae	taxon-1	0	0	8	0	0	0	0	0	Col	
Diptera	Athericidae	<i>Atherix</i>	0	0	0	0	1	11	2	0	Pre	
	Blephariceridae	<i>Paltostoma</i>	0	0	0	0	9	0	1	0	Scr	
	Ceratopogonidae	<i>Allaudomyia</i>	2	0	104	6	0	0	0	0	Pre	
	Chironomidae	Taxon-2	554	336	1037	1508	0	144	726	1114	Col	
	Empididae	<i>Chelifera</i>	0	0	0	0	0	31	0	0	Pre	
		<i>Neoplasta</i>	15	2	28	2	0	0	0	0	Pre	
	Muscidae	<i>Limnophora</i>	0	0	0	0	0	0	0	2	Pre	
	Psychodidae	<i>Pericoma</i>	24	3	2	0	0	0	0	0	Col	
	Simuliidae	<i>Gigantodax</i>	0	2	0	2	0	2	2	2	Col	
		<i>Simulium</i>	0	0	3	0	8	735	54	314	Col	
Tipulidae		<i>Hexatoma</i>	0	0	1	0	13	0	1	0	Pre	
		<i>Molophilus</i>	0	0	0	0	0	0	6	0	Shr	
		<i>Prionocera</i>	0	0	7	0	0	0	0	0	Shr	
		<i>Tipula</i>	0	0	0	0	2	8	1	2	Shr	

Table 3 continued

Order	Family	Genus	Upper montane			Montane			FFG		
			Forest		Pasture	Forest		Pasture			
			Benthos	Leaf bags		Benthos	Leaf bags				
Ephemeroptera	Baetidae	<i>Andesiops</i>	0	0	38	0	0	0	0	Shr	
		<i>Baetodes</i>	3	0	14	0	199	95	75	25	Ser
		<i>Mayobaetis</i>	0	0	0	0	2	5	0	0	Col
		<i>Zelusia</i>	0	0	0	0	70	0	209	6	Col
	Leptohyphidae	<i>Leptohyphes</i>	0	0	0	0	66	103	5	17	Col
		<i>Tricorythodes</i>	0	0	0	0	0	0	12	0	Col
	Leptophlebiidae	<i>Ecuaphlebia</i>	49	0	6	0	0	0	0	0	Col
		<i>Thraulodes</i>	0	0	0	0	424	9	98	3	Col
	Hydridae	<i>Hydra</i>	0	0	5	0	0	0	0	0	Pre
		taxon-3	18	0	0	0	0	1	0	0	Pre
Gordioidea	Tubificidae	<i>Tubifex</i>	231	200	451	776	2	4	22	Col	
Haplotaixida	Perilidae	<i>Anacroneuria</i>	0	0	0	0	179	9	4	0	Pre
		taxon-4	10	0	4	0	0	0	0	0	Ser
	Anomalopsychidae	<i>Phylloicus</i>	0	0	0	0	14	9	0	5	Shr
		<i>Helicopsyche</i>	5	0	26	0	42	0	4	0	Ser
	Calamoceratidae	<i>Atopsyche</i>	7	1	9	7	4	0	1	0	Pre
		<i>Neatopsyche</i>	0	0	0	0	2	0	0	0	Pre
	Hydropsychidae	<i>Leptonema</i>	1	0	11	0	0	0	0	0	Col
		<i>Smicridea</i>	0	0	0	0	8	0	0	1	Col
	Hydroptylidae	<i>Metrichia</i>	0	0	0	0	8	5	18	36	Ser
		<i>Ochrotrichia</i>	16	1	10	2	0	0	0	0	Ser
Leptoceridae	Leptoceridae	<i>Atanatolica</i>	0	1	1	1	0	0	0	0	Col
		<i>Grimichella</i>	0	0	0	0	316	22	7	8	Ser
	<i>Nectopsyche</i>	0	0	0	0	2	0	0	0	Shr	
		<i>Marilia</i>	0	0	0	0	4	2	0	1	Shr
	Xiphocentronidae	taxon-5	1	0	13	0	0	0	0	0	Col
		<i>Dugesia</i>	181	10	818	0	0	0	8	0	Pre
	Hydrachnidae	<i>Hydrachna</i>	64	3	15	9	0	0	0	0	Pre

FFG functional feeding group, Col collectors, Scr scrapers, Pre predators, and Shr shredders

