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## Altitudinal variation in fish assemblage diversity in streams of the central Andes of Colombia

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This study documents differences in fish assemblages for 32 freshwater streams located between 258 and 2242 m a.s.l. on the eastern slopes of the central range of the Colombian Andes. A total of 2049 fishes belonging to 62 species, 34 genera and 16 families were collected. Species richness declined rapidly with altitude; nearly 90% of the species were recorded between 250 and 1250 m a.s.l. Three of the four physico-chemical variables, of the water, temperature, dissolved oxygen and pH, explained 53.5% of the variation in species richness along the altitudinal gradient, with temperature the most important (37.6%). An analysis of species composition showed that the distinctiveness of the fish fauna increased with elevation, with the greatest turnover observed between 1000 and 1750 m a.s.l. On this altitudinal gradient, turnover was dominated by the loss of species rather than gain, and dominance by just a few species was greater at higher elevations. Turnover was also observed along the altitudinal gradient in the structure of the three functional groups (torrential, pool and pelagic species). The study focused on understanding the pattern of diversity of fish communities inhabiting the Andes in Colombia. Anthropogenic effects on the altitudinal distribution of fish species in the region, however, are largely unknown and would require further investigations.

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Key words: elevation gradients; fish distribution; neotropical mountains; temperature; turnover.

### INTRODUCTION

Altitude is frequently correlated with changes in diversity (Lomolino, 2001). Studies on these changes have included a wide range of organisms, including vertebrates, invertebrates and plants from many different geographic regions (Rahbek, 1995). Generally, the observed pattern is marked by a decrease in species diversity and the

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substitution of species as altitude increases; however, the processes that determine those patterns remain poorly understood (Lomolino, 2001). In the tropics, mountains act as ecological barriers that prevent colonization by lowland species into adjacent territories (Janzen, 1967). To maintain stable populations in high mountain environments, terrestrial and aquatic species must tolerate adverse conditions (Navas, 2003; Jacobsen, 2008). In aquatic ecosystems, low temperature, hydraulic, physical and chemical conditions influence fish species distribution (Buisson *et al.*, 2008a), and physiological and morphological adaptations such as low metabolic rates and hydrodynamic body forms are required (Beitinger *et al.*, 2000; Taniguchi & Nakano, 2000; Winemiller *et al.*, 2008).

Owing to the spatial correlation between environmental variables and elevation, it is often difficult to attribute changes in diversity over altitudinal gradients to a single variable (Brown, 2001). Several hypotheses have been proposed to explain such changes in diversity associated with altitude; most of them are based on only a few ecological factors. These can be summarized as: (1) reduction in the available area and environmental complexity, (2) greater severity of climatic conditions, (3) reduction in the diversity of available resources and (4) decrease in primary productivity with increasing altitude (Huston, 1994). There is no consensus on how these ecological factors co-vary and interact with environmental variables to generate the patterns of diversity observed in mountains (Nogués-Bravo *et al.*, 2008).

In their review of the factors that determine the structure of riverine fish assemblages in both temperate and tropical regions, Tejerina-Garro *et al.* (2005) found that the most important factors were river size, altitude, habitat complexity, water velocity, depth, conductivity and temperature. Studies on the effect of environmental variation on the composition of fish assemblages and species richness in South American tropical mountain regions are scarce. Bistoni & Hued (2002) showed that fish diversity is correlated with elevation and the distance from the origin of the water body, while Pouilly *et al.* (2006) observed that decreasing altitude plays a role similar to that of increasing stream size along a longitudinal gradient and that water temperature and stream slope influence fish diversity. Winemiller *et al.* (2008) found that at 81 sites between 50 and 3100 m, fish diversity was strongly correlated with physical and environmental variables related to the altitudinal gradient.

Colombia possesses the highest diversity of mountain fishes within of the Northern Andes region with 220 species, 37% of which are endemic. There have been few studies describing the ichthyofauna diversity patterns along the altitudinal gradients. Considering that 80% of the socioeconomic activity in Colombia is concentrated in the Andean region (Rodríguez *et al.*, 2004), it is important to improve knowledge of the diversity patterns of the freshwater fish fauna along the altitudinal gradients in order to understand how these patterns are affected by anthropogenic activities (*e.g.* hydroelectric dams, the introduction of exotic species, agriculture, deforestation and pollution). This information is required to generate effective conservation strategies and mitigate the effects of human activities.

Diversity of fish assemblages was assessed for 32 streams located along an altitudinal gradient on the eastern slopes of the central Andes range of Colombia, which form part of the middle Magdalena River drainage basin. The aims of the study were to (1) determine whether stream fish diversity varies with altitude, (2) assess which abiotic factors (physico-chemical water quality variables) influence species richness

and composition and (3) investigate how fish species composition varies across an altitudinal gradient.

## MATERIALS AND METHODS

### STUDY AREA

This study was carried out in streams on the eastern slopes of the central Andes mountain range in the Department of Antioquia, Colombia (5 to 7° N; 74 to 76° W; Fig. 1). The region spans a range of altitudes, from 150 to 2600 m a.s.l., resulting in a heterogeneous landscape with complex topography and geomorphology that includes Altiplano (high plain) as well as canyons, piedmonts and lowlands. Precipitation is 800–5500 mm year<sup>-1</sup>, temperatures are 6–35° C and soil lithology is dominated by granitic rocks of the Antioquian Batholite (Hermelín, 1992; González & Londoño, 2002). The region has a great wealth of rivers with the major drainage basins being the Nare, Claro, Manso and Miel Rivers, flowing into the middle section of the Magdalena River. These rivers are mostly torrential with clear water and reduced alluvial plains resulting from the spurs of the mountain range slopes that extend almost to the banks of the Magdalena River (Mojica *et al.*, 2006).

