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Limnology of Andean piedmont rivers of Venezuela

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Abstract. We sampled 6 rivers of the piedmont region of Venezuela during the dry seasons of 1997 and 1998 to compare physical, chemical, and biological features and evaluate the influence of natural and anthropogenic differences in their watersheds. These 6 watersheds lie in a northeast-to-southwest transect along the interior slope of the Andes. Human disturbance declines and elevation of river origin increases along this transect. All watersheds experience a pronounced dry season from December through March, but rivers to the southwest exhibit less pronounced seasonality in flow and higher water yields. Sediment concentrations were highest in the Río Acarigua, which experiences the greatest human disturbance, but also were high in the least disturbed Río Bumbun, apparently from natural causes. Dissolved nutrient concentrations were lowest in the Río Acarigua, whereas less disturbed rivers contained higher amounts of dissolved nutrients. We collected 46 taxa of invertebrates and 50 fish species. Invertebrates and fish exhibited greatest diversity in rivers intermediate in the gradient. These more diverse systems may experience an intermediate level of disturbance that favors higher diversity, compared to the 2 rivers in the least disturbed landscapes. Cluster analysis done separately using invertebrates and fish separated rivers in the northeast from those in the southwest. However, a full explanation of these trends will have to address the intertwined effects of the natural biogeographical differences and the different human impacts that occur along the gradient.

Key words: river, tropics, Venezuela, invertebrates, discharge, watershed.

Our knowledge of the ecology of tropical rivers has increased substantially over the last decade. Nevertheless, the limnology of tropical Andean streams remains remarkably understudied, although there are notable exceptions (e.g., Turcotte and Harper 1982, Flecker 1992, Flecker and Feifarek 1994, Jacobsen et al. 1997, Jacobsen 1998, 2003, 2004, Jacobsen and Encalada 1998, Monaghan et al. 2000, Sites et al. 2003). Relatively few studies have characterized the physical and biological features of tropical Andean streams despite the fact that the Andes represent the headwaters of some of the largest river systems in the world.

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We examined the comparative limnology of rivers in the Venezuelan Andean piedmont. This region interfaces between high-gradient montane systems of the northern Andes and lowland sites of the vast Venezuelan llanos. The Venezuelan piedmont contains species of conservation significance, yet it has virtually no legally protected status. Much of this region has been heavily influenced by human settlement and disturbance. Over the last ½ century, forest clearing has been extensive (Winemiller et al. 1996, Allan et al. 2002), and remaining patches of forest continue to be cleared today.

In a comparative analysis of land use within a series of watersheds over a northeastern-to-southwestern transect along the interior slope of the Venezuelan Andes, we documented a gradient in human disturbance and intrinsic features (Allan et al. 2002). Within the piedmont (200–800 m elevation zone), all river valleys were ~60% forested. However, at higher elevations, a pronounced trend toward increasing forest and decreasing disturbed land area was evident from the most northeastern location (Río Acarigua) to the most southwestern (Río Bumbun). The density of habitations (homes, schools, churches; used as a surrogate for population) and of roads both were correlated with the extent of disturbed land (Allan et al. 2002). Intrinsic features of these river systems also differed across this transect. In particular, watersheds to the southwest originate at much higher elevations than watersheds to the northeast and have a greater fraction of their watershed area above the piedmont, the steepest lateral valley slopes, and the least human disturbance.

Here we characterize the physical and biological features of 6 rivers sampled at similar elevations in the Andean piedmont. Our goals were 2-fold. First, we wanted to provide basic descriptive information on the comparative limnology of rivers in the Venezuelan piedmont region. Second, we asked whether characteristics of discharge and chemistry, as well as patterns of faunal diversity and abundance, could be attributed readily to the anthropogenic and natural gradients described above. We expected that adjacent rivers would be most similar and that the gradient in human disturbance would be apparent. However, if upstream processes are major drivers of biotic diversity and abundance, then piedmont rivers with vastly different characteristics in their upper reaches should display unique patterns of community structure.

Methods

Study region

The study region is located along the southern slope of the Andes, and includes 6 rivers in the upper watershed of the Río Apure, a major left-bank tributary of the Orinoco River. Rivers originate at elevations from >1200 m to nearly 4000 m and drain toward the interior of Venezuela (Table 1). Very steep gradients in the headwaters become more gradual in the piedmont zone, below ~800 m. At ~200 m elevation, rivers leave the foothills and begin their meandering traverse of the llanos before joining the Río Apure. All study sites reported here were located in the foothills and were upslope of the Llanos Alto Highway (Carretera Nacional 5) that roughly marks the boundary of the piedmont region and the llanos. Two sites were sampled on each of the 6 rivers. In the case of the Río Acequia, which is formed by the confluence of the Siniguis and the Acequia, the upper of the 2 sites was on the Siniguis, and the lower was below the confluence. Hereafter, we refer to this location as the Siniguis because our characterization of the watershed was limited to that valley, but we report hydrologic data as the Acequia because the gage was below the confluence.

The foothills are characterized by a well-demarcated dry season lasting from late December until early April. Precipitation increases with altitude until ~1000 m, and then declines and is less seasonal at higher elevations (Reaud-Thomas 1989). The watershed was covered originally by dry deciduous forest, but present land use includes some sugar cane and tobacco plantations where the piedmont meets the llanos; crops of banana, cassava, and maize; and some coffee

TABLE 1. Characteristics of 6 Venezuelan rivers. Watershed area was limited to area above the llanos, determined by a point 1 km below the Llanos Alto Highway. Elevation at origin was determined from 1:100,000 topographic maps. Elevation range reflects differences among tributaries. Percent forested area was estimated from 1995 Landsat TM images. Habitation and road densities were derived from 1:100,000 maps. See Allan et al. (2002) for further details.

	Acarigua	Morador	Las Marías	La Yuca	Siniguis	Bumbun
Watershed area (km^2)	988	608	331	262	258	358
Watershed area in piedmont zone (km^2)	328	355	289	213	23	125
Elevation at origin (m)	1600–2000	1200–1600	1200–1600	1200–1600	3600–4000	3600–3900
% forested	42.7	46.0	57.1	57.1	63.6	79.2
Habitations (/km^2)	1.80	1.22	0.98	0.34	0.17	0.02
Roads (/km)	0.46	0.48	0.53	0.15	0.14	0.04

and citrus crops (Allan et al. 2002). Extensive cattle pasture occurs throughout the region, as well as occasional tree plantations (*Eucalyptus*, *Pinus*).

Land cover and settlement density for the 6 watersheds are described by Allan et al. (2002). Rivers at the northeastern end of the gradient (Acarigua, Morador, Las Marías) originate at lower elevations, have wider, flatter valleys in the piedmont zone, and experience a greater overall level of human disturbance in their watersheds than rivers at the southwestern end of the gradient (Siniguis/Acequia and Bumbun). Rivers toward the southwestern end of the gradient originate at higher elevations, are more constrained by their valleys, and experience less human disturbance, particularly at higher elevations. All 6 watersheds have roughly similar forest cover (50–60%) in the 200–800-m-elevation piedmont zone. However, a greater fraction of total watershed area of the Acarigua, Morador, Las Marías, and La Yuca watersheds lies within the piedmont; the Siniguis and Bumbun watersheds originate at greater elevation.

