CHAPTER 5

HYDRO-ECOREGIONS OF THE BOLIVIAN AMAZON: A GEOGRAPHICAL FRAMEWORK FOR THE FUNCTIONING OF RIVER ECOSYSTEMS

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The Bolivian Amazonian basin is not a small piece of the puzzle. With 724 000 km^2, it accounts for one half of the Rio Madeira basin and 10% of the whole Amazon basin. It further comprises one quarter of the Andean Amazon catchments whose influence upon the hydrological functioning of the larger basin is significant (Fig. 5.1). The geography of the Bolivian Amazon is extraordinarily diverse, from rainforest to semi-desert and from glacier peaks to wetlands, and it shelters some of the planet's most important biodiversity refuges. It still contains extensive wild and almost depopulated zones, but it also includes Bolivia's three largest cities and a fast growing agro-industrial area. Both development and inappropriate practices tied to under-development generate conflicts between the aquatic resource conservation and development. Being unevenly distributed in the basin, water acts also as a strong determinant of human settlements and constitutes a major social stake; recent bloody riots flared over a conflict about water distribution. While environmental legislation is being implemented with difficulty, there is no scientific support for a global policy towards aquatic ecosystem management and conservation, and the geography of water problems remains blurred. A global view of hydrosystems, including biological aspects, is necessary to define sustainable development policies at the basin scale.

Integrated research management requires a strong scientific grounding. At the beginning of our research programme, in 1996, running water ecosystems of the Bolivian Amazon were still poorly investigated. Scientific knowledge was largely limited to two fields: hydrology and fish. The hydrology was investigated by PHICAB (hydrological joint research programme (1982–1992) for the Bolivian Amazonian basin), the main results of which were summarized in a water balance atlas (Roche *et al.*, 1990) with a description of hydrological regimes given by Bourges *et al.* (1993) and a detailed study of the hydrochemistry and sediment transport reported in Guyot (1993). More limited investigations concerning dissolved organic carbon (DOC) (Guyot & Wasson, 1994) and sedimentology (Guyot *et al.*, 1999) have been documented. In ichthyology, most of the data concerned the lowland rivers investigated during the "Convenio Piscicola" (Fish Research Agreement) joint research programme (1982–1987) on fish distribution, taxonomy, biology and production, which provided an inventory of almost 400 fish species in the Beni plain, including halieutic aspects (Lauzanne & Loubens, 1985; Lauzanne *et al.*, 1990, 1991). Pioneering work in the Andean rivers was done by Pearson (1924), and Sarmiento & Barrera (1997) recently produced a simple inventory of fish. Little was known about the invertebrate fauna in the basin, with the exception of the benthic invertebrates in a few mountain streams (Wasson *et al.*, 1998). Moreover, hydrology and biota have traditionally been studied independently, and the functional links between hydrology-dependant factors and biological structures—which constitute the basis of ecohydrology—had not been investigated.

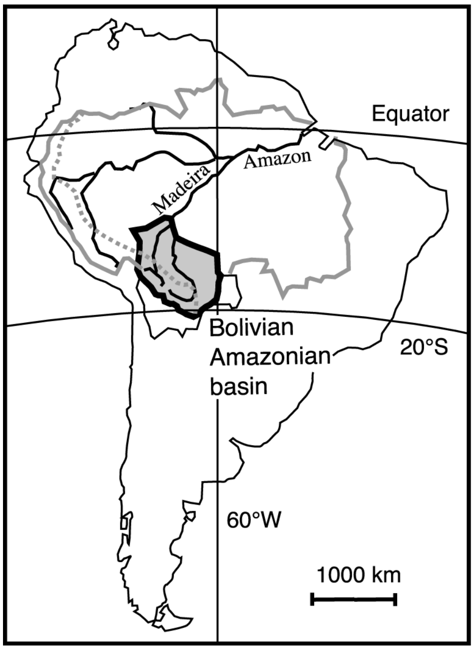

Fig. 5.1 Location of the Bolivian Amazonian basin (bold line) in South America; grey line: Amazon basin; dotted line: Andean border.