Within this altitudinal gradient, the streams are grouped into four categories based on characteristics described by Hermelín (2003, 2006), Rodríguez *et al.* (2004), Tobón *et al.* (2004) and Rodríguez & Armenteras (2005): (1) lowland streams (<1000 m) in areas of gentle slopes (<20°) that are characterized by wide, shallow channels, fine-grained substrata and a high proportion of backwaters and pools; (2) middle altitude streams (>1000–1500 m), where slope is moderate (20 to 60°), characterized by narrower, deeper channels and the presence of isolated rocks of various sizes; (3) highland streams (>1500–2000 m), where slope is steep (45 to 80°), with deep channels, a rocky substratum and the absence of backwaters; (4) the Altiplano streams (>2000 m) that have characteristics similar to those of the lowland water bodies in flat areas with little turbulence with deep, narrow channels over fine substrata.

### DATA COLLECTION

For the purpose of this study, streams of first to third orders that are distributed along the altitudinal gradient were selected from maps (scale 1:50 000). The site selection criteria of Pouilly *et al.* (2006) were applied to reduce any longitudinal effect on the fish assemblages. Streams were selected to limit size range (stream width and water depth). The 32 sites selected were located between 258 and 2242 m a.s.l., with a maximum depth and width of 1.5 and 12 m, respectively (Table I).

Sampling was carried out in September 2006, from a transitional period to the dry season. At each site, a 100 m stretch was delimited; one survey along each stretch in the downstream–upstream direction was conducted, using electrofishing (340 V, 1–2 A, d.c.) by wading and operated by the same person across sites.

Temperature (° C), conductivity ( $\mu\text{S cm}^{-1}$ ), dissolved oxygen ( $\text{mg l}^{-1}$ ) and pH were recorded using a portable multi-parameter (Hach sensION156; www.hach.com). The altitude and geographic coordinates were recorded at each site using a global positioning system (Garmin GPSMAP 60CSx; www.garmin.com).

In the field, specimens were anaesthetized in menthol solution (150  $\text{mg l}^{-1}$ ) for 10 min according to the procedures describe in Façanha & Gomes (2005) and then fixed in formalin (10%). In the laboratory, fishes were preserved in alcohol (75%) and identified using taxonomic keys (Eigenmann, 1918; Dahl, 1971; Géry, 1977; Vari & Harold, 2001; Román-Valencia, 2003; Armbruster, 2005; Maldonado-Ocampo *et al.*, 2005; Vari *et al.*, 2005) and by comparison with identified material in the fish collection of the Instituto de Investigaciones de Recursos Biológicos Alexander von Humboldt (IAVH-P). Once identified, specimens were deposited at IAVH-P and in the Universidad Católica de Oriente (CP-UCO).