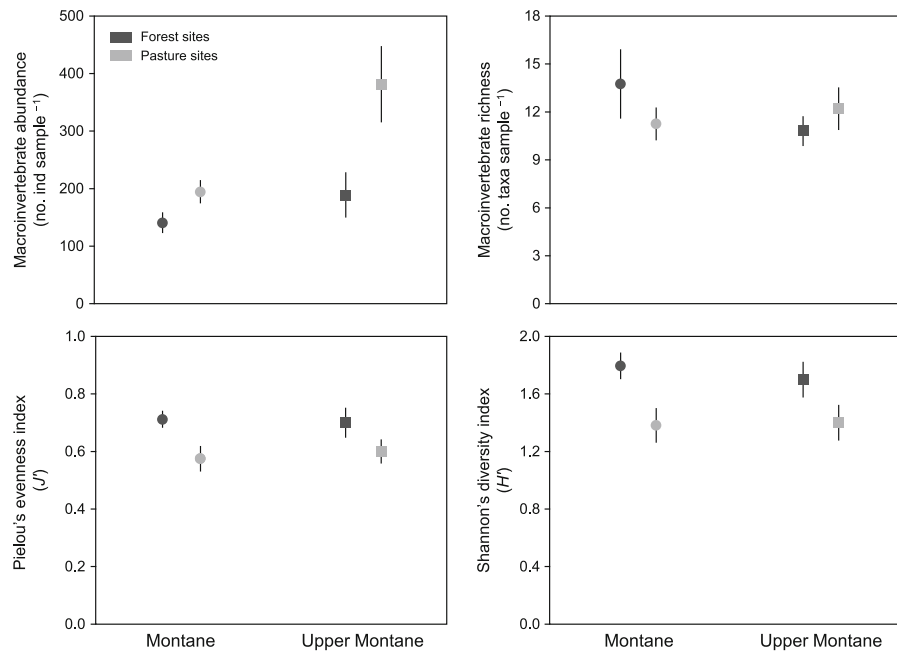


Fig. 3 Mean values ($\pm$ SE) of the abundance, richness, Pielou's evenness, and Shannon's diversity of benthic macroinvertebrates collected in montane and upper montane streams at forest

and pasture sites in the Ecuadorian Andes. Metrics for montane streams $n = 4$ and for upper montane streams $n = 5$

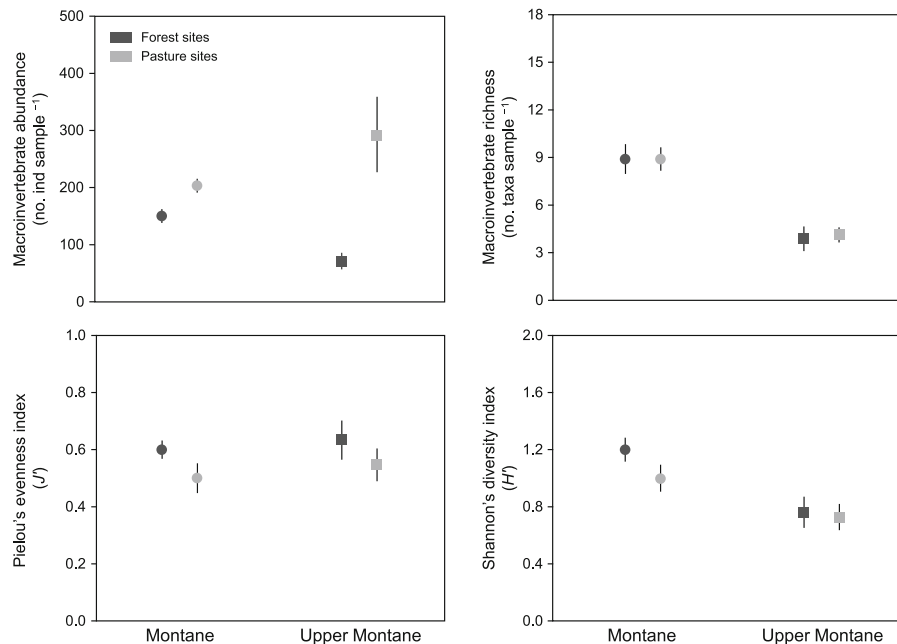


Fig. 4 Mean values ($\pm$ SE) of the abundance, richness, Pielou's evenness, and Shannon's diversity of leaf-associated macroinvertebrates collected in montane and upper montane streams at

