DISTRIBUTION OF EPHEMEROPTERA IN THE ANDEAN PART OF THE RIO BENI DRAINAGE BASIN (BOLIVIA): REGIONAL PATTERN OR CONTROL AT THE LOCAL SCALE?

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ABSTRACT

A regionalization of the Rio Beni Andean basin based on geomorphology and climate led to hydro-ecoregions (HER). Ephemeroptera were sampled in 13 streams representative of 6 HER. Abiotic factors included slope, granulometry, and chemical parameters. Fauna is dominated by 6 genera (*Baetodes, Camelobaetidius, Baetis, Leptohyphes, Tricorythodes, Thraulodes*). Ephemeropteran communities does not present a strong hydro-ecoregional pattern, but major trends were evidenced. At the stream scale, slope governs the densities. HER clearly discriminate the streams on their physical and chemical parameters, and constitute a valid framework to explain the densities of Ephemeroptera.

INTRODUCTION

Aquatic ecosystems of the Bolivian Amazonian drainage basin are still very poorly known, especially for the invertebrate fauna. A better knowledge of the ecology and distribution of Ephemeroptera of this region will be of great interest to better understand the functioning of these ecosystems, as mayflies generally play an important paper in the faunistic structure. Predicting the distribution pattern of Ephemeroptera in natural streams according to their regional characteristics will be also of critical importance to further develop bioindication tools. In the northern countries (North America and Europe), the taxonomy, ecology and distribution of mayflies are well known. In the tropical Andes, the taxonomy and distribution of Ephemeroptera is documented by works carried out mainly in Colombia and Argentina (Needham and Needham, 1978; Roldán, 1980, 1985, 1988; Domínguez, *et al.*, 1992,1995; Flowers and Domínguez, 1992; Rojas *et al.*, 1993; Zúñiga and Rojas, 1995). In

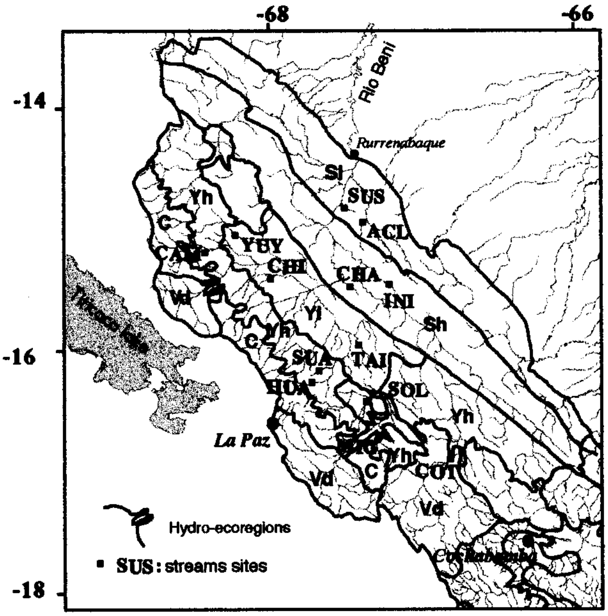

Fig. 1. Localization of the stream sites in the Hydro-ecoregions of the Rio Beni Andean basin.

Bolivia, the ephemeropteran fauna of the tropical Andean region is almost unknown. Thus, the aims of this paper are: 1) to get a preliminary list of the mayflies genera living in natural streams of the Andean Rio Beni drainage basin, 2) to give a quantitative distribution pattern of ephemeropteran fauna during low flow, and 3) to investigate at the regional and local scales the environmental factors that may explain this pattern.

STUDY AREA

Regionalization of the Basin

The Rio Beni is one of the main tributaries of the Rio Madeira in the Amazonian basin. The studied part of its basin (fig 1) encompasses all the geomorphologic structures of the eastern slope of the Bolivian Andes. Altitude ranges from 6400 m in the Cordillera Real to 200 m at the base of the Andes. The climate is mainly tropical humid, but some sheltered valleys are semi-arid. The anthropogenic alteration of the whole basin is very low, except in some areas of recent colonization, and extended areas are still covered with primary vegetation.

A preliminary regionalization of the basin (Gourdin, 1997), based on geology, geomorphology, climate and natural vegetation, led to the delimitation of hydro-ecoregions (HER *sensu* Wasson, 1996). These HER provide *a priori* a geographical frame for the regionalization of running waters ecosystems, with the hypothesis that physical and ecological structures, as well as the longitudinal gradient, will significantly differ from one region to another. The figure 1, derived from the definitive map of hydro-ecoregions of the Bolivian Andes (Wasson and Barrère 1999), presents the localization of the study sites in the HER of the basin. Main characteristics of the 6 studied regions are summarized in table 1.