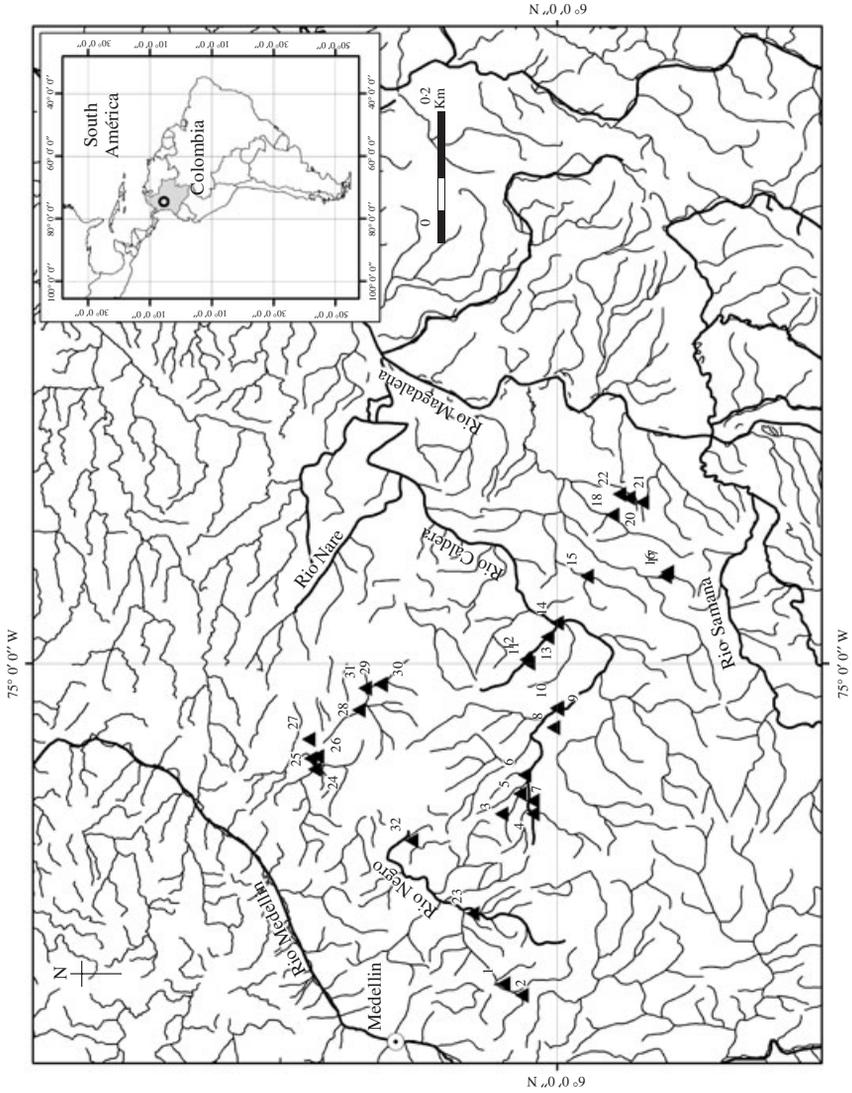


FIG. 1. Eastern slopes of the Central Andes mountain range region (Antioquia, Colombia), with sampling sites locations (▲) along the altitudinal gradient. Lowland streams, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 31; middle streams, 5, 6, 7, 8, 9, 10, 27, 28, 29, 30; highland streams, 4, 24, 25, 26; Altiplano streams, 1, 2, 3, 23, 32.

TABLE I. Main descriptors of diversity and the physico-chemical characteristics of each altitudinal level sampled on the eastern slopes of the central Colombian Andes. Values for the indices were statistically compared using the null model developed by Solow (1993). Values with different lower case letters correspond to statistically significant differences ( $P < 0.05$ )

	Streams categories					
	Lowland		Middle		Highland	Altiplano
Altitudinal levels	<500 m	1000 m	1250 m	1500 m	1750 m	>2000 m
Number of localities	9	4	7	3	4	5
Number of individuals	734	268	573	126	193	155
Number of families	15	5	9	2	4	4
Number of genera	30	8	15	3	7	6
Number of species (mean $\pm$ s.d.)	12.30 $\pm$ 5.62	7.50 $\pm$ 3.70	10.43 $\pm$ 4.65	3.33 $\pm$ 1.15	5.5 $\pm$ 1.29	4.8 $\pm$ 2.69
Diversity ( $\pm 95\%$ CI)						
Shannon ( $H'$ )	2.96 $\pm$ 0.16 <sup>a</sup>	2.41 $\pm$ 0.20 <sup>b</sup>	2.82 $\pm$ 0.16 <sup>c</sup>	1.26 $\pm$ 0.39 <sup>d</sup>	2.00 $\pm$ 0.14 <sup>e</sup>	1.93 $\pm$ 0.34 <sup>f</sup>
Simpson ( $D$ )	12.71 $\pm$ 2.83 <sup>a</sup>	9.04 $\pm$ 2.06 <sup>b</sup>	12.16 $\pm$ 2.55 <sup>a</sup>	2.72 $\pm$ 1.02 <sup>c</sup>	6.83 $\pm$ 1.54 <sup>d</sup>	4.79 $\pm$ 1.68 <sup>f</sup>
Evenness ( $J$ )	0.71 $\pm$ 0.04 <sup>a</sup>	0.58 $\pm$ 0.05 <sup>b</sup>	0.68 $\pm$ 0.04 <sup>a</sup>	0.30 $\pm$ 0.07 <sup>b</sup>	0.48 $\pm$ 0.03 <sup>c</sup>	0.46 $\pm$ 0.08 <sup>d</sup>
Physico-chemical variables (mean $\pm$ s.d.)						
Oxygen (mg l <sup>-1</sup> )	7.81 $\pm$ 0.04	8.25 $\pm$ 0.30	8.25 $\pm$ 0.19	10.45 $\pm$ 5.33	8.042 $\pm$ 0.65	7.77 $\pm$ 0.48
Temperature (°C)	25.48 $\pm$ 2.20	21.92 $\pm$ 1.37	21.20 $\pm$ 1.37	19.73 $\pm$ 1.18	20.74 $\pm$ 1.50	19.9 $\pm$ 1.71
Conductivity ( $\mu$ S cm <sup>-1</sup> )	32.32 $\pm$ 15.74	34.36 $\pm$ 17.27	26.25 $\pm$ 10.28	31.46 $\pm$ 23.57	27.15 $\pm$ 1.98	29.93 $\pm$ 15.31
pH	7.33 $\pm$ 0.34	7.16 $\pm$ 0.12	7.09 $\pm$ 0.34	7.16 $\pm$ 0.08	6.99 $\pm$ 0.22	7.12 $\pm$ 0.18

## STATISTICAL ANALYSIS

A simple linear regression analysis using the total species collected in each altitudinal level ( $n = 6$ ) was used to determine the rate of decrease (loss) and accumulation (gain) of species as altitude increased. Two estimators (Chao 1 and Chao 2) were used to assess the sampling efficiency in each altitudinal level because these are two of the most appropriate for estimating species richness from small samples (Colwell & Coddington, 1994). Inventory completeness at each altitudinal level was evaluated by comparing the percentage of species observed with that predicted by the estimators. For the direct comparison of species richness at each altitudinal level, the number of species observed  $\pm 95\%$  CI was calculated using the analytic equation proposed by Colwell *et al.* (2004). Both the value of the estimators as well as the CI (at 95%) for observed richness was calculated using the EstimateS v.7.5.0 software (Colwell, 2005).