forest and pasture sites in the Ecuadorian Andes. For all metrics, $n = 20$

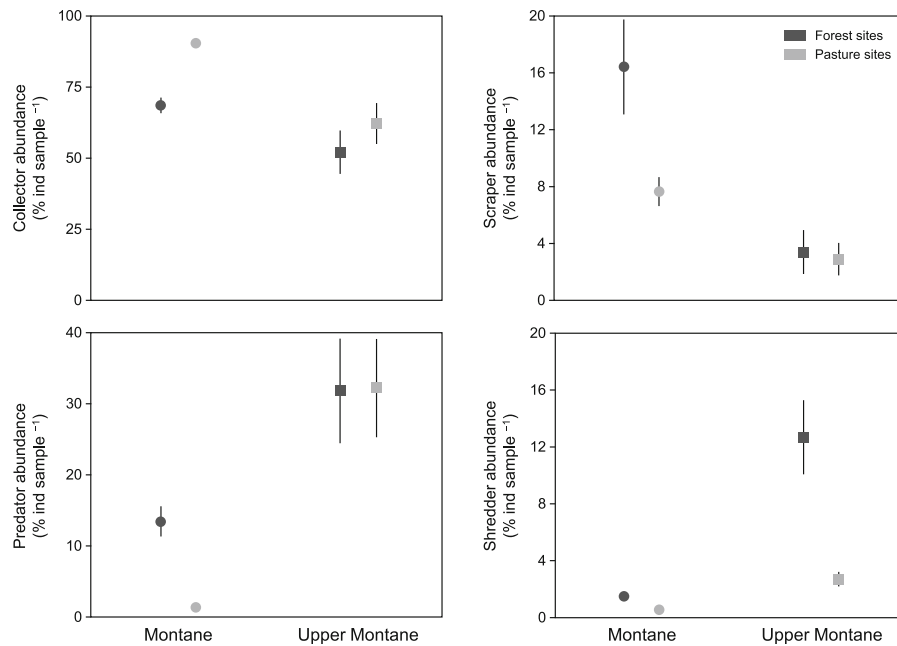


Fig. 5 Mean relative abundance ($\pm$ SE) of collector, scraper, predator, and shredder benthic macroinvertebrates in montane and upper montane streams at forest and pasture sites in

Ecuadorian Andes. Metrics for montane streams $n = 4$ and for upper montane streams $n = 5$. The extension of y-axis differs for all metrics

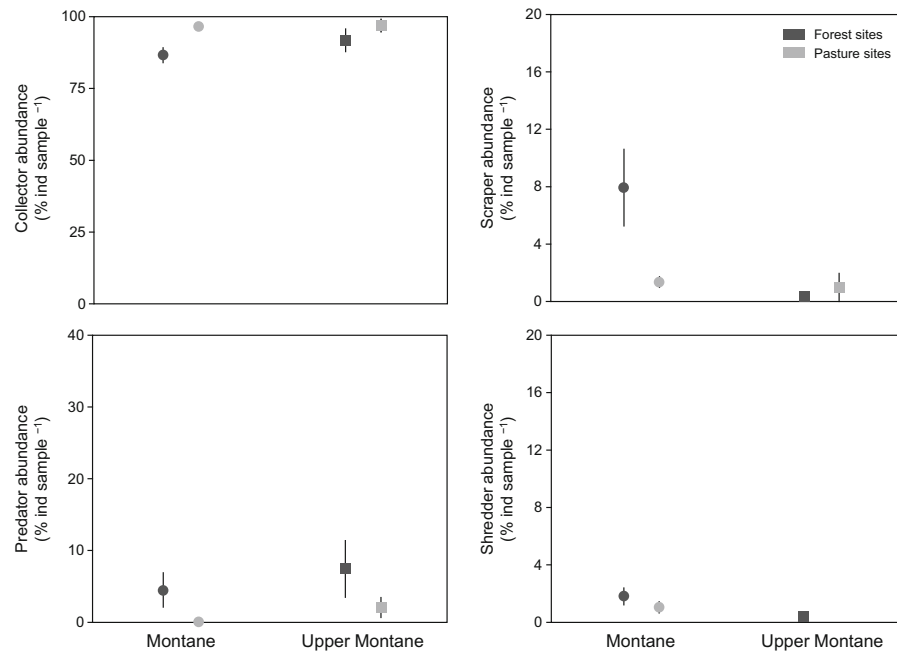


Fig. 6 Mean relative abundance ($\pm$ SE) of collector, scraper, predator, and shredder macroinvertebrates associated with leaf bags in montane and upper montane streams at forest and

pasture sites in Ecuadorian Andes. For all metrics, $n = 20$. The extension of y-axis differs for all metrics

Differences between stream ecosystems

The dissimilarity found in the taxonomic composition of both benthic and leaf-associated macroinvertebrates between the two ecosystem types is supported by other studies in Andean streams (Jacobsen and Encalada 1998; Jacobsen 2008; Lujan et al. 2013; Madsen et al. 2015). They have demonstrated that variations in the macroinvertebrate composition were statistically attributed to altitude and stream parameters directly correlated with the altitudinal gradient such as oxygen availability and water temperature. Our results confirmed those variations considering that the studied streams are located in a montane and an upper montane forest (ecosystem classification according to Sierra et al. 2002) with an altitudinal difference of around 1000 m which is also reflected in variations of the water temperature and dissolved oxygen between both stream ecosystem types.

Benthic macroinvertebrates suggested no differences in their structural composition between stream ecosystem types, while leaf-bag macroinvertebrates do. These contradictory findings can be explained by the fact that both sampling techniques target different macroinvertebrate assemblages and that a higher diversity of macroinvertebrates can be collected with benthic sampling. For instance, the main constraint of artificial substrates, such as leaf bags, is the collection of a part of the entire macroinvertebrate community (Murphy and Giller 2000; Di Sabatino et al. 2014). It can be evidenced by the very low diversity of macroinvertebrates collected in leaf bags compared to benthic samples in both ecosystem types. Another reason for this finding is probably the lower diversity of macroinvertebrates at higher altitudes in Andean streams (Jacobsen 2008; Lujan et al. 2013), which together with the known limitations of artificial leaf packs, makes the single use of this technique unsuitable to characterize the macroinvertebrate community at any stream ecosystem. However, the assessment of the macroinvertebrate diversity will be more accurate if more than one sampling technique is applied (Stein et al. 2008).