Table 1. Characteristics of the six Hydro-ecoregions studied. Stream sites endogenous of a single region are in the left column; sites in the right column have a significant part of their watershed in the region Cordillera (code Y+C). See table 2 for stream sites codes.

Hydro-ecoregions	code	Altitude	Relief	Geology	Rainfall	Stream sites	
Dry Valleys	Vd	1000 -4000	V shaped valley	sedimentary	500-1000	COT	
Cordillera	C	3000 -6000	Steep valleys	metamorphic	600-900		Y+C:
High Yungas	Yh	1000 - 3000	V shaped valley	metamorphic	1500-3000	SUA	HUA MIG SOL CAM
Low Yungas	Yl	500 - 2500	open valleys	both	1500-2500	TAI CHI YUY	
High Sub-Andean	Sh	400 - 2000	mountain ridges	sedimentary	1300-1700	INI CHA	
Low Sub-Andean	Sl	200 - 1500	depression	sedimentary	2000-2500	SUS ACL	

Studied Streams

A total of 13 stream sites of similar size (about 15 - 20 meters wide in low flow) were selected on three criteria: representative of a region, natural state or low anthropogenic alteration of the watershed, and accessibility of the site. Representativeness is based on the watershed extension : most of the studied streams are endogenous of single HER, but the watersheds of four streams sites situated in the region "High Yungas" encompasses also significantly the region "Cordillera" (see table 1). Due to the difficulty of access, two regions (High Yungas and Dry Valleys) have only one representative site sampled at the present time. To emphasize on the regional and local control factors, the well known effects of the altitudinal and thermal gradients were limited by selecting stream sites in a restricted altitudinal range, between 1300 and 240 m. The slopes of the studied sites lie in the range of median values for streams of similar size in each HER (Gourdin, 1997) (table 2).

METHODS

All streams were sampled once during the dry season (May-October 1997). Stream sites were selected to represent the morphodynamic features of the reach, each site including two major riffle/pool sequences. The total length of a site represents about 12 times the bankfull width. The physical habitat of the stream sites was characterized by slope and granulometry. The slope of the water level was measured using topographic instruments, and calculated for the whole site and each major morphodynamic units. By the same way was evaluated the percentage of lentic units. Surface granulometry was evaluated by measuring the B-axis of 50 randomly selected elements, in both rapid and flat morphodynamic units (100 elements measured in total). Instability of the substrate was evaluated from its structure and the shape of the stones. Chemical data included temperature measured over a 24 h period, pH and conductivity measured in the field with WTW portable equipment, alkalinity and suspended solids analyzed in the laboratory following standard methods (Laboratorio de Calidad Ambiental, Instituto de Ecologia, UMSA La Paz). Benthic fauna was sampled using a Surber net (area 0.1 m^2, mesh size 0.250 mm). Six samples were taken to represent the main morphodynamic features of the site. Samples were conserved in 10% formalin for the transfer to the laboratory, then Ephemeroptera were sorted and identified to the genus level using the keys of Roldán (1988), Edmondson (1959), and Domínguez *et al.* (1992, 1995). Data were analyzed using the software ADE-4 (Chessel and Doledec, 1996) for multivariate analysis and SYSTAT 5 for other statistical analyses.

Table 2. Characteristics and localization of the stream sites.

Stream	Code	Slope %	Altitude (m)	Latitude (S)	Longitude (W)
				decimal degrees	
Huarinilla	HUA	1.8	1300	16.2167	67.8333
Miguillas	MIG	1.33	1272	16.5926	67.3087
Solacama	SOL	2.01	1269	16.3982	67.4705
Camata	CAM	1.28	1100	15.2174	68.6464
Suapi (Yungas)	SUA	2.86	1271	16.1152	67.7864
Yuyo	YUY	0.73	720	15.0424	68.4593
Chimate	CHI	0.61	560	15.4058	68.1536
Taipiplaya	TAI	0.55	804	15.9136	67.5023
Cotacajes	COT	0.93	1100	16.7474	66.7399
Inicua	INI	0.76	531	15.5065	67.1678
Chamaleo	CHA	0.27	450	15.4142	67.5786
Suapi (subandino)	SUS	0.25	240	14.8346	67.6220
Agua Clara	ACL	0.29	240	14.9217	67.4292