With its biological richness, its wilderness and geographical diversity, the Bolivian Amazon constitutes a fantastic natural laboratory for ecohydrological research. A topic of growing interest concerns the factors controlling the distribution and maintenance of aquatic biodiversity at both regional and local scales. This was a major aim of BIOBAB, a joint research programme (1996–2000) on aquatic biodiversity in the Bolivian Amazonian basin, which was initiated in 1996 to provide basic knowledge for management and conservation. The first step of this project was to develop a global view of running water ecosystems at the basin scale, which included the distribution of fish and invertebrates in the Andean zone; other topics concerned the hydrological dynamics of wetlands (Bourrel *et al.*, 1999) and hydrosystem functioning in the lowland flood plain (Pouilly *et al.*, 1999), bioindication (Fossati *et al.*, 2001), and mercury contamination (see chapter 4 of this book—Maurice-Bourgoin & Quiroga, 2002). Another limnological research programme initiated simultaneously was the PROLIMCO joint research project, which was more oriented towards aquatic resources management, with an emphasis on invertebrate fauna and bioindication in mountainous streams, and aquatic biodiversity distribution in lowland river systems. The first results of both projects were published in the proceedings of the Bolivian Congress on Limnology and Aquatic Resources (1999) held at Cochabamba.

We present in this chapter the regional approach of the BIOBAB project, the aim of which was to define homogeneous regions as regards the ecological functioning of running waters. The approach consisted of identifying at different hierarchical levels the ecohydrological links between physical control factors and ecosystem structures. Such an approach should provide a global view of the natural diversity of aquatic ecosystems in the basin, and by understanding the distribution of the main functional types, to allow some spatial prediction of their most important physical characteristics and associated biota. We shall define, map, and briefly describe the "hydro-ecoregions" of the Bolivian Amazonian basin and present some important aquatic ecosystem characteristics of the morphology, hydrochemistry, and fish and invertebrate communities in the Andean zone. This work is the first attempt of regionalizing running water ecosystems in South America, with the aim of providing a geographical framework for management and conservation.

CONCEPTUAL FRAMEWORK

Regionalization differs from a mere typology of known objects, as the purpose is to delimit geographical entities in which, at the present case, unknown running water ecosystems should *a priori* present similar characteristics. Usually, regionalization is a bottom-up process done by spatial aggregation of numerous sites that have only a few parameters. But in the case of aquatic ecosystems, we deal at best with a limited number of sites described by a complex set of variables. So the regionalization developed here is a top-down approach, linking ecosystem functioning to the geographical features of their catchments. The approach requires a strong theoretical background, based upon the hydrosystems hierarchical control concept.

The geographical classification of terrestrial ecosystems began in Europe and Russia at the beginning of the twentieth century and has been further developed in the USA by Bailey (1976) who popularized the term "ecoregion" (see Bailey, 1996). This approach was adapted to aquatic ecosystems by Omernick (1987), in order to define regional goals for water quality and management (Hughes & Larsen, 1988); a good agreement was observed between these ecoregions and hydrochemistry, fish communities, and to a certain extent with benthic invertebrates (Rohm *et al*., 1987; Whittier *et al*., 1988). This approach is obviously interesting for management (Omernick & Griffith, 1991; Warry & Hanau, 1993), but as the functional links between geographical characteristics and ecosystem structures are not explicitly described, an explanation of the observed patterns is somewhat lacking.

The conceptual framework for regionalization is substantially improved by the theories of hydrosystem hierarchical control, and particularly the nesting of physical structures from the basin to the microhabitat scale proposed by Frissell *et al.* (1986) and Naiman *et al.* (1992) and based on the ideas expressed by Hynes (1975) and Lotspeich (1980). All of these authors recognized geology, relief and climate as the primary determinants of running water ecosystem functioning at the basin scale. More recently the role of temporal variability and spatial heterogeneity in structuring aquatic communities has been emphasized (Resh *et al*., 1988; Townsend, 1989; Ward & Stanford, 1983). The integration of these findings led to the hydrosystem concept, a four-dimensional dynamic structure ruled by hydrology and morphology (Amoros & Petts, 1993).