Discharge

Velocity and channel dimensions were measured at 2 transects at each of 2 sites/river under low-flow conditions during the 1997 dry season. Width and depth also were determined for the estimated bankfull channel. Discharge data were available (Ministerio del Ambiente y de los Recursos Naturales, MARN) for the Acarigua, Las Marías, La Yuca, and Acequia rivers at gauges located within a few hundred meters upstream of the Llanos Alto Highway, and ~5 to 16 km downstream of our study sites. Available data (1950 to 1993, depending on site) included monthly means and monthly instantaneous maximum and minimum discharges.

Chemistry

River water collected during the 1998 dry season was filtered through precombusted and preweighed 25-mm Whatman GF/F filters using a 60-mL syringe and filter holder. Filters were sun-dried in the field, then dried in the lab at 40°C (to prevent volatilization of organic compounds) and reweighed for determination of total suspended solids (TSS) dry mass and ash-free dry mass. Particulate organic C (POC) and particulate organic N (PON) were measured using a Perkin Elmer 2400 elemental analyzer from the same filters used for TSS. Water samples for dissolved organic C (DOC) and total dissolved P (TDP) were filtered through GF/F filters, preserved with 6N HCl, and kept in the dark. DOC was analyzed using high-temperature Pt-catalyzed combustion followed by infrared detection of CO_2 (Shimadzu TOC-5000), and total dissolved N (TDN) was measured on an Alpkem autoanalyzer after a potassium persulfate digestion (Kling et al. 2000). We were unable to conduct analyses of TDN with the 1998 water samples. Instead, an auxiliary set of water samples was collected from the lower sites of the study rivers in the 2004 and 2005 dry seasons. These auxiliary samples were analyzed for NH_4-N, NO_3-N, and soluble reactive P (SRP). Auxiliary water samples were filtered through Gelman A/E filters and analyzed in the field for NH_4-N by fluorometry (Holmes et al. 1999), using a Turner Designs Picofluor fluorometer. NO_3-N and SRP samples were frozen for subsequent laboratory analysis; concentrations of NO_3-N were measured using a DIONEX DX 2000 ion chromatograph, and concentrations of SRP were measured by the acid-molybdate method (APHA 1998) using a Shimadzu UV/VIS Mini 1240 spectrophotometer.

Aquatic invertebrates

Invertebrates on stone surfaces were sampled by collecting 30 stones throughout each study reach. We sampled primarily riffle habitats from a representative range of depths and currents, as well as shallow runs and pools. A handheld net (25×20 cm, 200-μm mesh) was placed immediately behind each stone as it was removed. The size of the net determined the upper size limit of individual stones that could be sampled. Length, width, and depth of each stone were recorded to the nearest 0.5 cm. The stone surface was rinsed thoroughly and hand-picked, and invertebrates were preserved in 95% ethyl alcohol in whirl-pack bags. Ephemeroptera, Plecoptera, and Trichoptera were identified to genus, Diptera and some Coleoptera to family, and remaining taxa to suborder or order. No invertebrate key exists for this region, so our identifications were based on multiple literature sources, and specimens were examined by specialists when possible.

Fishes

Fishes were sampled using a combination of backpack electrofishing (model 15-C; Smith-Root, Vancouver, Washington) and seine net. Each site received similar effort, which consisted of ~3 h of sampling of all available habitats. Collected individuals were returned to the Museo de Zoología, UNELLEZ, Guanare, Venezuela for identification and deposition of voucher specimens.

Statistical analyses

The landscape, river morphometry, and chemical data were examined by correlation analysis (all

TABLE 2. Dry-season discharge and channel dimensions of 6 Venezuelan rivers. Measurements are the mean of 2 transects at 2 sites/river, except as noted.

	Acarigua	Morador	Las Marías	La Yuca	Siniguis	Bumbun
Discharge (m^3/s)	6.2[a]	1.33	0.29	1.13	9.6[b]	6.9
Wetted width (m)	47.4	18.6	10.0	22.6	26.0	31.5
Bankfull width (m)	108.6	122.5	74.0	70.7	43.4	39.4

[a] Upper site only; an aqueduct withdraws water above the lower site, where discharge was 4.2 m^3/s
[b] Upper site only; the lower site is on the Acequia and is larger (38.6 m^3/s)

reported correlations were significant at $p < 0.05$, $n = 6$, unless otherwise noted).

Invertebrate species (taxon) richness was estimated from the 30 individual samples using EstimateS (version 5.0.1, http://viceroy.eeb.uconn.edu/estimates). EstimateS computes randomized taxon accumulation curves based on the n species $\times$ 30 samples species-abundance matrix. Taxon accumulation curves can be computed by a number of methods, all of which extrapolate to an estimate of the true number of taxa in the assemblage based on the number of rare taxa in the sample (Colwell and Coddington 1994).

Patterns in taxonomic composition across rivers and sites were examined using a Bray–Curtis cluster analysis of log-transformed abundances from the 12 collections (6 rivers $\times$ 2 sites). Cluster analysis was done separately for fish and invertebrates. Initial Bray–Curtis cluster analyses for invertebrates and fishes indicated that sites within rivers were very similar, so we pooled sites within rivers and repeated the analysis for the 6 rivers to better explore similarities across river systems. A Mantel test was used to compare the results of the 2 cluster analyses.

Results

Dry season discharge and channel dimensions

Based on dry-season discharge measurements, Las Marías is the smallest of the study rivers, Morador and La Yuca are intermediate, and the Acarigua, Siniguis, and Bumbun sustain the largest dry-season flows (Table 2). Estimates of dry season and bankfull widths parallel the pattern in measured discharge for the Acarigua to the La Yuca. However, the Siniguis and Bumbun rivers occupy steeper, more constrained valleys than the other rivers. This pattern is evident in their greater discharge relative to width and markedly narrower bankfull widths. These 2 rivers also have the highest dry-season discharge despite having 2 of the smallest watershed areas.

Hydrology

Hydrologic data for the Acarigua, Las Marías, La Yuca, and Acequia (below its confluence with the Siniguis) permit a more complete description of the flow regime of these rivers than of the other rivers (Table 3). Gauge data corresponded well with field measurements, taking into account that field sites were as much as 16 km upstream of the gauge location, tributary inputs were present in some instances, and water is withdrawn from the Acarigua for municipal use between upper and lower field sites. The rivers to the northwest (Acarigua, Morador, Las Marías) appeared to lose volume to groundwater recharge during the dry season as they left the foothills, and so dry-season flows at the gauge location may be less than flows recorded 10 to 20 km upstream.