RESULTS

Physical and Chemical Data

The 13 stream sites were classified according to 14 physical and chemical parameters using a normalized Principal Component Analysis (PCAn) (fig. 2). The first two axes summarize 67% of the total inertia (fig. 2C). Axis 1 is structured by the physical parameters: altitude, slope and granulometry on the positive side, opposite to temperature, substrate instability and percentage of lentic units on the negative side. Axis 2 correspond to chemical parameters, suspended and dissolved solids being strongly correlated (fig 2A), together with pH and alkalinity. When plotted on these first two axes, the stream sites grouped by HER spread out along the F1 according to a gradient of their physical characteristics (fig. 2B). Stream sites of the High Yungas and Cordillera (Yh, Y+C) present higher slopes and granulometry, while sub-Andean sites (Sh, Sl) are characterized by lower values for these parameters, substrate instability, a high proportion of lentic units, and higher temperature. The second axis differentiates the sites of two HER: the Cotacajes in the Dry Valleys (Vd) due to high dissolved and suspended solids concentrations, and the sites of the Low Yungas (Yl) characterized by low pH and alkalinity. As a whole, the different hydro-ecoregions are well separated by the physical and chemical parameters of their representative stream sites.

Ephemeropteran Fauna

Faunistic Distribution. A total of 5 families and 16 genera were identified, with total densities varying from 15 to 1073 ind./m^2 (table 3).

The table was analyzed by the mean of a centered PCA after logarithmic transformation of the density values (log x + 1) (fig. 3). The first two axes account for 68% of the total inertia (fig. 3A). The faunistic map separates three groups of Ephemeroptera (fig. 3B) : group I includes three genera of Baetidae (*Baetodes, Camelobaetidius* and *Baetis*) ; group II includes three genera of Leptohyphidae and Leptophlebiidae (*Leptohyphes, Tricorythodes* and *Thraulodes*); group III includes all remaining taxa. The six genera in groups I and II are situated on the negative side of F1 and are the most abundant. The genera of the group III, located near the origin of the axis, are less abundant and more evenly distributed. Among them, the genus *Euthyplocia* was found only in two sites of the High sub-Andean region (Sh).

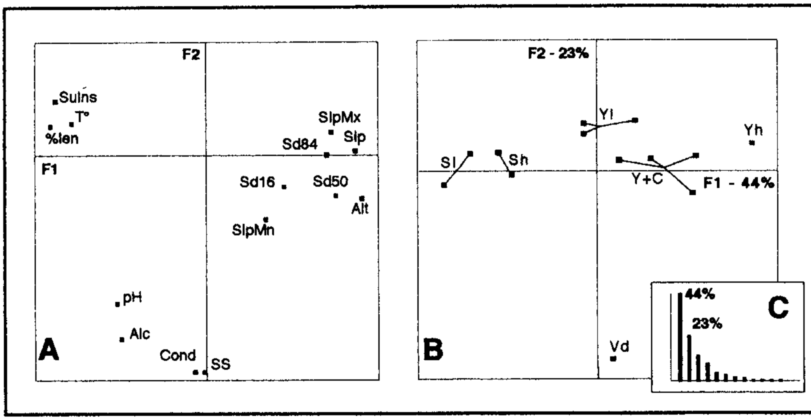

Fig. 2. Normalized PCA of the stream sites according to their physical and chemical characteristics.
A) Factor map of the 14 physical and chemical parameters. Alt: altitude (m); Slp: mean slope (%); SlpMx: maximum slope of the site; SlpMn: minimum slope of the site; Sd50: median granulometry (D50 of the granulometric curve); Sd84: coarse granulometry (D84); Sd16: fine granulometry (D16); SuIns: substrate instability, (qualitative evaluation, see text); T°: temperature; %len: percentage (in length) of lentic morphodynamic units. pH; Alc: Alkalinity; Cond: conductivity; SS: suspended solids ($mg.l^{-1}$).
B) Stream sites map. The 13 stream sites are grouped according to the hydro-ecoregions of their watershed. See table 1 for region codes.
C) Eigenvalues of the PCA axis.