We also found differences in the functional composition of macroinvertebrates of benthic samples and leaf bags between Mon and UMon streams. The relative abundance of shredder invertebrates was higher in Umon than in Mon streams, while the opposite occurred for scrapers. UMon streams were

smaller than Mon streams and showed a more closed tree canopy as well. Therefore, more abundant organic matter inputs and more shade provided by the riparian forest are expected in UMon than in Mon streams. This situation will probably reduce the food sources for scrapers (e.g., benthic algae) and favor shredder invertebrates feeding on allochthonous organic matter. Lujan et al. (2013) also showed a reduction of shredders and an increase of scrapers in Andean streams from higher to lower elevations where stream size and canopy cover increased along the altitudinal gradient as well. Therefore, shredder invertebrates appear to be more common at higher elevations because of food availability which suggest a general pattern for tropical streams as predicted by Dobson et al. (2002). However, we must emphasize that shredder invertebrates are rarer in macroinvertebrate communities in tropical streams compared to temperate streams (Irons et al. 1994; Tomanova et al. 2007). We also found that collector invertebrates dominated benthic and leaf-bag-associated macroinvertebrates in both ecosystem types. According to Greathouse and Pringle (2006), collectors tend to dominate the headwaters of tropical streams. However, an additional explanation can be that FPOM in headwater streams presents higher quality and heterogeneity than lower-elevation streams in the Andes (Lujan et al. 2013), increasing the attractiveness for collector invertebrates that consume large amounts of FPOM (Ramirez and Guitiérrez 2014). Evidently, these results are common for tropical streams (Boyero et al. 2011, 2015).

Differences between land uses

The strong effect of the riparian forest conversion to pasture land on macroinvertebrate taxonomic composition confirmed the advantage of using benthic communities not only to detect streams' impairment due to environmental pollution, but also to assess the effects of land-use change on ecological integrity of streams (Death and Collier 2009; Iñiguez-Armijos et al. 2014). Land-use change and its associated anthropogenic disturbances affect the macroinvertebrate communities in several pathways (Allan 2004). The replacement or elimination of some macroinvertebrate species (e.g., intolerant taxa) can lead to differences in taxonomic composition between forest and pasture streams in montane ecosystems (Encalada

et al. 2010; Iñiguez-Armijos et al. 2014; Astudillo et al. 2016). For instance, at Mon streams a total of 34 genera were sampled, 25 were common to both land uses, though some sensitive genera to human impacts in Andean streams (Ríos-Touma et al. 2014) such *Nectopsyche* and *Grumichella* were present only in forest sites, and conversely more tolerant genera such as *Limnophora* and *Dugesia* were only present in pasture sites.

The conversion of riparian forest to pasture land also increased the macroinvertebrate abundance in pastures reaches, similarly to other Andean (Encalada et al. 2010; Miserendino et al. 2011) and Amazon (Bojsen and Jacobsen 2003) streams. The riparian clearing increases the light penetration and nutrient input from pastureland favoring the dominance of generalist macroinvertebrates such as chironomids (Collier 1995). Because chironomids are generalist, they easily overcome the lack of both food sources and suitable microhabitats commonly occurring in deforested streams (Suga and Tanaka 2012). Therefore, a dominance of chironomids (i.e., disturbance-tolerant insects) promoted by habitat modifications or competition will result in significant changes in macroinvertebrate community of streams affected by riparian clearing (Sweeney and Newbold 2014). In our study, chironomids were more abundant in the pasture than in forest sites in both ecosystem types, and we believe that the dominance of Chironomidae larvae influenced on differences found in macroinvertebrate composition between land uses. As expected, the overall diversity and evenness were higher in forested than in pasture stream reaches. Higher macroinvertebrate diversity can be found in highly forested streams as reported in other studies in tropical (Bojsen and Jacobsen 2003; Lorion and Kennedy 2009; Iñiguez-Armijos et al. 2014) and temperate streams (Death and Collier 2009; Miserendino et al. 2011). Furthermore, significant differences were found in the functional organization of macroinvertebrate assemblages between forest and pasture stream reaches. In average, the relative abundance of shredder invertebrates in pasture reaches was lower than in forest reaches. This result can be attributed to less allochthonous material available in pasture streams compared to forested streams (Reed et al. 1994; Lecerf et al. 2005; Hagen et al. 2010; Iñiguez-Armijos et al. 2016). Because of an increase in periphyton biomass in open canopy streams (Allan 2004), it is expected a potential