The following is a summary of the hierarchical nesting of factors that determine running water ecosystem functioning (Fig. 5.2). At the local scale, aquatic biodiversity and

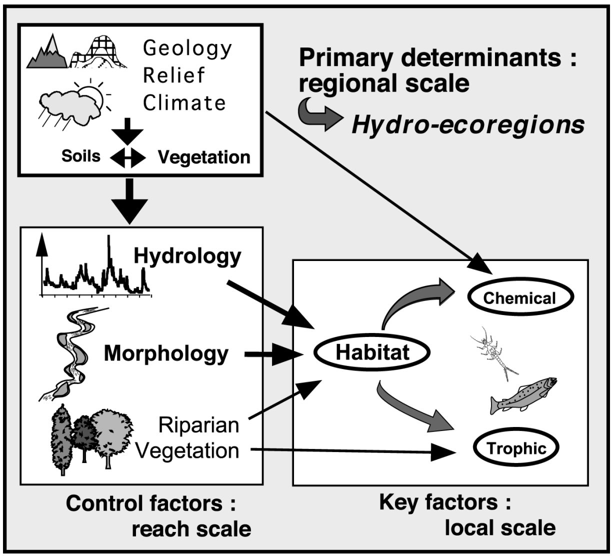

Fig. 5.2 Conceptual frame for the regionalization: schematic representation of the hierarchical control factors concept for running water ecosystems. See text for explanation.

productivity respond to “key factors” that can be grouped into three categories (Wasson, 1989): physical habitat (hydraulics, substrate), hydroclimate (light, temperature, dissolved gases, hydrochemistry etc.), and trophic resources (autochthonous production and allochthonous organic matter); however, the influence of physical conditions upon essential parameters such as oxygen or trophic resource availability leads on to assigning a central role to the habitat factor. At the reach scale, the distribution and dynamics of these key factors depend upon the hydro-sedimentological regime and valley geomorphology; these “control factors” rule the reach morphodynamics (river bed form and stability, substrate composition), the riparian vegetation structure, the lateral (flood plain) and vertical (hyporheic) connectivity, and the overall temporal variability of the system. Finally, at a regional scale, these control factors depend upon a limited set of “primary determinants”: geology (lithology), relief (geomorphology) and climate (temperature and precipitation). Soils and vegetal cover obviously affect the hydro-sedimentological balance, but they are ultimately determined by the geophysical and climatic characteristics.

This conceptual framework justifies an attempt to regionalize aquatic ecosystems in a large basin by delineating “hydro-ecoregions” (HER) on the basis of the primary determinants identified above (geology, relief, climate) (see Wasson 1996, Wasson *et al.* 1993). The underlying hypotheses are:

(a) within each HER, running water ecosystems should present a limited range of variation (as compared to the whole basin) for physical, chemical and biological characteristics, together with a similar pattern of longitudinal change;

(b) ecosystems of various regions should differ in at least one important abiotic parameter, leading to a consistent and significant difference in their biological structure. This should open the way to the definition of a limited set of ecological types in each region.

METHODOLOGY

The methodology for regionalization is detailed in Wasson & Barrère (1999), and here we shall merely point out some relevant aspects.

The approach is clearly based on a top-down control concept, following the principle that a classification is “better done according to the causes of the class differences than according to the effects that differences produce” (Strahler, 1975 cited in Lotspeich, 1980). This method also allows the definition of several hierarchical regional levels, and the identification of the control factors.

Basic parameters for regionalization are natural characteristics: geology, relief and climate. However, as we deal with existing data, their validity and relevance have to be carefully evaluated. For instance, the geological map has been interpreted in the light of lithological characteristics, such as rock hardness and chemical properties. The geomorphological structure was analysed by comparing three different sources: a broad digital elevation model (DEM), a specific study of remote sensing scenes, and a physiographical map. The climatic maps are very imprecise in Bolivia, and we used the vegetation as a geographically exact indicator of the climate. As vegetation cover is also a regulating factor for water and sediment fluxes, it emerges as an important parameter for regionalization and was analysed by comparing three different sources: an ecological map, a forest and agriculture map and a NOAA scene.