A forward stepwise multiple-regression model taking into account all samples ( $n = 32$ ) was used to estimate the relationship between the dependent variable ( $S$ , number of species) and the independent variables (*i.e.* physical–chemical characteristics of the water; Table I). Because the dependent variable was based on number of fishes, the complete model ( $S = \mu + T + O + C + p + \varepsilon$ , where  $T$  = temperature,  $O$  = oxygen,  $C$  = conductivity and  $p$  = pH) was obtained assuming a Poisson error distribution (function link = log; Crawley, 2007). The model was verified by examining the standardized residuals *v.* the fit values, in addition to the graphical distribution of errors (Crawley, 2007).

Changes in species composition along the altitudinal gradient were measured using presence and absence data and by calculating Whittaker beta-diversity index ( $\beta_w$ , Koleff *et al.*, 2003):  $\beta_w = (a + b + c) [0.5(2a + b + c)]^{-1}$  between adjacent pairs of altitudinal levels, where  $a$  is the total number of species that occur in any pair of adjacent sites along a transect, and  $b$  and  $c$  are the number of exclusive species (those that occur in each site but not in the adjacent one). This index is an indication of the degree of dissimilarity, so its values increase when sites differ more in their species composition. It gives values similar to other species turnover indices and is most appropriate because it provides a direct expression of differences in species composition for sites (or samples) along an environmental gradient (elevation in the present case), as well as being independent of local diversity and sample size (Shmida & Wilson, 1984; Koleff *et al.*, 2003). Because turnover indices do not indicate whether the change is produced by a loss or a gain of species, for each comparison the number of species lost or gained was calculated separately to determine the relative contribution of these different processes.

Changes in fish assemblage structure along the elevation gradient were evaluated using  $K$ -dominance curves in which the cumulative percentage of abundance is plotted against the range of species expressed as logarithms (Magurran, 2004). This graphic method allows for the visual comparison of the diversity among samples. In addition, the following descriptive indices were calculated for each altitudinal level: Shannon ( $H' = -\sum p_i \ln p_i$ ), Simpson ( $D = \sum n_i(n_i - N)[N(N - 1)]^{-1}$ ) and Evenness ( $J = H'(\log S)^{-1}$ , where  $p_i$  is the proportion of individuals found for the  $i$ th species,  $n_i$  is the number of individuals per species,  $N$  is the total number of individuals captured and  $S$  is the total number of species (Magurran, 2004). Values for the indices were statistically compared using the null model developed by Solow (1993) and the Species Richness and Diversity programme, v.3.0 (Henderson & Seaby, 2002).

As in the study on Andean fishes of Colombia (Maldonado-Ocampo *et al.*, 2005), species were assigned to three functional groups according to body form and habitat use: torrential, pelagic and pool species. Torrential fishes live on the bottom of rivers, have small-to-medium body sizes that are dorso-ventrally compressed, have morphological adaptations (*e.g.* sucker-mouths, opercular odontodes and reduced swimbladders) that permit them to adhere to rocks and move upstream in fast currents; pelagic fishes have a range of body sizes, live in the water column and have fusiform bodies with hydrodynamic shapes that allow them to swim in fast currents, and pool species live in isolated, temporary or permanent pools or in channels with slow currents, these fishes lack any specific adaptations to high water velocity. The information on habitat utilization for each species was complemented with field observations and information from the literature (Froese & Pauly, 2008; Winemiller *et al.*, 2008).

A  $\chi^2$  test for contingency table was used to determine whether the proportion of individuals in each group was the same across the altitudinal gradient. To detect the group of species for which the proportion of individuals differed among altitudinal levels, the contingency table was subdivided and the data were reanalysed with the same statistical test (Zar, 1996). The Bonferroni test was applied using the Dunn–Šidák method to correct the level of significance of alpha ( $\alpha$ ) for sequential non-independent comparisons (Sokal & Rohlf, 1981).

## RESULTS

A total of 2049 individuals belonging to 62 species (34 genera, 16 families) were collected. The genera best represented in the 32 streams were *Astroblepus* with 13 species, *Trichomycterus* with seven and *Chaetostoma* with four species. Most of the genera (67% of the total) were represented by only one species (Table II).

Although species richness decreased with altitude (Fig. 2), the latter did not explain the impoverishment of the fish assemblages along the gradient (coefficient of determination,  $R^2 = 0.60$ ;  $P > 0.05$ ). The rate of decrease in the number of species was 19.7 species per 1000 m, while the accumulation rate with increasing elevation was 13.1 species per 1000 m ( $R^2 = 0.88$ ;  $P < 0.01$ ; Fig. 2). The greatest species richness was found in lowlands at sites  $<1250$  m, and the lowest in the highlands, sites  $>1500$  m (Fig. 2 and Table I). About 93% of the total number of species recorded occurred between  $<500$  and 1250 m, above this the rate of species addition is very slow. The pattern of expected species richness, as estimated with Chao 1 and Chao 2 (Colwell & Coddington, 1994), was similar to the observed species richness (Fig. 2). The two estimators suggest that a significant percentage of the species present at each altitudinal level were captured ( $>75\%$ ), except at the Altiplano (above 2000 m), where only 67% of the total number of species present were collected (Fig. 2).

All physico-chemical variables were negatively correlated with elevation, although temperature was the only one that was statistically significant ( $r = -0.73$ ,  $P < 0.001$ ). To avoid co-linearity and thus redundancy in the interpretation of the results, altitude was eliminated as a predictor variable from the multiple regression analysis. This analysis indicated that three of the four physico-chemical variables measured, temperature, dissolved oxygen and pH, explained 53.5% of the observed change in species richness (Table III), with temperature the most important factor (37.6% of the variance).