Mean annual discharge for the period of record varied from 9.2 m^3/s for Las Marías to 43.8 m^3/s for the Acequia. This range is a result of differences in

TABLE 3. Discharge statistics for 4 Venezuelan rivers. Hydrologic data were not available for 2 of the study rivers. Water yield is mean annual discharge divided by watershed area.

	Acarigua	Las Marías	La Yuca	Acequia[a]
Period of record	1950–1989	1957–1973	1952–1983	1970–1993
Mean annual discharge (m^3/s)	32.6	9.2	13.0	43.8
Water yield (m/y)	1.06	0.88	1.55	2.89
Range of annual discharge (m^3/s)	9.7–75.5	4.8–12.8	7.4–24.8	35.5–60.5
Maximum discharge during period of record (m^3/s)	4500	560	2200	2500
Mean seasonal maximum discharge (m^3/s)	75	25	20	70
Mean seasonal minimum discharge (m^3/s)	4.4–5.2	0.1	2–4	10.4–13.2

[a] Watershed area of the Acequia and Siniguis combined = 478 km^2

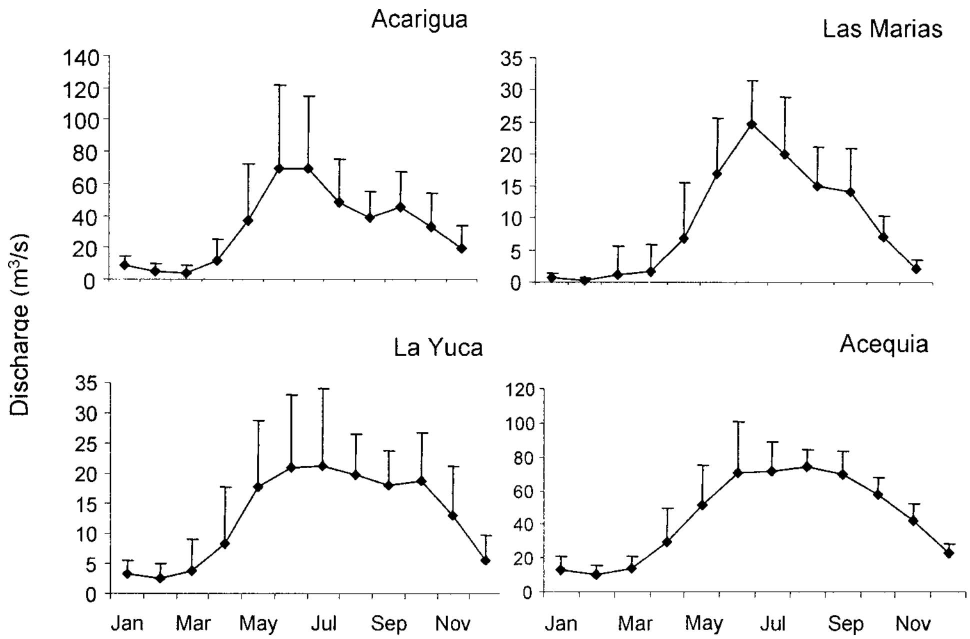

FIG. 1. Mean (+1 SE) monthly discharge for 4 Andean piedmont rivers.

watershed area and water yield. Las Marías and La Yuca have smaller watersheds than the Acarigua and Acequia, and this size difference explains most of the difference in discharge. However, water yield (mean annual discharge divided by watershed area) also varies by a factor of ~2 to 3 (Table 3). The 2 easternmost of the 4 watersheds in Table 3, the Acarigua and the Las Marías, originate at low elevations (Table 1) and have water yields of ~1 m/y. La Yuca originates at an elevation similar to the Acarigua and Las Marías (Table 1) but has a moderately higher water yield (~1.5 m/y), and the Acequia has a much higher origin (3500 m for the Acequia, 3900 m for the Siniguis branch) and a water yield ~3 m/y. The higher water yield of the Acequia and other watersheds to the southwest probably is a consequence of their greater area at high elevations where precipitation data show a less pronounced seasonality and where evapotranspiration also may be reduced because of lower temperatures. However, the Acequia's water yield may be overestimated if our calculation of watershed area is low. Based on data presented in Reaud-Thomas (1989), mean annual precipitation is typically 2500 to 3000 mm for locations at 1000 to 2000 m elevation and 1500 mm for locations in the lower piedmont, and mean annual temperatures increase from ~8°C at 3000 m to 16°C at 2000 m and 27°C in the lower piedmont.

Discharge in these Andean piedmont rivers is strongly seasonal (Fig. 1). Flows are low from December through April, the driest months of the year. Discharge increases steadily from April until July and August, then declines gradually through the remainder of the year. Based on average monthly discharge for the periods of record, seasonally high flows appear more restricted to the July and August period in the Acarigua and Las Marías, whereas high wet-season flows appear to be more seasonally extended in La Yuca and the Acequia.

The mean seasonal maximum discharge is considerably lower in Las Marías (25 m^3/s) and La Yuca (20 m^3/s) than in the Acequia (70 m^3/s) and Acarigua (75 m^3/s; Table 3). The largest flood on record for the Acarigua, 4500 m^3/s in September 1984, was nearly 2× the recorded maximum for the Acequia of 2500 m^3/s, also in September 1984 (Table 3).

Detection of synchrony among rivers in the timing of peak events is hampered by differences in periods of record. However, the data series for Las Marías and La Yuca overlap extensively, and they partly overlap early records from the Acarigua. Concordance among rivers in peak events and high values for mean annual discharge were few (JDA, unpublished data). A relationship between the El Niño Southern Oscillation (ENSO) index and discharge has been noted for larger Venezuelan rivers (Castillo et al. 2004), but examination of data since 1950 for our study rivers did not show a clear relationship between discharge events and the ENSO index. This lack of correlation is consistent with the variability among rivers in their timing of peak events.

Minimum flows generally occurred in March, which typically marks the end of the dry season. The seasonal

TABLE 4. Selected chemical variables for 6 Venezuelan rivers. Data were collected during February to March 1998 except for NO_3, NH_4, and soluble reactive P (SRP), which were collected during 2004 and 2005. TSS = total suspended solids, DOC = dissolved organic C, POC = particulate organic C, PON = particulate organic N, TDP = total dissolved P.