Regionalization deals with some striking natural boundaries (geomorphological and climatic) obvious in the landscape but also with pluviometry and altitude gradients. For the latter, we have singled out regionalization by structural (geomorphological) massif, with the hypothesis of a predictable longitudinal evolution of running waters in these massifs.

Delineating regions along a climatic gradient is more arbitrary, and in this case we followed important changes in the vegetation cover.

Running waters integrate rapidly the microscale (*sensu* Bailey 1996, i.e. at a kilometric scale) heterogeneity of their basin, which constitutes a great advantage for their regionalization. Such heterogeneity, for instance in rock composition, can be considered statistically as a component of HER characteristics. Landscape heterogeneity (10–100 km^2), such as rain shadow effects in mountainous area, is more difficult to deal with, but this was considered in the same manner. Consequently we recognize a fairly high internal heterogeneity in some regions. In every case the variation range for a given parameter must be predictable, and lower within a HER than between HERs.

Finally, such a regionalization approach remains an hypothesis until it has been validated at the running water ecosystem level on the basis of independent physical, chemical and biological parameters. Obviously, the basic hypotheses described above are valid only for small- and medium-sized reaches occurring entirely within a single region, but these ecosystems, which are often poorly known, account for a very high percentage of the total hydrographic network. For high-order reaches or systems crossing various regions, the analysis—and thus the prediction of their characteristics—must evidently be done in considering the proportion of the various HERs encompassed by their catchment.

The following thematic layers were used and processed within a geographical information system (GIS) with ArcView® and IDRISI®: **Geology**: Geological map, 1/1 000 000, SERGEOMIN* 1998. **Relief**: DEM GTOPO30, 30″, US Geological Survey EROS Data Center (http://edcdaac.usgs.gov/gtopo30/gtopo30.html); physiographic map, 1/1 000 000, GEOBOL 1996; specific analysis of 1/450 000 ERTS scenes by Gourdin (1997) for the Andean zone and Binet (1998) for the lowlands. **Climate**: Temperature and precipitation map from the PHICAB Atlas, 1/5 000 000 (Roche *et al*., 1990). **Vegetation**: Vegetation and ecoregions map, 1/1 500 000 (Rivera *et al*., 1996); forest map including agriculture, 1/1 500 000, CUMAT 1996; NOAA scene (23 May 1998) and the normalized differential vegetation index (NDVI), ABTEMA. **Soils**: Preliminary soils map for the Beni lowlands, 1/1 000 000, MDS/OT 1999. **Hydrography**: Hydrographic map, 1/1 500 000, IGM 1986.

Some of these sources, such as the vegetation map, carry interesting typological information but are geographically very imprecise. Others, such as the physiographic map, present important distortions; the DEM is also really inaccurate in the humid regions. The hydrographic network and the forest map were used to correct some geographical distortions. All the maps were reduced to a 1/2 000 000 scale for the HER delineation. The most obvious geomorphological and climatic boundaries were first used to define a first level of hydro-ecoregions (HER-1). Then, we looked within the most heterogeneous HER-1 for identifiable regional structures to delineate a second level (HER-2) that could be considered at present to be the most precise significant regionalization attainable with existing sources. Finally, these HERs were grouped into a few large geoclimatic domains.

For validation at the hydrosystems level, three types of independent data were used:
(a) geomorphologic characteristics of valleys and river beds,
(b) hydrochemical parameters and
(c) a hydro-ecological study of 25 stream sites in the Andean zone.
The methods will be described in the corresponding sections.