The analysis of turnover in species composition between adjacent altitudinal levels clearly shows an increase in the distinctiveness of the fish fauna with increasing altitude. The highest turnover values were observed between 1000 and 1750 m ( $\beta_w$ : 0.41–0.75; Fig. 3). A remarkable number of species disappear when moving up from the lowlands to  $>1000$  m (Fig. 3). Also notable is a significant gain of species from 1000 to 1250 m and at sites  $>1750$  m. Overall, more species were lost (mean  $\pm$  s.d.:  $13.40 \pm 13.60$ ) than gained (mean  $\pm$  s.d.:  $9.60 \pm 3.78$ ) with increasing altitude.

Only four species (6.3%) of all those captured were found at all altitudes: *Bryconamericus huilae* Román-Valencia, *Bryconamericus* sp. 2, *Hemibrycon boquiae* (Eigenmann) and *Astroblepus homodon* (Regan). About half of the species were found only at the lowlands streams and 75% of these were found exclusively below 500 m (Table II). The opposite was observed at the highest elevations ( $>1750$  m); four species were restricted to this level: *Astroblepus* cf. *fissidens* (Regan),

TABLE II. Species and abundance of fishes collected at each altitudinal level and functional group (T, torrential species; Pe, pelagic species; Po, pool species) of the eastern slopes of the central Andes Colombia

Species	Altitudinal levels (m a.s.l.)						Total	Functional groups
	<500	1000	1250	1500	1750	>2000		
Order Characiformes								
Family Parodontidae								
<i>Parodon suborbitalis</i>	2						2	T
<i>Saccodon dariensis</i>			8				8	T
Family Crenuchidae								
<i>Characidium phoxocephalum</i>	4		16				20	T
<i>Characidium</i> sp.	25						25	T
Family Gasteropelecidae								
<i>Gasteropelecus maculatus</i>	5						5	Po
Family Characidae								
<i>Argopleura diquensis</i>	2	10					12	Pe
<i>Argopleura magdalenensis</i>	2	3					5	Pe
<i>Astyanax fasciatus</i>	9						9	Pe
<i>Astyanax gisleni</i>			1	21	24		46	Pe
<i>Brycon henni</i>			5		44	1	50	Pe
<i>Bryconamericus caucanus</i>					18	5	23	Po
<i>Bryconamericus huilae</i>	9	11	10		15	28	73	Po
<i>Bryconamericus</i> sp. 1		6	11			5	22	Pe
<i>Bryconamericus</i> sp. 2	65	43	92	9	21	54	284	Pe
<i>Creagrutus affinis</i>	62						62	Po
<i>Gephyrocharax melanocheir</i>	5						5	Pe
<i>Hemibrycon boquiae</i>	63	33	6		1	5	108	Pe
<i>Roeboides dayi</i>	5						5	Po
<i>Saccoderma hastatus</i>	1						1	Pe
Family Erythrinidae								
<i>Hoplias malabaricus</i>	7						7	Po
Order Siluriformes								
Family Cetopsidae								
<i>Cetopsis othonops</i>	3						3	Po
Family Trichomycteridae								
<i>Trichomycterus banneau</i>	20		73				93	T
<i>Trichomycterus</i> cf. <i>banneau</i>	61						61	T
<i>Trichomycterus caliense</i>	2		8		41	36	87	T
<i>Trichomycterus latistriatus</i>		3	5			1	9	T
<i>Trichomycterus</i> cf. <i>regani</i>		1					1	T
<i>Trichomycterus striatus</i>	1	5					6	T
<i>Trichomycterus</i> sp.						1	1	T
Family Astroblepididae								
<i>Astroblepus chapmani</i>			1	1		1	3	T
<i>Astroblepus chotae</i>			21		17	2	40	T
<i>Astroblepus cirratus</i>	2	5	1			1	9	T
<i>Astroblepus cyclopus</i>			1				1	T

TABLE II. Continued

Species	Altitudinal levels (m a.s.l.)						Total	Functional groups
	<500	1000	1250	1500	1750	>2000		
<i>Astroblepus cf. fissidens</i>						2	2	T
<i>Astroblepus grixalvii</i>	9	11	8				28	T
<i>Astroblepus homodon</i>	9	42	30	2		3	86	T
<i>Astroblepus micrescens</i>		1	1	1		4	7	T
<i>Astroblepus trifasciatus</i>		13	17	22		5	57	T
<i>Astroblepus</i> sp. 1		2					2	T
<i>Astroblepus</i> sp. 2			15				15	T
<i>Astroblepus</i> sp. 3		2	10	70			82	T
<i>Astroblepus</i> sp. 4	11						11	T
Family Loricariidae								
<i>Ancistrus centrolepis</i>			15				15	Po
<i>Chaetostoma fischeri</i>	1						1	T
<i>Chaetostoma leucomelas</i>	27	42	7				76	T
<i>Chaetostoma milesi</i>	8		9				17	T
<i>Chaetostoma</i> sp.	37	33	50				120	T
<i>Cordylancistrus</i> sp.	2		8		12		22	T
<i>Lasiancistrus caucanus</i>	142	1	61				204	T
<i>Sturisoma aureum</i>	26						26	T
Family Heptapteridae								
Heptapteridae sp.*	2						2	Po
<i>Pimelodella chagresi</i>	18						18	Po
<i>Rhamdia quelen</i>	6						6	Po
Order Gymnotiformes								
Family Sternopygidae								
<i>Sternopygus</i> sp.	9						9	Po
Order Cyprinodontiformes								
Family Rivulidae								
<i>Rivulus cf. boehlkei</i>	3						3	Po
Family Poeciliidae								
<i>Poecilia caucana</i>	9		2				11	Po
<i>Poecilia reticulata</i>		1	65				66	Po
Order Synbranchiformes								
Family Synbranchidae								
<i>Synbranchus marmoratus</i>	1		5				6	Po
Order Perciformes								
Family Cichlidae								
<i>Aequidens latifrons</i>	2						2	Po
<i>Caquetaia kraussii</i>	2						2	Po
<i>Caquetaia umbrifera</i>	9						9	Po
<i>Geophagus steindachneri</i>	46		11				57	Po
Family Centrarchidae								
<i>Micropterus salmoides</i>						1	1	Po
Total	734	268	573	126	193	55	2049	