The site map separates also three clusters of stream sites (fig. 3C). The cluster located on the positive side of the F1 includes the sites with a poor Ephemeropteran fauna, i.e. with 1 to 4 genera and less than 100 ind./m^2. The second cluster, negative on F1 and positive on F2, corresponds to stream sites dominated by the family Baetidae, with high ephemeropteran densities (500 to 1000 ind./m^2), and 5 or 6 genera. The third cluster, negative on F2, is dominated by genera of the families Leptohyphidae and Leptophlebiidae, have intermediate densities (200 to 800 ind./m^2), but the highest number of genera (8 to 11). One stream site (SUS) lies in an intermediate position.

When grouping the stream sites by hydro-ecoregions (fig. 3D), the streams sampled in the High Yungas but coming from the Cordillera (Y+C), appears with a dominance of Baetidae (group I) and relatively isolated from the others. Comparatively, the stream (SUA) endogenous from the High Yungas (Yh), although also supporting a high density of Baetidae (group I), presents a dominance of Leptohyphidae and Leptophlebiidae (group II). Another stream, the Cotacajes (COT) flowing in the Dry Valleys region (Vd), lies apart due to its very poor fauna dominated by *Baetodes*. The three other regions are not separated by their Ephemeropteran fauna, although a slight gradient might appear from the Low Yungas to the Low sub-Andean with increasing abundance and diversity, and increasing dominance of Leptohyphidae and Leptophlebiidae (group II).

Quantitative analysis. At the site level, control factors of the Ephemeropteran fauna quantitative structure were investigated using regression models on raw data. The entries of the models were the number of genera, total density, densities of each family, and densities of the groups I and II as dependent variables, and as independent variables the 14 physical and chemical parameters. The only significant regressions ($p< 0.05$) were: total density vs. mean slope (fig 4A), densities of Baetidae vs. mean slope ($r^2 = 0.601$, $p = 0.002$) and altitude ($r^2 = 0.527$, $p = 0.005$), density of group I (Baetide) vs. mean slope ($r^2 = 0.610$, $p = 0.002$) and altitude ($r^2 = 0.542$, $p = 0.004$), and densities of Euthyplociidae vs. fine

Table 3. Densities of Ephemeroptera per stream site (number of individuals / m^2). See table 2 for sites codes.

Taxa	Code	Stream sites												
		HUA	MIG	SOL	CAM	YUY	SUA	TAI	COT	INI	CHA	SUS	ACL	CHI
Euthyplociidae														
Euthyplocia	Eut	0	0	0	0	0	0	0	0	13	1,7	0	0	0
Leptohyphidae														
Leptohyphes	Lep	463	168	78	8.3	0	137	68	0	1.7	160	32	58	0
Tricorythodes	Tri	0	0	0	0	0	78	1.7	0	0	225	6.7	3.3	0
Leptophlebidae														
Thraulodes	Tra	230	35	3.3	57	25	233	53	3.3	1.7	28	63	100	17
Traverella	Trv	0	0	0	0	0	0	0	0	0	1.7	0	0	0
Terpides	Ter	0	0	0	0	0	10	0	0	0	0	0	0	0
Ulmeritoides	Ulm	0	1.7	0	0	0	0	0	0	0	0	0	0	0
Farrodes	Far	0	0	0	0	0	0	3.3	0	0	0	0	0	0
Meridialaris	Mer	12	0	0	0	0	0	17	0	0	3.3	1.7	47	0
Baetidae														
Baetis	Bae	90	8.3	23	0	0	6.7	12	0	0	40	0	1.7	8.3
Baetodes	Bao	263	185	248	17	0	248	5	12	0	10	27	0	0
Moribaetis	Mor	0	0	3.3	0	0	0	0	0	0	0	0	0	0
Cloeodes	Clo	0	0	0	0	0	0	1,7	0	0	0	0	6.7	0
Camelobaetidius	Cam	15	77	5	0	0	0	0	0	0	5	1.7	0	5
Paracloedoes	Par	0	0	0	0	0	5	0	0	0	5	0	5	0
Caenidae														0
Brachycercus	Bra	0	0	0	1.7	0	1.7	0	0	0	1.7	0	3.3	0
Total density		1073	475	362	83	25	720	162	15	17	482	132	225	30
Nb of genera		6	6	6	4	1	8	8	2	3	11	6	8	3

granulometry ($r^2 = 0.881$, $p = 0.000$) and percentage of lentic units ($r^2 = 0.330$, $p = 0.040$). However, the regressions for Euthyplociidae are only driven by one station (INI). For the family Baetidae and group I, regressions are significant with both altitude and mean slope but these two parameters are highly correlated ($r = 0.84$). When using a multiple regression analysis which eliminates the effect of partial correlation, only the mean slope enters in the regression model to explain the densities of both Baetidae and group I. The two models are very similar, as the 3 genera of the group I (*Baetodes, Camelobaetidius, Baetis*) make up more than 90% of the Baetidae in all sites except one (ACL); so only the regression for Baetidae is given in fig 4B.