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* Acronyms used in this paragraph are as follows:
SERGEOMIN: Servicio de Geología Minería (Geology and Mining Service (formerly GEOBOL)
GEOBOL: Servicio de Geológico de Bolivia (Bolivian Geological Service)
CUMAT: acronym of a private environmental office
ABTEMA: Asociación Boliviana de Teledetección para el Medio Ambiente (Bolivian Association for Environmental Teledetection)
MDS/OT: Ministerio de Desarrollo Sostenible/Ordenamiento Territorial (Sustainable Development Ministry/Land Planning Board)
IGM: Instituto Geográfico Militar (Military Geographical Institute)

THE HYDRO-ECOREGIONS OF THE BOLIVIAN AMAZON BASIN

Geoclimatic domains

The main geomorphological and climatic structures delineate nine hydro-ecological domains (Fig. 5.3 and Table 5.1). The Andes cordillera is divided into two geomorphological zones, the first internal and the second external or "subandean". The mountainous internal zone is principally made up of primary rocks, more or less consolidated, interspersed with an intrusive granitic axis in the north, some volcanic deposits and localized calcareous formations in the south. The V-shaped valleys run perpendicular to the main cordillera axis, and the altitude extends from 500–1000 m up to more than 6000 m. The subandean zone comprises a succession of lower altitude ranges (2000–2500 m), parallel to the main axis, of secondary poorly consolidated rocks, often calcareous. These ranges, called "Serranías", delineate wide valleys and large depressions filled with Tertiary