\*Possible new genus.

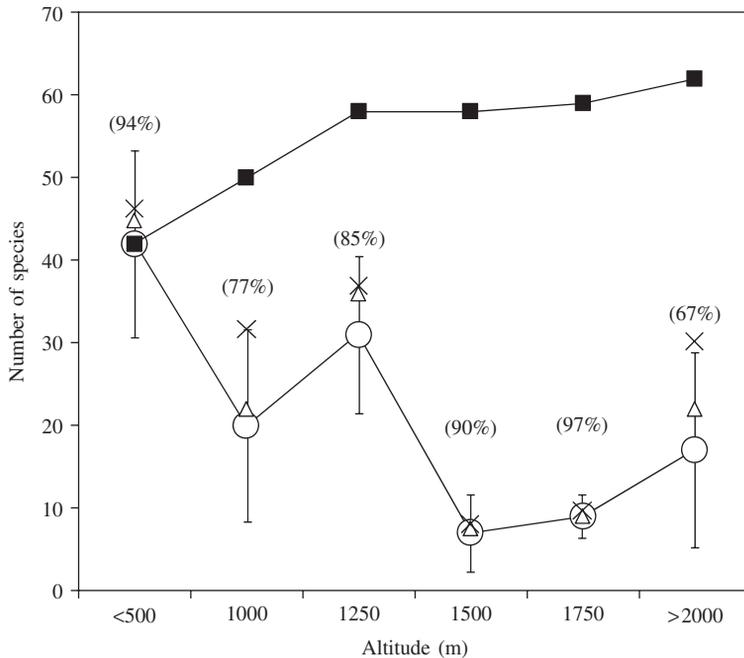


FIG. 2. Cumulative number of species (■) and variation in total species richness (○;  $\pm 95\%$  CI) with increasing elevation. Also shown are values of Chao 1 (X) and Chao 2 (Δ) (estimators of sampling efficiency; Colwell & Coddington, 1994). The values in parentheses are the expected percentages of species richness for each altitudinal level.

*Bryconamericus caucanus* Eigenmann, *Trichomycterus* sp. and a non-native species, *Micropterus salmoides* (Lacépède) (Table II).

Visual inspection of the  $K$ -dominance curves (*i.e.* per cent accumulation of species abundance) indicated that fish assemblage structure changed with increasing elevation (Fig. 4 and Table III). The general pattern observed was a sharp reduction in diversity, an increase in dominance of a few species and, as a consequence, a decrease

TABLE III. Summary of the multiple-regression analyses to examine the effects of four physico-chemical variables [temperature ( $T$ ), Oxygen ( $O$ ), conductivity ( $C$ ) and pH ( $p$ )] of water quality on species richness ( $S$ ). For this analysis, a generalized linear model (GLM) with a Poisson type error distribution (link function = log) was used. Deviance values are given as a measure of the model's fit (Crawley, 2007). The complete adjusted model was:

$$S = \mu + T + O + C + p + \varepsilon$$

Factor	d.f.	S: deviance	$P$
Temperature ( $^{\circ}$ C)	1	37.365	<0.001
Oxygen ( $\text{mg l}^{-1}$ )	1	7.693	<0.01
Conductivity ( $\mu\text{S cm}^{-1}$ )	1	2.379	>0.05
pH	1	8.510	<0.01
Error	28	44.03	

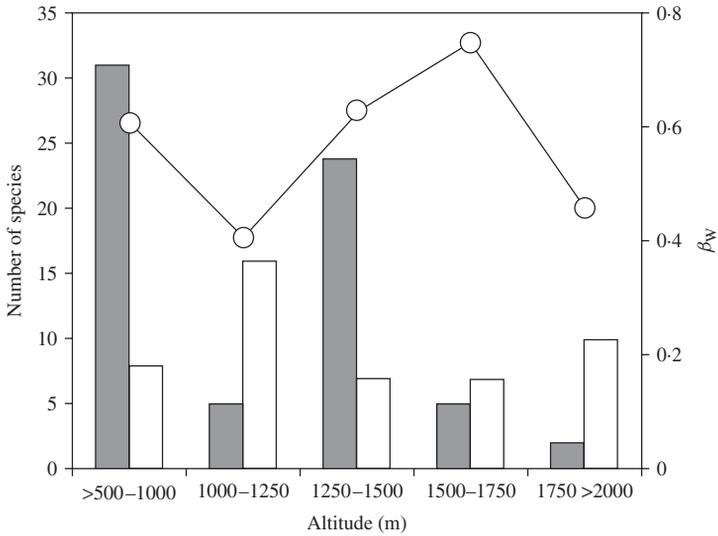


FIG. 3. Species turnover estimated with the Whittaker index ( $\beta_w$ ; ○) between adjacent altitudinal levels. Also shown is the number of species lost (■) and those gained (□) for each comparison.

in the evenness of the fish assemblages (Table I and Fig. 4). This trend was more evident when comparing sites above 1500 m. At this altitudinal level, three species *Astroblepus trifasciatus* (Eigenmann), *Astroblepus* sp. 3 and *Astyanax gisleni* Dahl, account for 90% of the individuals captured (Tables I and II and Fig. 4).