The pattern of mayflies densities was also investigated at the region scale. As the slope appears as a main factor in discriminating the stream sites of the different hydro-ecoregions, mean densities were plotted against HER ranked following their position along the F1 of the PCAn on physical and chemical parameters (fig. 5). The global pattern evidences at the region scale the positive relationship between the total density of Ephemeroptera and the position of HER along the F1 axis, that integrates the physical characteristics of the streams sites in these regions. However, the two HER previously discriminated in the PCAn by their chemical particularities (Low Yungas and Dry Valleys) appears also with densities much lower than expected only by their position along the F1.

The differences in Ephemeropteran densities between HER were tested with an ANOVA. We used the logarithm of number of individuals per Surber sample, in order to downsize the problem of the small number of stream sites by HER. Differences were tested with a Mann-Whitney's test (0.05 significance level) for total densities of Ephemeroptera (Table 4), and for the densities of the two dominant groups I and II identified in the faunistic

PCAc. Despite the few number of samples, the results indicate that the stream sites of both Low Yungas and Dry Valleys differ significantly from those of the other Yungean regions (High Yungas and Yungas + Cordillera) in almost every case (11/12). The differences between the High Yungean sites (Yh and Y+C) and the Sub-Andean ones (Sh and Sl) are significant for 2/3 of the tested cases.

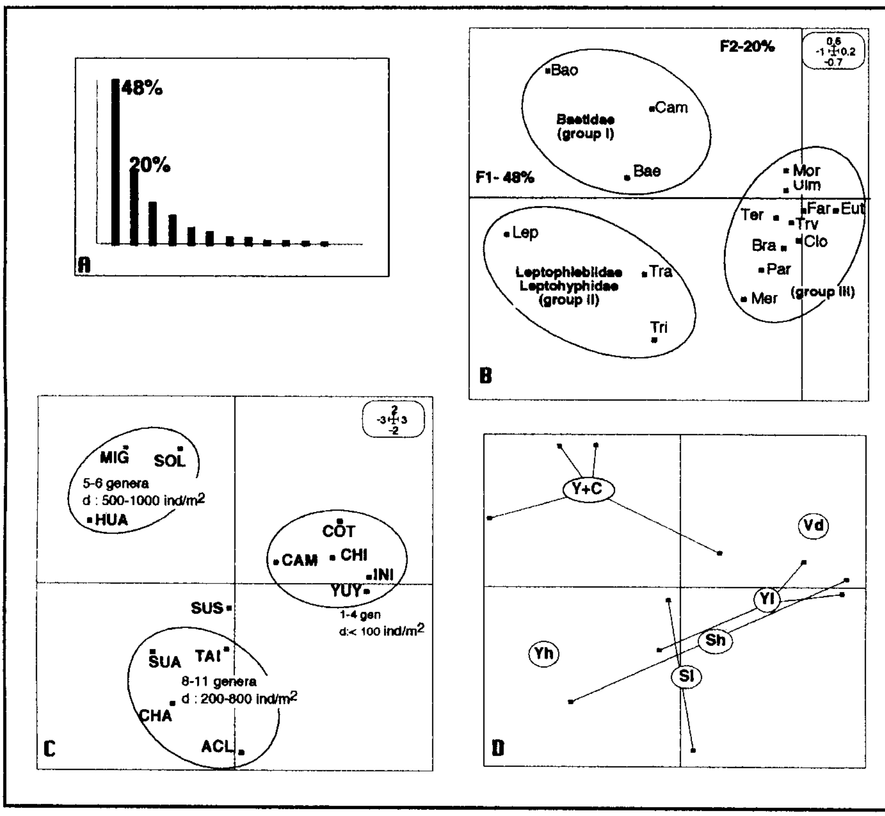

Fig. 3. Centered PCA of the stream sites according to their Ephemeropteran fauna.
A) Eigenvalues of the PCA axis.
B) Factor map of the 16 Ephemeropteran genera. See table 3 for genera codes and text for explanations.
C) Map of the 13 stream sites. See table 2 for sites codes.
D) Map of the 13 stream sites grouped according to the hydro-ecoregions of their watershed. See table 1 for region codes.