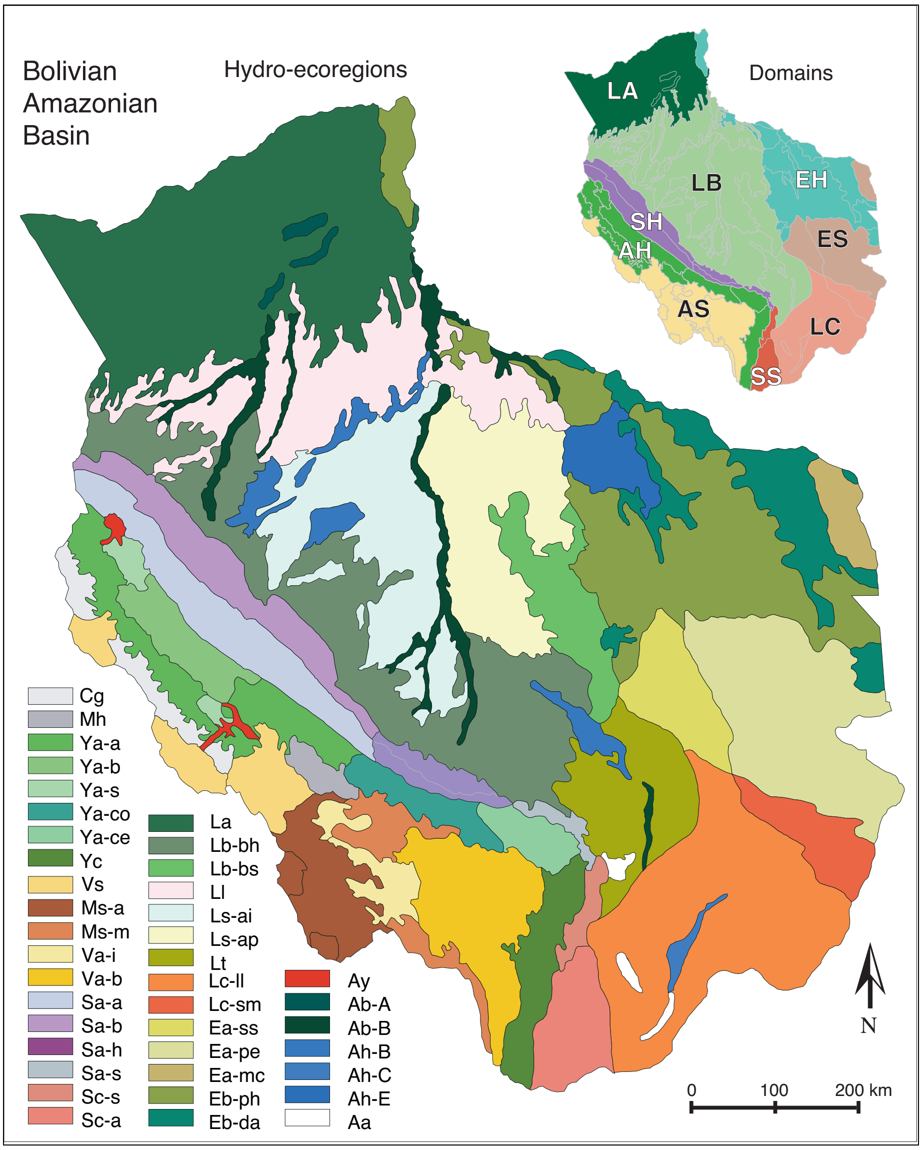

Fig. 5.3 Hydro-ecoregions of the Bolivian Amazonian basin, and geoclimatic domains (upper right). For the hydro-ecoregions map, the first two letters of the code correspond to the first level (HER-1) and the other letters to the second level (HER-2). See text for explanation and Table 5.1 for definition of codes.

sediments. On this longitudinal geomorphological structure is superimposed a well-defined transversal climatic boundary. The main axis of the eastern cordillera, oriented northwest–southeast, blocks the wet air mass coming from the central Amazon, thus separating a very humid domain northward from a semiarid one southward. This major divide corresponds to the limit between two (dry and tropical humid) of the four major climatic domains recognized at the global scale by Bailey (1996).

The lowlands comprise a vast central plain, called "Llanos", and the edge of the Brazilian shield in the east. The Llanos plain is filled with Quaternary sediments and is divided into three domains:

Table 5.1 Names and codes of hydro-ecoregions of the Bolivian Amazonian basin. Original Spanish terms have been conserved for local use and homogeneity with previous publications.

Domains	HER level 1	Code	HER level 2	Code
AH—Andino húmedo	Cordilleras glaciares	Cg	Cordilleras glaciares	Cg
	Montañas húmedas	Mh	Montañas húmedas	Mh
	Yungas peri-amazónicos	Ya	Ya—altos	Ya-a
			Ya—bajos	Ya-b
			Ya—subhúmedos	Ya-s
			Ya—"Chapare" hyper-húmedo	Ya-co
			Ya—"Chapare" subhúmedo	Ya-ce
	Yungas peri-chaqueños	Yc	Yungas perichaqueños	Yc
AS—Andino seco	Valles secos intra-andinos	Vs	Valles secos intra-andinos	Vs
	Montañas secas	Ms	Ms—altas	Ms-a
			Ms—medianas	Ms-m
	Valles semi-áridos	Va	Valles semi-áridos internos	Va-i
			Valles semi-áridos bajos	Va-b
SH—Subandino húmedo	Subandino peri-amazónico	Sa	Sa—húmedo alto	Sa-a
			Sa—húmedo bajo	Sa-b
			Sa—hyper-húmedo	Sa-h
			Sa—subhúmedo	Sa-s
SS—Subandino seco	Subandino peri-chaqueño	Sc	Sc—semi-seco	Sc-s
			Sc—seco	Sc-a
LA—Llanos amazónicos	Bosque amazónico del Pando	La	Bosque amazónico del Pando	La
LB—Llanos del Beni	Bosques inundables de llanos	Lb	Lb—Bosque húmedo peri-andino	Lb-bh
			Lb—Bosque subhúmedo peri-chiquitano	Lb-bs
	Sabanas lateríticas de llanos	Ll	Sabanas lateríticas de llanos	Ll
	Sabanas alcalinas de llanos	Ls	Ls—Sabanas alcalinas inundables	Ls-ai
			Ls—Sabanas alcalinas de palmeras	Ls-ap
	Zona de transición Beni Chaco	Lt	Zona de transición Beni Chaco	Lt
LC—Llanura del Chaco	Llanura seca del Chaco	Lc	Lc—Llanura xérica del Chaco	Lc-ll
			Lc—Serranías y mesas Chiquitanas	Lc-sm
ES—Escudo subhúmedo	Escudo subhúmedo alto	Ea	Ea—Serranías subhúmedas	Ea-ss
			Ea—Penillanura subhúmeda estacional	Ea-pe
			Ea—Meseta del Cerrado	Ea-mc
EH—Escudo húmedo	Escudo húmedo bajo	Eb	Eb—Penillanura húmeda boscosa	Eb-ph
			Eb—Depresiones aluviales	Eb-da
AH	Azonal—Valles secos de Yungas	Ay	Valles secos de Yungas	Ay
LA	Azonal—Bosque galería	Ab	Bosque galería Amazónicos	Ab-A
LB			Bosque galería del Beni	Ab-B
LB	Azonal—Humedales	Ah	Humedales del Beni	Ah-B
LC			Humedales del Chaco	Ah-C
EH			Humedales del Escudo	Ah-E
LC	Azonal—Arenales	Aa	Arenales	Aa