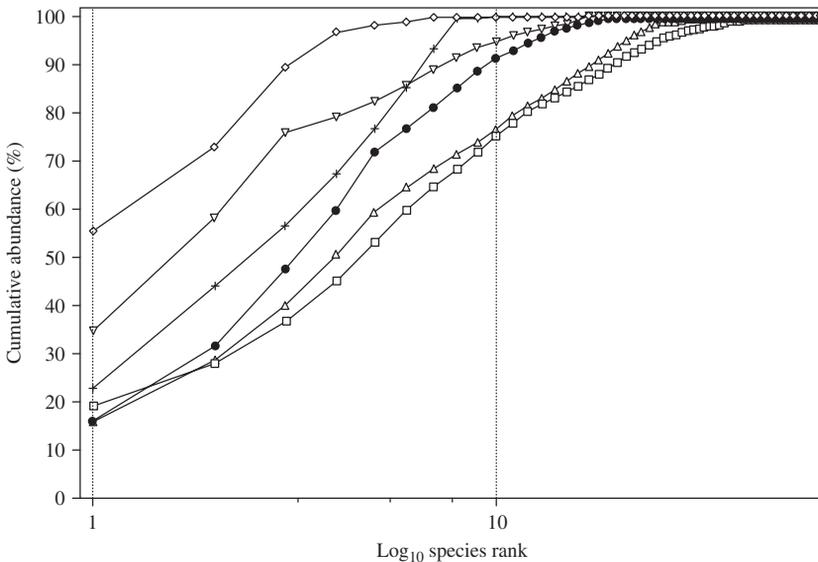


FIG. 4. *K*-dominance curves for each altitudinal zone [ $<500$  (□), 1000 (●), 1250 (△), 1500 (◇), 1750 (+) and  $>2000$  (▽) m].

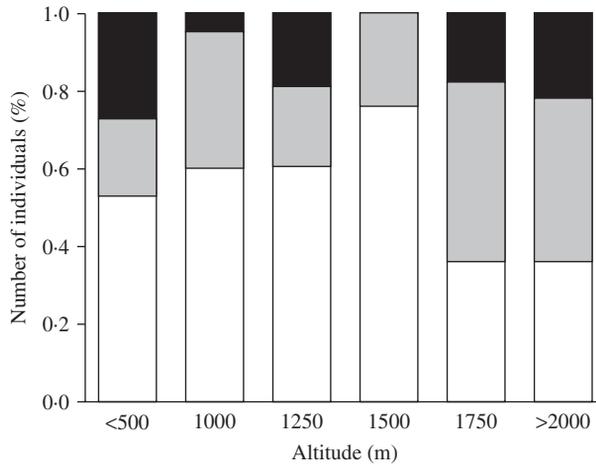


FIG. 5. Percentage of individuals from each functional group [torrential (□), pelagic (▒) and pool (■) species] in each altitudinal zone and the characteristics of the types of streams found at different elevations.

The percentage of individuals from each functional group (groups based on body shape and habitat use) was different at different altitudes ( $\chi^2 = 191.20$ , d.f. = 10,  $P < 0.001$ ; Fig. 5). Torrential species increased in abundance above 1500 m, but then decreased in abundance above 1750 m ( $\chi^2 = 38.42$ , d.f. = 5,  $P < 0.001$ ). Above this altitudinal level, fusiform fishes were more abundant and represented c. 45% of the total abundance ( $\chi^2 = 72.56$ , d.f. = 5,  $P < 0.001$ ). Species that inhabit pools are more abundant in lowland and high altitude streams ( $\chi^2 = 80.17$ , d.f. = 5,  $P < 0.001$ ) (Fig. 5).

## DISCUSSION

The decrease in species richness and increase in taxonomic distinctiveness with increasing altitude is a well-documented phenomenon in the flora and fauna of tropical mountains (Rahbek, 1995; Lomolino, 2001). The type of response differs among taxonomic groups, relating to differences in evolutionary history, which precludes the occurrence of just one pattern of response (Brown, 2001). The freshwater fish fauna of the eastern slopes of the central Colombian Andes changes from very diverse at lower altitudes (<1250 m) to impoverished communities, dominated by very few species at higher altitudes (>1750 m) where only 33% of all species were found.

A similar pattern has been reported for Andean water bodies elsewhere (Argentina: Bistoni & Hued, 2002; Colombia: Álvarez-León & Ortiz-Muñoz, 2004; Bolivia: Miranda-Chumacero, 2004; Pouilly *et al.*, 2006; Venezuela: Hoenighaus *et al.*, 2004). According to those studies, species diversity in the highlands (>1000 m) decreased significantly, with a reduction of 3.3–17.0% of the total number of species present along the altitudinal gradient. This indicates that the environmental conditions of the high altitudes may serve as a barrier to dispersion and the colonization of adjacent

drainage basins by lowland fishes. Nevertheless the differences in the percentage of loss in the number of species, it is not yet clear how the specific topographic, geographic and climate conditions of a mountain affect the observed patterns of species loss and gain with altitude.