increase in the scraper abundance from forest to pasture stream reaches because they feed on periphyton (Cummins et al. 2005; Tomanova et al. 2007). Encalada et al. (2010) and Lorion and Kennedy (2009) have reported higher scraper abundance in the pasture than in forest sites in other tropical montane streams. In contrast, we found a decrease of scraper invertebrates in streams affected by riparian forest conversion to pasture land alike in other Andean streams (Iñiguez-Armijos et al. 2014). We believe that this result may be attributed to the lost or decreasing of sensitive taxa and the dominance of intolerant macroinvertebrates as a result of riparian deforestation. Scrapers invertebrates in pastures sites were dominated by *Baetodes*, whose family (Baetidae) is commonly found in impacted Andean streams (Ríos-Touma et al. 2014). Of course, there are scraper invertebrates (and shredders) sensitive to perturbation such as *Paltostoma*, and they can be used as indicator species in ecological assessment studies (Barbour et al. 1999; Rawer-Jost et al. 2000). Nevertheless, we think that the use of scrapers as reliable indicators of land-use effects on Andean stream ecosystems deserves further attention.

Implications of sampling techniques

The application of different techniques favors and discriminates the collection of certain taxa (Buss et al. 2015). We found that benthic sampling was a more efficient technique than leaf bags regarding the collection of higher taxonomic diversity in both ecosystem types and land uses. Moreover, we found important differences in the functional composition of benthic and leaf-bag macroinvertebrates. The relative abundance of the shredder, scraper, and predatory invertebrates was higher in the benthic samples, while collector invertebrates (mostly Chironomidae larvae) were more abundant in leaf bags. This dominance can be explained by the preference of chironomids to colonize natural and artificial leaf packs (Murphy and Giller 2000; Dangles et al. 2001; Di Sabatino et al. 2014). We found a lower relative abundance of shredder invertebrates in leaf bags than in benthic samples as in other Andean streams (Encalada et al. 2010; Dangles et al. 2011). We believe that the low shredder abundance found in leaf bags can be explained by the little attraction of artificial leaf packs to shredders; by abiotic (e.g., discharge) and biotic (e.g., decomposition stage) factors that may influence

the colonization process (Tiegs et al. 2008; Di Sabatino et al. 2014; Tonin et al. 2014). Therefore, we suggest that benthic sampling is more appropriate for bioassessment purposes and that the application of several sampling techniques is recommend to assess the macroinvertebrate diversity of stream ecosystems.

Conclusions

Our study on the integrity of benthic and leaf-associated macroinvertebrates in Andean streams across the different ecosystem types, riparian land use, and their interactions is the first of its kind in the tropical Andes. Although, we show significant effects of many factors. We highlight the significant effect of riparian forest conversion to pasture land on aquatic communities. The existing accelerated deforestation affects many Andean countries (Brandt and Townsend 2006; Rodríguez Eraso et al. 2013; Tapia-Armijos et al. 2015); nonetheless, land-use management and restoration programs are scarce along this region. Therefore, we believe that the application of conservation programs recommended for Andean ecosystems, such the restoration/protection of riparian margins, is an urgent task to mitigate the effects of deforestation on stream communities and ecosystem processes.

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Authors’ contributions CIA, HH and LB conceived and designed the experiments. CIA and HH performed the experiments. CIA analyzed the data. CIA, HH, LB wrote the manuscript.

References

- Allan JD (2004) Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annu Rev Ecol Evol Syst* 35:257–284. <https://doi.org/10.1146/annurev.ecolsys.35.120202.110122>
- Anderson MJ (2001) A new method for nonparametric multivariate analysis of variance. *Austral Ecol.* <https://doi.org/10.1111/j.1442-9993.2001.01070>
- Astudillo MR, Novelo-Gutiérrez R, Vázquez G et al (2016) Relationships between land cover, riparian vegetation, stream characteristics, and aquatic insects in cloud forest streams, Mexico. *Hydrobiologia* 768:167–181. <https://doi.org/10.1007/s10750-015-2545-1>
- Barbour MT, Gerritsen J, Snyder BD, Stribling JB (1999) Rapid bioassessment protocols for use in streams and Wadeable rivers: periphyton, benthic macroinvertebrates, and fish, 2nd edn. US Environmental Protection Agency, Office of Water, Washington DC
- Bates D, Maechler M, Bolker B, Walker S (2017) lme4: linear mixed-effects models using “Eigen” and S4. R package version 1.1-13
- Bojsen BH, Jacobsen D (2003) Effects of deforestation on macroinvertebrate diversity and assemblage structure in Ecuadorian Amazon streams. *Arch für Hydrobiol* 158:317–342. <https://doi.org/10.1127/0003-9136/2003/0158-0317>
- Bolker BM, Brooks ME, Clark CJ et al (2008) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135
- Boyer L, Pearson RG, Dudgeon D et al (2011) Global distribution of a key trophic guild contrasts with common latitudinal diversity patterns. *Ecology* 92:1839–1848. <https://doi.org/10.1890/10-2244.1>
- Boyer L, Pearson RG, Swan CM et al (2015) Latitudinal gradient of nestedness and its potential drivers in stream detritivores. *Ecography (Cop)* 38:949–955. <https://doi.org/10.1111/ecog.00982>
- Brandt JS, Townsend PA (2006) Land use—land cover conversion, regeneration and degradation in the high elevation Bolivian Andes. *Landsc Ecol* 21:607–623
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. *Ecol Monogr* 27:325–349
- Buss DF, Carlisle DM, Chon T-S et al (2015) Stream biomonitoring using macroinvertebrates around the globe: a comparison of large-scale programs. *Environ Monit Assess* 187:4132. <https://doi.org/10.1007/s10661-014-4132-8>
- Buytaert W, Cuesta-Camacho F, Tobón C (2011) Potential impacts of climate change on the environmental services of humid tropical alpine regions. *Glob Ecol Biogeogr* 20:19–33. <https://doi.org/10.1111/j.1466-8238.2010.00585.x>
- Carter JI, Resh VH, Hannaford MJ, Myers MJ (2006) Macroinvertebrates as biotic indicators of environmental quality. In: Hauer FR, Lamberti GA (eds) *Methods in stream ecology*, 2nd edn. Academic Press, London, pp 805–833
- Cole E, Newton M (2013) Influence of streamside buffers on stream temperature response following clear-cut