	Acarigua	Morador	Las Marías	La Yuca	Siniguis	Bumbun
TSS (mg/L)	16.20	1.88	0.93	1.73	1.21	4.45
Alkalinity (meq/L)	1.74	1.66	0.83[a]	1.31	0.37	0.37
DOC (mg/L)	0.98	1.24	1.37	1.50	0.96	1.00
POC (mg/L)	0.72	0.29	0.27	0.23	0.15	0.11
PON (mg/L)	0.077	0.063	0.059	0.040	0.018	0.055
Molar POC:PON	10.8	5.4	5.3	6.7	9.8	2.4
TDP (μg/L)	0.62	0.77	8.8	8.95	53.3	31.9
NO_3-N (μg/L)	<1.0	2.0	13.9	2.0	98.4	101.8
NH_4-N (μg/L)	<1.0	2.5	15.7	3.1	9.2	10.8
SRP (μg/L)	0.3	2.6	9.2	2.4	42.8	37.0
Molar N:P[b]	–[c]	3.9	7.1	4.7	5.6	6.7

[a] Taken in March when the river was barely flowing
[b] Ratio of dissolved inorganic constituents
[c] Ratio not calculated because individual values were near limits of detection

minimum discharge was highest in the Acequia and lowest in Las Marías (Table 3). An episode of zero flow occurred only once in the Acarigua, in 1988, when the river apparently ceased to flow for ≥4 mo. Episodes of zero flow occurred more frequently at Las Marías, and in all likelihood, extended for longer time periods.

Chemistry

TSS concentrations differed among rivers (Table 4), especially for the Acarigua where values were roughly an order of magnitude greater than other rivers. This pattern was consistent with its status as the most disturbed river valley (Allan et al. 2002). The TSS in the Bumbun was ~2× that of the remaining rivers, a result that was unexpected because the upper watershed of the Bumbun is unquestionably the least anthropogenically disturbed of the study systems. Fine sediment deposits were evident on the substrate of the Bumbun and presumably were of natural origin.

Other chemical measurements were indicative of a low dissolved load of materials (Table 4). Alkalinity declined from the Acarigua (1.74 meq/L) to the Siniguis and Bumbun (0.37 meq/L). POC also suggested a northeast-to-southwest gradient, from a high of 0.72 mg/L in the Acarigua to a low of 0.11 in the Bumbun. DOC concentrations (0.96–1.50 mg/L) were lower than values reported for other Venezuelan rivers, even the clearwater type (Lewis 1989, Castillo et al. 2004), but there were no strong patterns among the rivers. PON (0.018–0.077 mg/L) appeared to decrease from northeast to southwest, except for the higher value from the Bumbun. POC (0.11–0.72 mg/L) was markedly higher in the Acarigua, and also decreased from northeast to southwest. TDP values were very low and similar for the Acarigua and Morador, higher and similar for Las Marías and La Yuca, and highest for the Siniguis and Bumbun. Likewise, SRP and dissolved inorganic N (DIN = NO_3-N + NH_4-N) increased along the northeast-to-southwest gradient, with the range of concentrations spanning 2 orders of magnitude (SRP range: 0.3–42.8 mg/L, NO_3 range: <1.0–101.8 mg/L, DIN range: <2.0–112.5 mg/L).

Water yield was negatively correlated ($r = -0.96$, $n = 4$) with watershed area in the piedmont. Large watersheds and watersheds with high watershed area in the piedmont had more habitations than small watersheds and watersheds with low watershed area in the piedmont ($r = 0.87$ and 0.85, respectively). Habitations were inversely correlated with % forested area ($r = -0.88$). Thus, the 6 study watersheds exhibited 2 pronounced gradients. Rivers to the southwest had a greater watershed area above the piedmont, greater water yield and, in the case of the Siniguis and Bumbun, originated at considerably greater elevation than rivers to the northeast. The 6 watersheds lay along a gradient of human disturbance from the northeast to southwest (as seen in the increase in % forested area and decrease in habitations; Table 1).

Several chemical measures were significantly correlated with these overall gradients. TSS was correlated with wetted river width measured in the dry season ($r = -0.93$). The highest TSS values were observed in the Acarigua and the Bumbun, which fell at the 2 ends of the gradient, suggesting that the explanation for the high TSS values differed between the 2 rivers. In the Acarigua, the high TSS may have been a result of the highly disturbed landscape, but in the Bumbun, the explanation is unknown. Alkalinity was negatively correlated with % forest area ($r = -0.90$) suggesting a

TABLE 5. Summary of invertebrate collections for 6 Venezuelan rivers, based on combined data from 2 sites (30 samples/site) in each river. EPT = Ephemeroptera, Plecoptera, Trichoptera taxa.

	Acarigua	Morador	Las Marías	La Yuca	Siniguis	Bumbun
No. of taxa	31	36	36	39	33	31
No. of individuals/stone	59.8	32.6	62.3	79.6	18.5	108.0
Estimated no. of taxa	32.9	39.3	37.8	43.5	38.6	33.8
Shannon Index	1.96	2.65	2.69	2.69	2.2	1.69
Ephemeroptera genera	8	9	10	9	10	10
Trichoptera genera	8	10	10	11	10	8
Diptera families	3	5	4	6	4	5
EPT/Diptera (by number of individuals)	1.75	4.42	4.10	2.03	1.31	1.16

response to human disturbance, and also to watershed area in the piedmont ($r = 0.86$). DOC concentrations were negatively correlated with dry-season discharge ($r = -0.89$), and POC concentrations were positively correlated with habitations ($r = 0.95$) and negatively correlated with % forested area ($r = -0.90$). PON concentrations also were positively correlated with watershed area ($r = 0.84$) and watershed area in the piedmont ($r = 0.85$). TDP was positively correlated ($r = 0.87$) with % forested area and negatively correlated with habitations ($r = -0.92$). This pattern was consistent with the correlation of SRP and elevation ($r = 0.90$) and of both SRP and TDP with watershed area in the piedmont ($r = -0.91$ and -0.83, respectively). These patterns illustrate that underlying geology and rainfall are more important than anthropogenic sources of P in these rivers.

Aquatic invertebrates

A total of 21,638 invertebrates in 46 taxa were collected across the 12 sites on 6 rivers (Appendix 1). Those individuals identified at the level of order or above were excluded from further consideration. The remaining individuals were identified to taxa that usually could be assigned to genus (Ephemeroptera: 14, Trichoptera: 13, Plecoptera: 1, Megaloptera: 1, Lepidoptera: 1) or family (Diptera: 8, Coleoptera: 3). Some small or damaged specimens were included in order-level analyses (e.g., total EPT) when we could identify specimens to order but not to genus, but these individuals were excluded from measures of taxon diversity. Overall, 94% to 100% (average 97%) of the total sample could be identified to genus within the orders Ephemeroptera, Plecoptera, or Trichoptera (EPT), to family within the order Diptera, or could be placed in one of the higher categories used in taxon analyses (Appendix 1).

Total abundance varied widely among sites and among rivers (Table 5). The total number of individuals/stone averaged for the 2 sites/river ranged from 18.5 (Siniguis) to 108.0 (Bumbun). Average stone surface area varied only modestly among sites (overall mean = 293.6 cm^2, range: 263 cm^2 at Bumbun to 323 cm^2 at Siniguis), suggesting minimal influence of stone surface area on numbers of individuals collected. Invertebrate abundances were higher at downstream than at upstream sites at 5 of the 6 rivers.