Water temperature best explained the observed changes in the diversity of fish assemblages. The highest species diversity, 93% of all species and 76% of total individuals collected, occurred in the altitudinal level where the water temperature was 21.2 to 25.4° C (Table I). Below this temperature, there was a notable decrease in diversity at different scales of the taxonomic hierarchy (15 *v.* five families, 32 *v.* eight genera, 58 *v.* 20 species) (Tables I and II). Since water temperature directly affects the metabolism, breeding, development and growth, and behaviour of fishes (Buisson *et al.*, 2008a) and thermal variation and daily fluctuations of temperature are pronounced at higher elevations, it is reasonable to think that temperature is one of the most important factors limiting the diversity of fishes in tropical mountains at greater altitudes (Jacobsen, 2008). According to Janzen (1967), the effectiveness of an altitudinal barrier to the migration of species depends on the relative altitude, *i.e.* the difference between the ancestral thermal regime (experienced by the lineage in the past) and the new thermal regime being experienced by potential colonizing species. Studies on the physiological tolerance of related lineages, especially their response to changes in the temperature of water, are necessary to understand why different taxa have differentially extended their distribution ranges among the rivers flowing from mountains.

The species richness of the streams on the eastern slopes of the central Colombian Andes shows a similar pattern to that described by Osborne & Wiley (1992) in three Illinois drainage systems. They found that within the same drainage basin, local species richness and similarity are greater in streams located in the lower portion of the drainage that are connected to the main river channel than those of similar size located higher up in the drainage basin. Migration is a possible mechanism for explaining this pattern, since the rate of species exchange between the sites that are connected to the main channel (the source of colonists) is greater (Osborne & Wiley, 1992). Lomolino (2001) proposed that diversity decreases with elevation as immigration rate declines with the increasing isolation of high-elevation communities. The isolation and reduced capacity for dispersion of species from adjacent lowlands is a recognized cause of faunal differentiation and also explains the high endemism that characterizes fish communities of high mountain streams (Fu *et al.*, 2004).

Topography and climate determine the geomorphology and flow dynamics of water bodies (Allan, 1995). In the mountain altitudinal gradient, the drainage of rivers and streams changes from very swift, turbulent, cold and highly oxygenated in the highest reaches to less turbulent, more turbid and warmer in the lowest reaches (Jacobsen, 2008). These changes seem to be reflected in the structure and composition of fish assemblages in terms of morphology and habitat use. In the altitudinal gradient studied here, in lowland streams (below 500 m), species of Cichlidae, Sternopygidae, Cetopsidae and Heptapteridae dominated and were primarily associated with pool habitat (Table II). A transition occurred in middle altitude streams (between 1000 and 1500 m) with fewer species common to pools, while more fusiform or tor-rential species appear, such as representatives of Characidae, including the genera *Astyanax*, *Bryconamericus* and *Brycon* (Table II). Winemiller *et al.* (2008) described

a similar distribution pattern of these genera for rivers and streams of tropical mountains.

Highland (>1750 m) and Altiplano streams (>2000 m) were associated with a decrease in slope and a re-emergence of pool species. How might the presence of some species that have no particular morphological adaptations (such as dorso-ventrally compressed bodies, suckermouths or opercular odontodes) that would favour their presence by dispersion from lowland areas in high mountain environments (Altiplano), such as those of the genus *Bryconamericus*, be explained? If the distributional range of freshwater fish species along the altitudinal gradients is greatly affected by a combination of environmental factors acting at different scales (Buisson *et al.*, 2008a), the presence of these species could be the consequence of historical process related to the orogenesis of the Andean region in Colombia, more specifically, the process of valley uplift that isolated some species at high altitudes, as mentioned by Maldonado-Ocampo *et al.* (2005). This is of great relevance as it emphasizes the findings of Robinson & Rand (2005) on the existence of discrete changes in the rivers related to changes in geomorphology, which can influence the fish community structure along the altitudinal gradients.

In spite of the general reduction observed in the values of species abundance with altitude increased, only a few species increase in dominance, especially above 1500 m (Table II). The increasing dominance of a few species at high altitudes seems to be a compensating mechanism for adjusting populations to the available resources (Matthews, 1998).

The observed changes in various attributes of fish community structure in response to changes in the aquatic environment appear related to altitude. Climate change and human land use are two of the main external forces recognized to influence the fish diversity patterns along the altitudinal gradients (Dudgeon *et al.*, 2006; Becker *et al.*, 2007; Buisson *et al.*, 2008b; Buisson & Grenouillet, 2009). It is important to determine the effect of human activities, as they may modify altitudinal species distribution patterns (Orrego *et al.*, 2009), and therefore the way in which the patterns of species diversity along the altitudinal gradients are interpreted (Nogués-Bravo *et al.*, 2008). The amount of information on the effect and consequences of these forces in tropical mountains in countries such as Colombia is scarce. More data are needed to determine the real interaction of climate, physical factors and human land use on fish community structure along the altitudinal gradients and may allow better strategies to be developed for conservation of fish diversity in aquatic ecosystems in tropical mountains.

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