- harvesting in western Oregon. *Can J For Res* 43:993–1005. <https://doi.org/10.1139/cjfr-2013-0138>
- Collier KJ (1995) Environmental factors affecting the taxonomic composition of aquatic macroinvertebrate communities in lowland waterways of Northland, New Zealand. *N Z J Mar Freshwater Res* 29:453–465. <https://doi.org/10.1080/00288330.1995.9516679>
- Collier KJ, Hamer M (2012) The ecological condition of Waikato wadeable streams based on the Regional Ecological Monitoring of Streams (REMS) Programme. Waikato Regional Council, Technical Report, Waikato
- Cortes RMV, Abelho M, Rebelo SB (1997) The macroinvertebrate colonization of leaf bags: is there a pattern? *Limnetica* 13:71–75
- Cummins KW, Merritt RW, Andrade PCN (2005) The use of invertebrate functional groups to characterize ecosystem attributes in selected streams and rivers in south Brazil. *Stud Neotrop Fauna Environ* 40:69–89. <https://doi.org/10.1080/01650520400025720>
- Danger AR, Robson BJ (2004) The effects of land use on leaf-litter processing by macroinvertebrates in an Australian temperate coastal stream. *Aquat Sci* 66:296–304
- Dangles O, Guerold F, Usseglio-Polatera P (2001) Role of transported particulate organic matter in the macroinvertebrate colonization of litter bags in streams. *Freshw Biol* 46:575–586. <https://doi.org/10.1046/j.1365-2427.2001.00693.x>
- Dangles O, Gessner MO, Guerold F, Chauvet E (2004) Impacts of stream acidification on litter breakdown: implications for assessing ecosystem functioning. *J Appl Ecol* 41:365–378. <https://doi.org/10.1111/j.0021-8901.2004.00888.x>
- Dangles O, Crespo-Pérez V, Andino P et al (2011) Predicting richness effects on ecosystem function in natural communities: insights from high elevation streams. *Ecology* 92:733–743. <https://doi.org/10.1890/10-0329.1>
- Death RG, Collier KJ (2009) Measuring stream macroinvertebrate responses to gradients of vegetation cover: when is enough enough? *Freshw Biol* 55:1447–1464. <https://doi.org/10.1111/j.1365-2427.2009.02233.x>
- Di Sabatino A, Cristiano G, Pinna M et al (2014) Structure, functional organization and biological traits of macroinvertebrate assemblages from leaf-bags and benthic samples in a third-order stream of Central Apennines (Italy). *Ecol Indic* 46:84–91. <https://doi.org/10.1016/j.ecolind.2014.06.005>
- Dobson M, Magana A, Mathooko JM, Ndegwa FK (2002) Detritivores in Kenyan highland streams: more evidence for the paucity of shredders in the tropics? *Freshw Biol* 47:909–919. <https://doi.org/10.1046/j.1365-2427.2002.00818.x>
- Encalada AC, Calles J, Ferreira V et al (2010) Riparian land use and the relationship between the benthos and litter decomposition in tropical montane streams. *Freshw Biol* 55:1719–1733. <https://doi.org/10.1111/j.1365-2427.2010.02406.x>
- Environmental Protection Agency (2013) National rivers and streams assessment 2008–2009: a collaborative survey. Draft February 28. Washington
- European Environment Agency (2012) European waters—assessment of status and pressures. EEA Report No. 8. Copenhagen