(a) the Amazonian Llanos in the north, a very humid region where tropical forest lies on undulating lateritic formations;
(b) the "Beni" Llanos in the centre, a flat plain where central savannas and wetlands are surrounded by humid forests; and
(c) a xeric domain in the south, the "Chaco" with its characteristic shrubby vegetation.

The Brazilian shield, made up of late Palaeozoic rocks, is inclined northward. It can be divided into a seasonally dry and more dissected plateau in the south and a humid peneplain surrounding wide sedimentary depressions and wetlands in the north.

Hydro-ecoregions level 1

Inside of the defined domains, the first level of regionalization results in 17 main hydro-ecoregions (nine HER-1s in the Andes and eight in the lowlands) and four types of "azonal" formations (Fig. 5.3).

Andes In the humid Andes we define a "glacial cordillera" region (Cg) and another "humid mountains" region (Mh) devoid of the glaciers that constitute an essential factor of hydrological regulation. In the intermediate zone of humid tropical mountains called "Yungas" we define the very humid "Amazonian Yungas" (Ya) in the north, and the somewhat dryer "Chaco Yungas" (Yc) in the south exposed to less abundant rainfall coming from Argentina. The same climatic dichotomy is encountered in the subandean zone (Sa and Sc). In the dry Andes, we must distinguish three HER-1s: northward, a "dry valleys" region (Vs) sheltered from Amazonian air masses, deeply incised in unconsolidated rocks with huge erosion rates; southward, in the Rio Grande basin, we define a peripheral "dry mountains" region (Ms) of rather high altitude, including calcareous and volcanic formations, that tightly surround a lower region of "arid valleys" (Va) often deeply incised and heavily eroded.

Llanos and Brazilian shield The "Amazonian Llanos" (La) and the "Chaco" (Lc) constitute homogeneous regions, but the central Beni plain must be divided into four HER-1s. A peripheral region of tropical humid "Llanos forest" (Lb), partially vulnerable to flooding, surrounds an extensive savanna landscape. The seasonally flooded savannas of the central zone can be separated according to very different soils and hydrogeology encountered on both sides of a geophysical fault, known as "the Bala-Rogagua line". This uprising fault divides the Beni plain into a northern region (Ll) characterized by lateritic acidic soils and a deeper (15 m) groundwater table, and a southern region (Ls) crossed by the Rio Mamore, lying upon recent sedimentary alkaline soils with more superficial phreatic waters (Hanagarth, 1993). Between the Beni plain and the Chaco Llanos is a transition region (Lt) characterized by fertile, unflooded soils favourable for intensive agriculture (the soybean belt, east of the city of Santa Cruz). The Brazilian shield is divided into a higher seasonally dry and a lower humid region (Ea and Eb), following the geoclimatic domains.

The "azonal" formations correspond to very particular mesoscale physical conditions, driving to such a point the hydrosystem properties that they override the ecoregional context. We have separated some very dry valleys interspersed in the Yungas region due to a rain shadow effect (Ay), and in the Llanos the gallery forests (Ab), the permanent wetlands (Ah), and some aeolian dune formations (Aa).

Hydro-ecoregions level 2

The majority of HER-1s have sufficient heterogeneity in geomorphological or climatic parameters to justify a second level of regionalization. For instance, the Amazonian Yungas (Ya) are climatically fairly heterogeneous, as rainfall varies from 1500 to 5000 mm year^{-1} due to the orientation of the massifs, and geomorphologically the landscapes are more or less incised due to variations in lithological composition. This region is divided into six HER-2s and one azonal formation. Similarly, the subandean zone can be separated into four HER-2s on the basis of rainfall and geomorphology. All the Andean regions are more precisely described in Wasson & Barrère (1999).