Cumulative taxon richness appeared to be adequately estimated by the 30-stone samples, based on the relationship between sample size and taxon richness. Various estimators of expected taxon richness indicated that the 30-stone sample size underestimated the number of taxa/site by 2 to 7 taxa (mean observed taxon richness across sites = 28.1, mean estimated taxon richness = 32.0; Table 5).

The ratio of EPT/Diptera individuals, often used as an indicator of disturbed conditions, varied among sites and rivers (Table 5). The lowest EPT/Diptera ratios were observed at the 2 Acarigua sites and the downstream sites of La Yuca, Siniguis, and Bumbun. Members of the Chironomidae made up 72 to 98% of the Diptera except at the Bumbun, which was unusual in having a very large number of Simuliidae that made up 60% (upper) and 14% (lower) of individuals at the sites. Simuliidae were present at both sites on La Yuca, were found in very low numbers at one site on each of the Siniguis and Morador, and were not recorded elsewhere.

Abundance patterns were evaluated by graphing the rank order of relative abundances (Fig. 2). Dominance of a few species in a collection often is regarded as an indication of disturbed conditions. The 3 sites that had the highest number of taxa (Morador, Las Marías, and La Yuca) also had relative abundance curves with the most gradual slopes. The remaining sites had fewer taxa and had relative abundance curves with steeper slopes, an indication of greater dominance by a few, very abundant species.

With the exception of some rare taxa (mean abundances <1 individual/site) that could not be expected to be found at all sites, most taxa were

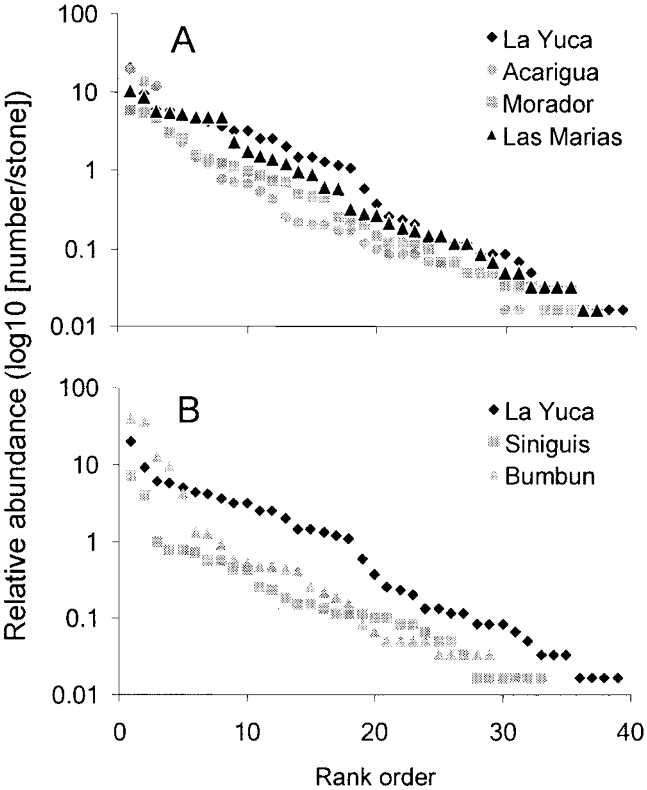

FIG. 2. Relative abundance of invertebrates for each of 6 Venezuelan rivers, based on 2 sites/river (n = 30 stones sampled at each site). La Yuca, the richest site, is shown in both panels to permit comparison of the northeastern (A) and southwestern (B) rivers.

broadly distributed (Appendix 1). *Polyplectropus* (Trichoptera) was found only at La Yuca, where it was common. *Smicridea* (Trichoptera) was very abundant in the rivers to the northeast and appeared to decline in the southwestern direction. *Leptonema* (Trichoptera) was absent from the northeastern rivers and present, although rare, in the southwestern rivers. Two genera of Ephemeroptera, *Camelobaetidius* and *Baetodes*, were most abundant in the Acarigua and Bumbun rivers, which are furthest apart geographically but similar in having higher TSS than the other rivers. Several taxa seemed to be most abundant in the 3 rivers in the middle of the gradient (Morador, Las Marías, and La Yuca). These rivers generally had the highest taxon richness as well. The ephemeropterans *Leptohyphes* and *Tricorythodes*, the trichopterans *Alisotrichia* and *Zumatrichia*, some dipterans, and the invertebrate predator *Corydalus* were more abundant in the middle rivers.

Fish assemblages

A total of 50 species and 3894 individual fishes were collected at the 12 sites and 6 rivers (Appendix 2). The 10 most common species in descending order were *Bryconamericus cismontanus*, *Chaetostoma milesi*, *Creagrutus taphorni*, *Chaetostoma anomalum*, *Parodon apolinari*, *Hemibrycon metae*, *Odontostilbe pulcher*, *Cetopsorhamdia shermani*, *Ancistrus triradiatus*, and *Characidium boavistae*. The greatest number of individuals and of species was collected at Las Marías and La Yuca, 2 rivers in the middle of the northeast-to-southwest gradient (Table 6). However, these rivers also were the 2 smallest and logistically easiest to sample for fish. Some fish taxa, such as *Prochilodus mariae*, were present at all sites but often were difficult to collect using a backpack electrofisher.

Similarities in assemblage composition among rivers

The 2 cluster analyses (fish and invertebrates) were highly similar based on the Mantel test ($p < 0.01$). Both cluster analyses reflected a strong influence of the northeast-to-southwest gradient, providing strong evidence that taxonomic composition within rivers was a result of their position along the gradient.

Invertebrates.—Invertebrate assemblages in the 4 eastern-most rivers clustered together, but the assemblage in the Acarigua was the least similar among the 4. The Siniguis and Bumbun formed a separate cluster, but differed substantially (Fig. 3A). Assemblages were distributed roughly along a northeast-to-southwest gradient that was the result of the presence of Blephariceridae (Diptera) and *Terpides* (Ephemeroptera) only in the Siniguis and Bumbun, and a gradient in abundance of Simuliidae (Diptera) from La Yuca to the Bumbun. Invertebrate taxa that characterized the Acarigua, Morador, Las Marias, and La Yuca included *Tricorythodes* and *Leptohyphes* (Ephemeroptera), *Corydalus* (Megaloptera), Hydrophilidae (Coleoptera), *Petrophila* (Lepidoptera), and Zygoptera. These taxa were absent or much reduced in abundance in the 2 western-most rivers.

Several invertebrate taxa, primarily Trichoptera, contributed to the dissimilarity between the Acarigua

TABLE 6. Species richness and diversity for fishes collected from 6 Venezuelan rivers (2 sites/river).