- Fenoglio S, Bo T, Cucco M, Malacarne G (2006) Leaf breakdown patterns in a NW Italian stream: effect of leaf type, environmental conditions and patch size. *Biologia (Bratisl)* 61:555–563. <https://doi.org/10.2478/s11756-006-0090-0>
- Fernández HR, Domínguez E (2001) Guía para la determinación de los artrópodos bentónicos sudamericanos. Universidad Nacional de Tucumán, Tucumán
- Flannagan JF, Rosenberg DM (1982) Types of artificial substrates used for sampling of freshwater benthic macroinvertebrates. In: Cairns J (ed) Artificial substrates. Ann Arbor Science Publishers Inc., Kent, pp 237–266
- Fugère V, Kasangaki A, Chapman LJ (2016) Land use changes in an afrotropical biodiversity hotspot affect stream alpha and beta diversity. *Ecosphere* 7:e01355. <https://doi.org/10.1002/ecs2.1355>
- Gessner MO, Chauvet E (2002) A case for using litter breakdown to assess functional stream integrity. *Ecol Appl* 12:498–510
- Greathouse EA, Pringle CM (2006) Does the river continuum concept apply on a tropical island? Longitudinal variation in a Puerto Rican stream. *Can J Fish Aquat Sci* 63:134–152. <https://doi.org/10.1139/f05-201>
- Hagen EM, McTammany ME, Webster JR, Benfield EF (2010) Shifts in allochthonous input and autochthonous production in streams along an agricultural land-use gradient. *Hydrobiologia* 655:61–77. <https://doi.org/10.1007/s10750-010-0404-7>
- Hauer FR, Resh VH (2006) Macroinvertebrates. In: Hauer FR, Lamberti GA (eds) Methods in stream ecology, 2nd edn. Academic Press, London, pp 435–454
- Hladyz S, Åbjörnsson K, Chauvet E et al (2011) Stream ecosystem functioning in an agricultural landscape: the importance of terrestrial-aquatic linkages. In: Woodward G (ed) Advances in ecological research, 44th edn. Elsevier, London, pp 211–276
- Iñiguez-Armijos C, Leiva A, Frede H-G et al (2014) Deforestation and benthic indicators: how much vegetation cover is needed to sustain healthy Andean streams? *PLoS ONE* 9:e105869. <https://doi.org/10.1371/journal.pone.0105869>
- Iñiguez-Armijos C, Rausche S, Cueva A et al (2016) Shifts in leaf litter breakdown along a forest-pasture-urban gradient in Andean streams. *Ecol Evol* 6:4849–4865. <https://doi.org/10.1002/ece3.2257>
- Irons JG, Oswood MW, Stout RJ, Pringle CM (1994) Latitudinal patterns in leaf litter breakdown: is temperature really important? *Freshw Biol* 32:401–411. <https://doi.org/10.1111/j.1365-2427.1994.tb01135.x>
- Jacobsen D (2008) Low oxygen pressure as a driving factor for the altitudinal decline in taxon richness of stream macroinvertebrates. *Oecologia* 154:795–807. <https://doi.org/10.1007/s00442-007-0877-x>
- Jacobsen D, Encalada AC (1998) The macroinvertebrate fauna of Ecuadorian high-land streams in the wet and dry season. *Arch für Hydrobiol* 142:53–70
- Lecerf A, Dobson M, Dang CK, Chauvet E (2005) Riparian plant species loss alters trophic dynamics in detritus-based stream ecosystems. *Oecologia* 146:432–442. <https://doi.org/10.1007/s00442-005-0212-3>