DISCUSSION

Validity of the Regionalization

Hydro-ecoregions were delimited on the basis of macro-scale determinants: geology, geomorphology, climate, and natural vegetation, available on maps or by remote sensing. We assume that these highest control factors will determine the basic physical and chemical characteristics of the streams, and the gradient of their longitudinal evolution. Thus, the hypothesis is that streams of similar size will present different physical and chemical

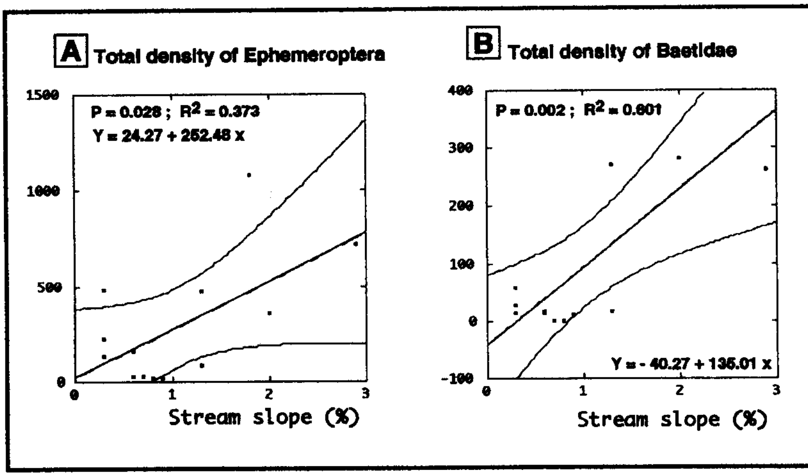

Fig. 4. Linear regressions models between A) total density of Ephemeroptera (Ind./m^2) and B) density of Baetidae (Ind./m^2) vs. mean stream slope (%).

characteristics according to the HER they flow through. Despite the small number of stream sites studied at the present time, the results obtained with physical and chemical parameters measured at the local scale support this hypothesis. The discrimination of HER by these parameters is good as evidenced by the PCAn (fig. 2B). This discrimination is in accordance with the global characteristics of HER. The geomorphologic sequence of HER along the eastern slope of the Bolivian Andes determines the gradient of physical characteristics of the stream sites (evidenced by the F1 axis of the PCAn). Noticeably, this gradient is not equivalent to a longitudinal or altitudinal zonation, as the streams of similar size were selected in different watersheds, without longitudinal relations between them. Another important point is the following: the hydro-ecoregions encompassed by the watersheds must be taken into account to explain the physical characteristics at the stream scale. In the High Yungas region, the endogenous stream (Yh) presents different characteristics (greater slope and granulometry) than the other streams flowing down from the Cordillera (Y+C). The climatic features, regulating the vegetal cover, explain some important variations in the chemical characteristics, such as the high dissolved and suspended solid content in the Dry Valleys region (Vd) where erosion is very high. Similarly, the low pH could be expected from the soil and vegetation characteristics; in the Yungean region, the humid tropical forest cover generates the accumulation of organic matter upon superficial uncarbonated rocks, thus leading to acid soils (Ribera *et al.* 1996). However, the lowest pH registered in the Low Yungas region (Yl) are probably related to the presence of pyrite veins in some basins (Guyot 1993), hardly predictable on the basis of the macro-scale determinants we used. Despite that, we assume that the hydro-ecoregions provide a valid frame for the regionalization of the physical and chemical characteristics of the streams. Such a correspondence has yet been observed in the Loire river basin (France) (Wasson, 1996). Now, the question is to what extent the Ephemeropteran fauna is controlled by this abiotic frame?

Distribution of Ephemeropteran Communities

All the genera identified in this study are encountered either in northern Argentina, or in Colombia. Thus we did not observed a particularity of the Bolivian fauna at the genus level. Globally speaking, the most salient feature of the mayflies fauna is the predominance of two

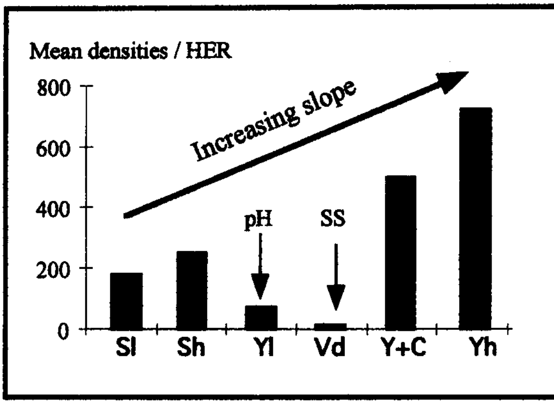

Fig. 5. Histogram of the mean total densities of Ephemeroptera by hydro-ecoregion. HER are ranked following their position along the axis F1 of the PCAn on physical and chemical parameters (fig. 2B). See table 1 for region codes.