River	Acarigua	Morador	Las Marías	La Yuca	Siniguis	Bumbun	Total
Number of species	19	29	42	31	18	23	50
Number of individuals	309	793	1094	727	474	497	3894
Shannon Index	1.47	2.49	2.99	2.52	1.57	1.82	2.93

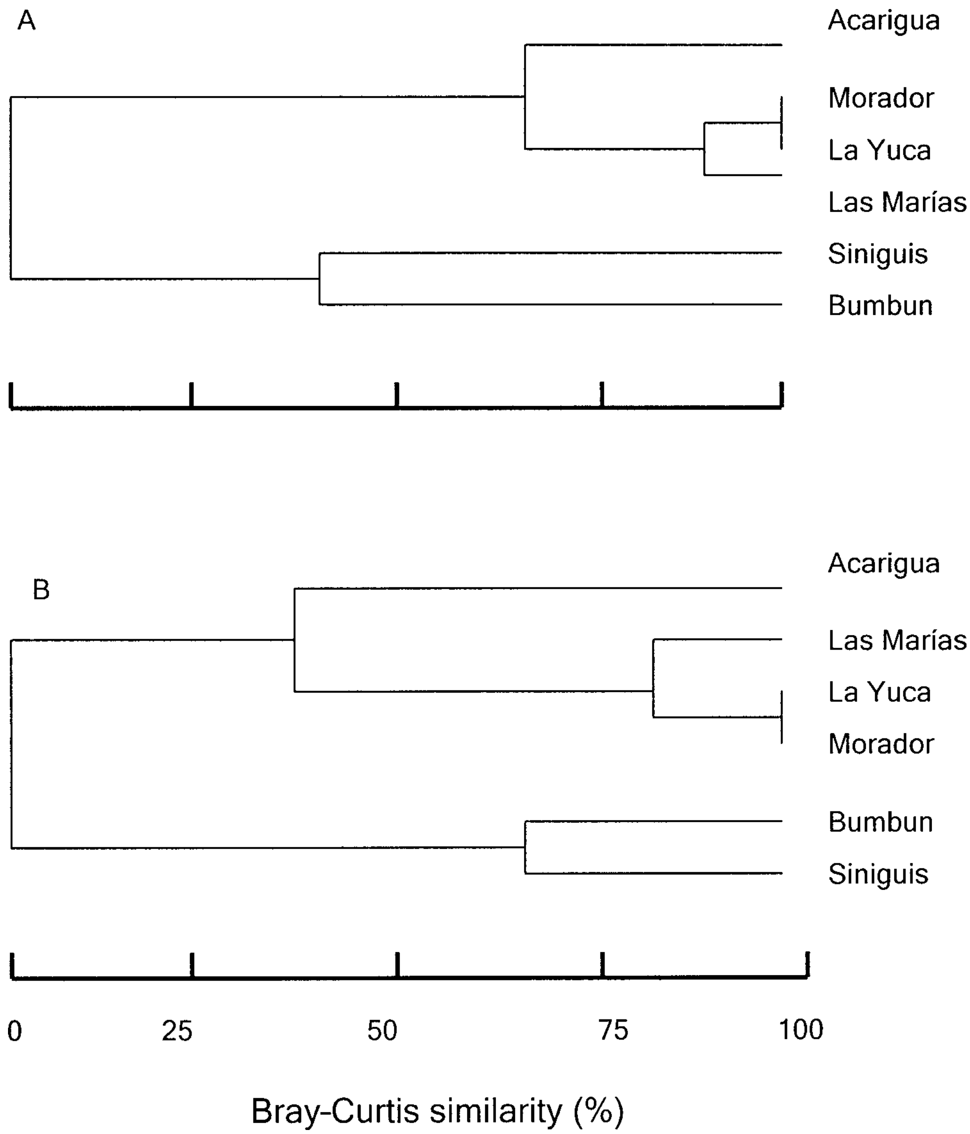

FIG. 3. Bray–Curtis similarity of 6 Venezuelan rivers based on relative abundances of invertebrates (A) and fishes (B).

and neighboring rivers. *Leucotrichia* was not collected in the Acarigua, and *Alisotrichia*, *Zumatrichia*, and *Chimarra* were less common in the Acarigua than in the Morador, Las Marías, and La Yuca. *Smicridea*, Elmidae (Coleoptera), and Empididae (Diptera) were more common in the Acarigua than in the Morador, Las Marías, and La Yuca. *Camelobaetidius* was a very abundant genus of Ephemeroptera at all sites, but reached its highest abundances at the Acarigua and Bumbun. These otherwise dissimilar sites had the greatest amount of sedimentation associated with the substrate, suggesting that *Camelobaetidius* is very tolerant of fine particles embedded amongst the coarser substrate.

The Bumbun had the greatest total abundance of invertebrates by far. Most of the individuals in the Bumbun were *Camelobaetidius* and Simuliidae, each of which made up $> \frac{1}{3}$ of the total abundance, and larvae of the Chironomidae. Together these 3 taxa contributed nearly 80% of the total number of individuals collected. Invertebrate taxon richness was lower in the Acarigua than in the other 3 eastern-most rivers.

Fishes.—Fish-assemblage similarity among rivers also followed a gradient that roughly corresponded to the geographic gradient (Fig. 3B). The 4 eastern-most rivers formed a cluster to which the Acarigua conformed least well, possibly because of its greater human influence. The Siniguis and Bumbun formed a separate cluster, but differed from one another because several species occurred only in the Siniguis.

Species responsible for the northeast-to-southwest gradient included *Leporinus striatus*, which was collected from the Acarigua to Las Marías, and *Chaetos-*

toma milesi and *Cetopsorhamdia shermani*, which were present in the Acarigua to La Yuca, but absent from remaining rivers. In contrast, *Chaetostoma anomalum* was found only from La Yuca to the Bumbun, and *Astyanax bimaculatus*, *Pyrrhulina lugubris*, and *Astroblepus* sp. were collected only in the Siniguis.

Fish species richness in the Acarigua (the largest of the eastern rivers) was similar to that observed in the Siniguis and Bumbun, but was strikingly lower than in the other eastern rivers. Only 19 fish species were found at the 2 Acarigua sites combined. Thirteen of these fish species were represented by $\leq$5 individuals, and all rare species encountered in the Acarigua were more abundant in nearby rivers. *Bryconamericus cismontanus* was common in all but the Bumbun, but it was most abundant in the Acarigua. In contrast, several species were common in all rivers except the Acarigua, where they were absent. These species included *Parodon apolinari*, *Hemibrycon metae*, and *Characidium boavistae*.

Discussion

Natural and anthropogenic gradients

The valleys of these 6 rivers occupy a northeast-to-southwest geographical transect along the interior slope of the Venezuelan Andes, forming a rough gradient in human disturbance and natural features (Allan et al. 2002). River valleys toward the northeast were settled earlier and road and habitation densities were higher than in river valleys to the southwest. Within the piedmont (200–800 m elevation), all 6 valleys were ~60% forested with the remaining land in pasture and agriculture, but the overall human presence was less evident in river valleys to the southwest. The trend toward increasing forest and decreasing disturbed land area from the Acarigua to the Bumbun was especially pronounced in the extent of undisturbed land upstream of our study sites.