- Lorion CM, Kennedy BP (2009) Relationships between deforestation, riparian forest buffers and benthic macroinvertebrates in neotropical headwater streams. *Freshw Biol* 54:165–180. <https://doi.org/10.1111/j.1365-2427.2008.02092.x>
- Lujan NK, Roach KA, Jacobsen D et al (2013) Aquatic community structure across an Andes-to-Amazon fluvial gradient. *J Biogeogr* 40:1715–1728. <https://doi.org/10.1111/jbi.12131>
- Madsen PB, Morabowen A, Andino P et al (2015) Altitudinal distribution limits of aquatic macroinvertebrates: an experimental test in a tropical alpine stream. *Ecol Entomol* 40:629–638. <https://doi.org/10.1111/een.12232>
- Miserendino ML, Masi CI (2010) The effects of land use on environmental features and functional organization of macroinvertebrate communities in Patagonian low order streams. *Ecol Indic* 10:311–319. <https://doi.org/10.1016/j.ecolind.2009.06.008>
- Miserendino ML, Casaux R, Archangelsky M et al (2011) Assessing land-use effects on water quality, in-stream habitat, riparian ecosystems and biodiversity in Patagonian northwest streams. *Sci Total Environ* 409:612–624. <https://doi.org/10.1016/j.scitotenv.2010.10.034>
- Murphy JF, Giller PS (2000) Seasonal dynamics of macroinvertebrate assemblages in the benthos and associated with detritus packs in two low-order streams with different riparian vegetation. *Freshw Biol* 43:617–631. <https://doi.org/10.1046/j.1365-2427.2000.00548.x>
- Neill C, Deegan LA, Thomas SM, Cerri CC (2001) Deforestation for pasture alters nitrogen and phosphorus in small Amazonian streams. *Ecol Appl* 11:1817–1828. [https://doi.org/10.1890/1051-0761\(2001\)011\[1817:DFPANA\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2001)011[1817:DFPANA]2.0.CO;2)
- Oksanen J, Blanchet FG, Kindt R et al (2014) Vegan: community ecology package. R package version 2.2-0
- R Development Core Team (2017) R: a language and environment for statistical computing
- Ramírez A, Guitiérrez P (2014) FFG of aquatic insect families in Latin America: a critical analysis and review of existing literature. *Rev Biol Trop* 62:155–167
- Rawer-Jost C, Böhmer J, Blank J, Rahmann H (2000) Macroinvertebrate functional feeding group methods in ecological assessment. *Hydrobiologia* 422–423:225–232
- Reed JL, Campbell IC, Bailey PCE (1994) The relationship between invertebrate assemblages and available food at forest and pasture sites in three south-eastern Australian streams. *Freshw Biol* 32:641–650. <https://doi.org/10.1111/j.1365-2427.1994.tb01154.x>
- Ríos-Touma B, Encalada AC, Prat Fornells N (2011) Macroinvertebrate assemblages of an Andean high-altitude tropical stream: the importance of season and flow. *Int Rev Hydrobiol* 96:667–685. <https://doi.org/10.1002/iroh.201111342>
- Ríos-Touma B, Acosta R, Prat N (2014) The Andean Biotic Index (ABI): revised tolerance to pollution values for macroinvertebrate families and index performance evaluation. *Int J Trop Biol* 62:249–273
- Rodríguez Eraso N, Armenteras-Pascual D, Retana Alumbrosos J (2013) Land use and land cover change in the Colombian Andes: dynamics and future scenarios. *J Land Use Sci* 8:154–174. <https://doi.org/10.1080/1747423X.2011.650228>
- Roldán Pérez G (2003) Bioindicación de la calidad del agua en Colombia. Uso del método BMWP/Col. Editorial Universidad de Antioquia, Medellín
- Rosenberg DM, Resh VH (1982) The use of artificial substrates in the study of freshwater benthic macroinvertebrates. In: Cairns J (ed) *Periphyton of freshwater ecosystems*. Ann Arbor Science Publishers Inc., Kent
- Sierra R, Campos F, Chamberlin J (2002) Assessing biodiversity conservation priorities: ecosystem risk and representativeness in continental Ecuador. *Landsc Urban Plan* 59:95–110
- Stein H, Springer M, Kohlmann B (2008) Comparison of two sampling methods for biomonitoring using aquatic macroinvertebrates in the Dos Novillos River, Costa Rica. *Ecol Eng* 34:267–275. <https://doi.org/10.1016/j.ecoleng.2007.06.010>
- Suga CM, Tanaka MO (2012) Influence of a forest remnant on macroinvertebrate communities in a degraded tropical stream. *Hydrobiologia* 703:203–213. <https://doi.org/10.1007/s10750-012-1360-1>
- Sweeney BW, Newbold JD (2014) Streamside forest buffer width needed to protect stream water quality, habitat, and organisms: a literature review. *J Am Water Resour Assoc* 50:560–584. <https://doi.org/10.1111/jawr.12203>
- Tapia-Armijos MF, Homeier J, Espinosa CI et al (2015) Deforestation and forest fragmentation in South Ecuador since the 1970s—losing a hotspot of biodiversity. *PLoS ONE* 10(9):e0133701. <https://doi.org/10.1371/journal.pone.0133701>
- Tiegs SD, Peter FD, Robinson CT et al (2008) Leaf decomposition and invertebrate colonization responses to manipulated litter quantity in streams. *J North Am Benthol Soc* 27:321–331. <https://doi.org/10.1899/07-054.1>
- Tomanova S, Goitia E, Helešić J (2006) Trophic levels and functional feeding groups of macroinvertebrates in neotropical streams. *Hydrobiologia* 556:251–264. <https://doi.org/10.1007/s10750-005-1255-5>
- Tomanova S, Tedesco PA, Campero M et al (2007) Longitudinal and altitudinal changes of macro-invertebrate functional feeding groups in neotropical streams: a test of the River Continuum Concept. *Fundam Appl Limnol* 170:233–241. <https://doi.org/10.1127/1863-9135/2007/0170-0233>
- Tonin AM, Hepp LU, Restello RM, Gonçalves JF (2014) Understanding of colonization and breakdown of leaves by invertebrates in a tropical stream is enhanced by using biomass as well as count data. *Hydrobiologia* 740:79–88. <https://doi.org/10.1007/s10750-014-1939-9>
- Tremblay A, Ransijn J (2015) LMER convenience functions: model selection and post-hoc analysis for (G)LMER models. R package version 2.10
- Voß K, Schäfer RB (2017) Taxonomic and functional diversity of stream invertebrates along an environmental stress gradient. *Ecol Indic* 81:235–242. <https://doi.org/10.1016/j.ecolind.2017.05.072>