groups of taxa (fig. 3B). Group I is composed of three genera of Baetidae (*Baetodes, Camelobaetidius* and *Baetis*) and group II by three genera of Leptophlebiidae and Leptohyphidae (*Leptohyphes, Tricorythodes* and *Thraulodes,*). These two groups account for most of the faunistic structure. When looking at the stream scale, three groups of sites can be distinguished (fig. 3C). The group "poor" as regarding Ephemeroptera includes sites where the fauna is impoverished for various reasons: low pH (CHI, YUY), high suspended solids content (COT), extended sandy substrate (INI). The second group of sites, whose ephemeropteran fauna is dominated by Baetidae, is formed by three streams flowing down from the Cordillera. The third group of sites, with high abundance of Leptophlebiidae and Leptohyphidae, includes only streams endogenous from the Yungean or Sub-Andean regions.

When searching for regional differentiation, the distribution of Ephemeropteran communities does not match very tightly the hydro-ecoregional structure. Three HER might appear with a relatively particular faunistic structure. The clearest one is that of the High Yungean streams flowing down from the Cordillera (Y+C), with a fauna dominated by the group I (Baetidae), and 4 to 6 genera. The endogenous stream of the High Yungas (Yh) differs from the former in sheltering both group I (Baetidae) and group II (Leptophlebiidae and Leptohyphidae) with high densities and 8 genera. The Dry Valleys (Vd) lies apart of the other regions due to its very poor fauna (2 genera and the lowest density) dominated by the genus *Baetodes*. The three other regions present only a slight gradient of differentiation, with high internal variability. Thus, these results did not evidence a strong differentiation of the Ephemeropteran communities on the basis of the Hydro-ecoregions, at least at the generic level. A high variability of the faunistic composition occurs at the local scale.

However, a general trend appears with the dominance of the Baetidae (group I) in the streams coming from the Cordillera, and of Leptophlebiidae and Leptohyphidae (group II) in the others. This could be related to a thermal effect, as streams flowing down from the Cordillera arrive in the Yungas valleys with mean water temperature much lower than the temperature of the air, and probably 2°C lower than the endogenous streams of this region (Wasson *et al.* 1989). Thus, the distribution of the family Leptophlebiidae, typically known as polystenotherm (Dominguez *et al.* 1995), could be limited in these streams by a colder mean temperature.

More sites and more precise data would be necessary to evidence a stronger hydro-ecoregional pattern of the ephemeropteran fauna, if it does exist. An interesting question is if the identification of species would lead to a better regional differentiation. The six genera that make up most of the faunistic structure are relatively common and widespread in the neotropical area, and presumably some species will tolerate a narrower range of abiotic conditions than the genus they belong to. Unfortunately, this question will remain unanswered for a while due to taxonomic limitations.

Table 4. Non parametric ANOVA (Mann-Whitney) for total density of Ephemeroptera between hydro-ecoregions. Probabilities for non-significant differences based on log transformed densities by Surber samples.

	Y + C	Yh	Yl	Vd	Sh	Sl
Y + C	1	0.565	0.001	0.002	0.141	0.149
Yh		1	0.001	0.006	0.008	0.004
Yl			1	0.095	0.442	0.442
Vd				1	0.047	0.003
Sh					1	0.73
Sl						1

Quantitative Structures of the Ephemeropteran Fauna

This high variability at the local scale oriented the investigation in search of quantitative models that could at least explicate the general parameters of the Ephemeropteran communities: total densities and number of genera. As a result, once eliminated the effects of partial or auto-correlation between abiotic parameters, the only significant relationships were found between stream slope vs. total mayflies densities, and slope vs. densities of the family Baetidae. However, even if these relationships are not doubtful, plotting the data (fig. 4) evidences the limited predictive capacity of these models at the local scale. Despite of that, the relationship between mayfly densities and stream slope is interesting because its offers a causal factor explaining the quantitative pattern of Ephemeroptera at the regional scale, as evidenced in the figure 5. Among the various parameters that contribute to the ranking of the six HER according to their physical characteristics, stream slope rises up as the only one significant in explaining the correlative increase of mayfly densities. The altitudinal effect seems less important as it disappears behind the slope effect in the multiple regression models, and we did not observe a significant difference between the two lowest HER (Sh and Sl) that could be related to the transition observed at 300 m by Flowers (1991) in the Ephemeropteran fauna of Panama.