The anthropogenic and natural gradients clearly were not independent. The gradient in human disturbance was accompanied by an imperfect gradient in a number of natural features. The 2 watersheds to the southwest, the Siniguis and Bumbun, originate at 3600 to 4000 m in the páramo, a region of montane meadows dominated by grasses and *Espletia* (Asteraceae). These watersheds have most of their watershed area above the piedmont and steep lateral-valley slopes (Karwan et al. 2001). Large boulders within the channel characterized both rivers. However, the substrate in the Bumbun contained a surprising amount of embedded fine sediments that could not be attributed to any human activity. Based on data from 4 rivers, water yields were markedly higher in the rivers to the southwest and declined towards the Acarigua. Clays and fine sediments generally appeared higher towards the northeastern end of the gradient. The Acarigua and Morador had larger watersheds than the other rivers.

Hydrologic records indicate that the seasonality is more pronounced and water yield lower for the Acarigua and Las Marías, compared with La Yuca and the Acequia (representing the confluence of the Siniguis and Acequia), which can be attributed to differences in rainfall and evapotranspiration at higher elevations. Inspection of long-term records also reveals more pronounced floods and droughts in the Acarigua in particular, which may reflect its longer history of forest disturbance.

Water chemistry

The most pronounced pattern in river chemistry, as related to the main northeast-to-southwest gradients of disturbance and elevation of origin, was in nutrient concentrations. TDP, SRP, NO_3, and NH_4 all were markedly higher in the Siniguis and Bumbun, which have the greatest water yields and extent of forest in their upper watersheds. In a study of small and large streams in Amazonia, Biggs et al. (2004) reported that TDP increased as the % of watershed deforested increased. In another study of small Amazonian streams, Thomas et al. (2004) showed a similar, but less distinctive, pattern of lower dissolved organic P in streams flowing in forests vs streams in pastures. Our data show an opposite pattern, in that the most disturbed and least forested catchments Acarigua and Morador had the lowest values of TDP. Clearly, disturbance is only one factor determining TDP concentrations in our study rivers. The highest TDP concentrations also occurred in watersheds with the highest elevation and, thus, the greatest and most consistent rainfall (Siniguis and Bumbun). Likewise, these rivers also had the highest concentrations of DIN. The controls on stream-water P may operate similarly to those for N, in that the dissolved forms tend to be higher in less-disturbed, forested areas with greater rainfall, as has been noted for dissolved organic N in other South American rivers (Lewis et al. 1999, Perakis and Hedin 2002).

All rivers had consistently low molar N:P ratios (molar N:P range: 3.9–7.1) regardless of the concentrations of DIN and TDP. These ratios are well below the Redfield ratio and are consistent with the notion that rivers in the Andean Piedmont region often are N limited. This conclusion also was reached in detailed studies of nutrient limitation of autotrophs in Río Las Marías, where different lines of evidence over consecutive years consistently pointed to N limitation throughout the dry-season months (Flecker et al. 2002).

Biotic diversity

Our assessment of biotic diversity was limited by incomplete taxonomic knowledge, particularly of the invertebrates, and by the moderate effort of snapshot sampling. Aquatic insects were identified to the genus level, which unquestionably under-represents species richness. For example, we identified only one stonefly, *Anacroneuria*, but a minimum of 31 species has been described from Venezuela based on adult collections (Stark 1995). In all likelihood, lumping also occurred at the genus level. However, based on species-pooling approaches, we believe that the collection of 30-stone samples from 2 sites on each river adequately characterized invertebrate diversity for the purposes of comparing relative patterns among sites. Melo and Froehlich (2000) used 25-stone samples to characterize invertebrate richness for a series of streams in Brazil and were able to compare sites and seasonal patterns using this sampling method. Nevertheless, increased sampling effort resulted in greater taxon richness, and they continued to add taxa to species accumulation curves even when as many as 150 individual stones had been sampled locally at a site (Melo and Froehlich 2001). Our species accumulation curves leveled off by 30 stones; thus, we are reasonably confident that the greatest invertebrate diversity is found in Las Marías and La Yuca (Shannon Index; Table 5), the 2 rivers in the middle of the transect. These rivers may experience an intermediate level of disturbance that favors higher diversity. The Morador and especially the Acarigua are disturbed systems, as is clearly indicated by the high TSS loads in the Acarigua (Table 4). The 2 rivers of least disturbed landscapes may be low in diversity for different reasons: the Siniguis was sampled at higher elevations and the Bumbun had finer substrate and a great deal of sediment of unknown origin.

In general, we found fewer invertebrate families at each site than has been reported for streams found elsewhere in tropical South America (e.g., Stout and Vandermeer 1975, Melo and Froehlich 2000, 2001, Rincón and Cressa 2000, Jacobsen 2004). Part of the reason for the smaller number of families might be related to our methods. Sampling was limited to individual stones and did not include other substrates and interstitial spaces. There is no question that we have underestimated taxon richness, but our comparatively low number of families may not be only methodological artifact. Invertivorous fish were abundant at all of our piedmont-river sites, and intense predation on exposed stone surfaces could have caused low species richness at these sites. Moreover, most invertebrates in our collections were extremely small bodied (<1 mm length). This size distribution could have been driven by high predation risk at piedmont sites. The small body size of most insects at our sites undoubtedly constrained, to some degree, our capacity to distinguish many of the taxa in our samples, although this problem generally did not occur at the family level.

We can evaluate the effectiveness of single-visit field sampling when characterizing fish assemblages because we have extensive, long-term sampling of Río Las Marías and high confidence in our fish identifications. We collected 42 species of fish in Las Marías in our single-visit sampling. This number represented slightly $>$½ of the 82 fish species we have found at Las Marías through repeated dry-season sampling since 1987 (ASF, unpublished data). Many of the fish species that were not represented in our single-visit sampling are species that have been very irregular in our collections. It is clear that our fish sampling effort was not complete, but it was effective for the purposes of comparing patterns of species richness among sites.

Separate cluster analyses of the invertebrate and fish assemblages in the 6 rivers had similar outcomes (Fig. 3). The Siniguis and Bumbun had assemblages that were different from assemblages in the other 4 rivers. La Yuca, Morador, and Las Marías were highly similar, but the Acarigua was less similar among rivers at the northeastern end of the transect, presumably reflecting its greater human disturbance.

Our results suggest that local landuse patterns alone are not the dominant factors driving patterns of species richness of river biota of the Andean piedmont. Forest cover was comparable among our piedmont sites, but we found distinct groups of rivers on the basis of fish and invertebrate assemblages. Considerable variation in human disturbance and natural features exists in the upper portions of our watersheds, in contrast to the piedmont region. Differences in the upper portions of our watersheds appear to override similarities in local downstream land use within the piedmont. The relative role of upstream vs downstream processes has important implications for the management and conservation of Andean rivers. Our work corroborates the notion that downstream reaches integrate processes occurring upstream, and their conservation requires that attention be paid to broader rather than local scales.