But the stream slope alone does not predict the significantly lower densities in the two regions Dry Valleys (Vd) with high suspended solids, and Low Yungas (Yl) with low pH. Although pH and suspended solids were included in the entry parameters of the regression models, they did not contribute to the explanation of densities, perhaps because although they are inversely correlated, they have the same negative biological effect. The inverse relationship between suspended sediment and benthic fauna density has been clearly evidenced in the Yungean region following the impact of road construction on a clear water river (Salinas *et al.* 1999). Although not surprising, the effect of the low pH provides an interesting insight in the functioning of aquatic ecosystems in the Andean zone, and urges to pay more attention to the pH factor even in fast flowing streams. In fact, if the effects of a low pH are well documented in the lower Amazonian basin, we are not aware of any case study in natural streams of the Andean part of this basin.

Thus, the explanation of the density pattern of Ephemeroptera in the six HER appears relatively evident: there is a general trend of increasing densities with increasing stream slope, but limiting chemical factors such as pH and suspended solid can alter this pattern in lowering significantly the densities. Therefore, as these three parameters, stream slope, pH and suspended solids are fairly well predicted by HER, we assume that the hydro-ecoregions make up a valid frame to predict a range of abundance of Ephemeroptera at the stream scale.

CONCLUSION

The Andean part of Rio Beni drainage basin, with its largely pristine state over a wide range of geomorphologic and climatic features, constitute a choice laboratory for ecological studies on stream ecosystems. Our data present the first insight on Ephemeropteran fauna, identified at the genus level, in natural streams of this basin. This faunistic list including 16 genera may serve as a reference for future bioindication studies.

The aim of this work was to identify at the regional and local scales the control factors that may explain the distribution and quantitative structure of Ephemeropteran communities. A previous regionalization of the basin led to the delimitation of hydro-ecoregions on the basis of geological, geomorphologic and climatic features. Ours results demonstrate that hydro-ecoregions make up a valid frame to regionalize the basic physical and chemical characteristics of the streams. The sites studied in the different hydro-ecoregions are well discriminated on the basis of abiotic features measured at the stream scale, including slope, granulometry, temperature, dissolved and suspended solids, and pH. The question was to what extent the Ephemeropteran fauna do respond to this abiotic frame ?

On the basis of the faunistic distribution, we did not observed a strong regional pattern. However, some trends are relatively clear, such as the dominance of Baetidae in streams flowing down from the Cordillera, and Leptohyphidae and Leptophlebiidae in the other regions. The High Yungas region and the Dry Valleys appear also different from the others, but here our dataset is presently too weak to lead to definitive conclusions. In many regions, the internal variability of the Ephemeropteran communities is very high, due to the influence of local factors or limited sampling.

When looking at the quantitative structure of theses communities, two HER (Dry Valleys and Low Yungas) appear with densities much lower than the others. In regression models, the mean slope rise up as the only control factor explaining the abundance of Ephemeroptera at the stream scale; but if this fâctor can explain the difference between Yungean (Yh, Y+C) and Sub-Andean (Sh, Sl) regions, it cannot explain the low densities in the Dry Valleys and Low Yungas. In fact, both physical and chemical parameters governs the abundance of Ephemeroptera. Although not doubtful, the general trend of increasing abundance with increasing stream slope is a poor predictor of the quantitative structure, which may be significantly altered by adverse chemical parameters such as suspended solids or low pH.

As a whole, when looking both qualitative and quantitative characteristics, five of the six studied HER are discriminated on the basis of their Ephemeropteran fauna; only the two Sub-Andean regions (Sh, Sl) appear with undifferentiated communities. Thus, hydro-ecoregions allow a rather good regionalization of the Ephemeropteran communities, and to some extent the prediction at the stream scale of abiotic factors that explain important differences in their quantitative structure. We expect similar or even stronger results when taking into account the whole invertebrate fauna. These preliminary results support, at least partially, the hypothesis that hydro-ecoregions provide a valid frame for the regionalization of stream ecosystems. In such a large and almost unknown basin, this result will be of critical importance to develop bioindication tools, and to recommend management practices adapted to the regional ecosystems characteristics.

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