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APPENDIX 1. Number of invertebrates by taxon for each of 6 Venezuelan rivers. Numbers represent total individuals collected from 30 stones sampled at each of 2 sites/river.

	Acarigua	Morador	Las Marías	La Yuca	Siniguis	Bumbun
Ephemeroptera						
Baetidae A	32	6	103	63	8	0
Baetidae B	39	26	9	85	33	0
Camelobaetidius	695	269	318	262	234	2142
Baetodes	310	67	82	149	47	735
Leptohyphes	86	177	278	185	46	13
Tricorythodes	25	28	280	76	7	15
Thraulodes	71	147	71	549	59	31
Total[a]	1292	763	1294	1393	454	2947
Plecoptera						
Anacroneuria	15	29	36	35	15	35
Trichoptera						
Alisotrichia	12	73	306	243	14	241
Leucotrichia	0	4	2	22	1	3
Neotrichia	0	7	17	0	2	9
Ochrotrichia	4	3	7	1	6	0
Zumatrichia	1	42	339	217	11	77
Smicridea	806	344	289	354	33	28
Leptonema	0	0	0	2	4	3
Marilia	0	7	2	4	0	0
Chimarra	7	84	53	333	42	54
Polyplectropus	0	0	0	70	0	0
Glossosomatidae	12	14	1	15	9	0
Psychomyidae	5	92	136	85	7	24
Total[b]	848	670	1152	1346	129	439
Megaloptera						
Corydalus	3	15	19	7	0	0
Lepidoptera						
Pyralidae						
Petrophila	42	58	615	293	1	1
Diptera						
Chironomidae	1177	321	505	1197	435	564
Simuliidae	0	9	0	147	5	2335
Ceratopogonidae	10	2	58	12	0	5
Empididae	45	0	0	7	3	0
Tipulidae	0	2	0	5	0	0
Blephariceridae	0	0	0	0	6	28
Deuterophlebiidae	0	0	7	1	0	26
Psychodidae	0	1	16	0	0	0
Total[c]	1233	335	586	1369	450	2958
Coleoptera						
Psephenidae	3	7	35	8	5	4
Elmidae	136	51	90	118	25	75
Hydrophilidae	13	1	3	1	0	0
Total[d]	3588	1956	3738	4774	1106	6476

[a] Includes *Apobaetis*, *Pseudocloeon*, *Chloroterpes*, *Terpides*, *Hermanella*, *Euthyplocia*, *Hagenulopsis*, and unidentified Ephemeroptera
[b] Includes *Atopsyche*
[c] Includes unknowns
[d] Includes Anisoptera, Zygoptera, Hemiptera, Gerridae, and Isoptera

Appendix 2. Number of fish by taxon collected in each of 6 Venezuelan rivers. Numbers for each river are the total from 2 sites/river.

Species	Total all sites	Acarigua	Morador	Las Marías	La Yuca	Siniguis	Bumbun
Anostomidae							
Leporellus vittatus	7	0	1	1	5	0	0
Leporinus striatus	12	2	1	9	0	0	0
Characidae							
Astyanax bimaculatus	20	0	0	0	0	20	0
Astyanax integer	28	0	0	28	0	0	0
Astyanax metae	66	1	40	8	11	4	2
Brycon whitei	2	0	0	1	1	0	0
Bryconamericus beta	57	0	4	53	0	0	0
Bryconamericus cismontanus	721	185	141	115	160	13	107
Cheirodontops geayi	27	0	20	7	0	0	0
Corynopoma riisei	1	0	0	0	0	0	1
Creagrutus melasma	14	0	0	11	3	0	0
Creagrutus taphorni	396	19	17	38	51	47	224
Gephyrocharax valencia	62	8	3	50	0	0	1
Hemibrycon metae	192	0	82	57	3	45	5
Odontostilbe pulcher	188	0	60	101	1	0	26
Crenuchidae							
Characidium boavistae	98	0	21	58	3	9	7
Characidium zebra	26	0	23	2	1	0	0
Erythrinidae							
Hoplias malabaricus	5	0	1	3	0	1	0
Lebiasinidae							
Pyrrhulina lugubris	19	0	0	0	0	19	0
Parodontidae							
Parodon apolinari	293	0	72	136	64	17	4
Prochilodontidae							
Prochilodus mariae	21	1	0	20	0	0	0
Apteronotidae							
Apteronotus albifrons	30	0	5	4	5	4	12
Aspredinidae							
Bunocephalus amaurus	3	0	0	3	0	0	0
Hoplomyzon sexpapilostoma	13	1	0	3	8	0	1
Astroblepidae							
Astroblepus sp.	3	0	0	0	0	3	0
Cetopsidae							
Pseudocetopsis cf. *plumbeus*	10	1	0	4	2	0	3
Loricariidae							
Ancistrus triradiatus	136	0	0	63	60	2	11
Chaetostoma anomalum	371	0	0	0	32	281	58
Chaetostoma milesi	472	55	180	136	101	0	0
Farlowella vittata	29	3	7	2	3	2	12
Hypostomus sp.	53	0	4	5	44	0	0
Lasiancistrus sp.	14	0	3	11	0	0	0
Panaque maccus	7	0	0	5	2	0	0
Rineloricaria caracensis	5	0	0	1	0	0	4
Spatuloricaria gymnogaster	39	4	18	2	15	0	0

APPENDIX 2. Continued.

Species	Total all sites	Acarigua	Morador	Las Marías	La Yuca	Siniguis	Bumbun
Pimelodidae							
Cetopsorhamdia insidiosa	18	0	2	6	6	0	4
Cetopsorhamdia rosei	61	1	0	45	14	0	1
Cetopsorhamdia sp. 'large'	44	12	10	10	5	1	6
Cetopsorhamdia shermani	160	3	55	4	98	0	0
Heptapterus tapanahoniensis	1	0	0	0	1	0	0
Microglanis iheringi	4	0	2	2	0	0	0
Pimelodella sp. A	14	0	1	13	0	0	0
Pimelodella sp. B	39	3	13	11	9	2	1
Pseudopimelodus bufonias	5	1	3	0	0	0	1
Trichomycteridae							
Ochmacanthus alternus	1	0	0	1	0	0	0
Trichomycterus sp.	33	2	1	21	1	3	5
Poeciliidae							
Poecilia reticulata	9	6	0	3	0	0	0
Cichlidae							
Aequidens pulcher	25	0	0	24	1	0	0
Caquetia kraussi	1	0	0	0	1	0	0
Crenicichla geayi	39	1	3	17	16	1	1
No. of species	50	19	29	42	31	18	23
No. of individuals	3894	309	793	1094	727	474	497