In the lowlands, the geographical structure is less heterogeneous. However, the savannas situated on both parts of the Rio Mamore differ sufficiently in terms of precipitation and vulnerability to flooding to be separated into the western region (Ls-ai) with significantly more flooding (Bourrel *et al.*, 1999) than the eastern region (Ls-ap) interspersed with palm-tree assemblages (Rivera *et al.*, 1996). The same phenomenon occurs for the eastern part of the Llanos forest (Lb-bs), which is dryer than the piedmont region (Lb-bh). In the Brazilian shield, the second level of hydro-ecoregions has been defined mainly on the basis of relief and geomorphology. In the lower region, the granitic peneplain (Eb-ph) is separated from the alluvial depressions (Eb-da), and in the higher region, we distinguished the peneplain (Ea-pe), the mountainous ranges (Ea-ss) and the very particular “Cerrado” plateau (Ea-mc). For the azonal formations, gallery forest and wetlands have been separated according to the geoclimatic domain to which they pertain.

On the whole, 33 HERs have been identified at the second level (19 in the Andes and 14 in the lowlands), and seven types of azonal formations. The global figures reflect some outstanding structures, such as the geological domains (Andes, Llanos, Brazilian shield), the wet/dry climatic boundary in the Andes or the savanna/forest limit in the Llanos. But other important boundaries are much less obvious in the landscape, and the transition between two regions is sometimes blurred. However, in every case the variations in the parameters used to delineate the regions are expected to involve significant differences at the river level in a combination of morphodynamic and chemical characteristics.

In the same way as a typology is best defined by the barycentre of the object classes rather than their limits, HERs are defined by their dominant characteristics rather than their boundaries. We have not derived an independent set of “predictions” about the aquatic ecosystem characteristics in each region, but we assume that such predictions are possible. Nevertheless, HERs could be used for predictive spatial extrapolation, i.e. the probability for an unknown system to match a given ecological type (and a limited range of variation for a set of important parameters) according to the HER it belongs to. In the following section we present the validation of the regional hypothesis at the aquatic ecosystem level.

VALIDATION: REGIONAL CHARACTERISTICS OF RUNNING WATER ECOSYSTEMS

Ideally, the validation should be made first on the hydrological and morphological control factors, but as hydrometric data are very poor in Bolivia for small and medium sized rivers, the characterization of hydrological regimes at the HER scale remains questionable. Conversely, the topographic map coverage, although incomplete, is sufficient to provide quantitative information on river and valley morphology for most HERs.

Geomorphologic characteristics

The methods and detailed results for the Andean and lowland zones are described in Gourdin (1997) and Binet (1998), respectively. Geomorphological parameters were measured from available topographic maps (1/50 000) for reaches about 5 km long, thus the data source is independent from those used for the regionalization. The database includes 520 reaches for the Andes and 306 for the lowlands where the map cover is more scattered. The parameters were selected to describe the valley morphology and as far as possible the structure and dynamics of the river beds. Structural parameters were the stream order (Strahler), the hill-slope gradient, the valley bottom slope and width, the fluvial form and sinuosity coefficient, and the transversal valley profile in the lowlands. The reach dynamics were evaluated differently in the two zones. In the Andes, the active strip was defined as a ratio between the total (active) and ordinary (wet) mapped river-bed width; in the lowlands, we used the nature and width of the river corridor, and the density of oxbow lakes. On the basis of these variables, a typical (statistical) longitudinal profile has been defined in all HERs with sufficient cartographic coverage (at least five reaches analysed by stream order classes). As a first conclusion, the geomorphological identity of the HER was validated on the basis of a dichotomous differentiation using four or five parameters. This result is quite clear in the Andes even at level 2, while in the lowlands the discrimination is good only at the first level, because of a much less heterogeneous landscape and a less complete database.

We present below the most significant results related to the structure and dynamics of medium-sized reaches. The parameters illustrated have been selected for their particular relevance in terms of ecological functioning: the slope determines hydraulic conditions and

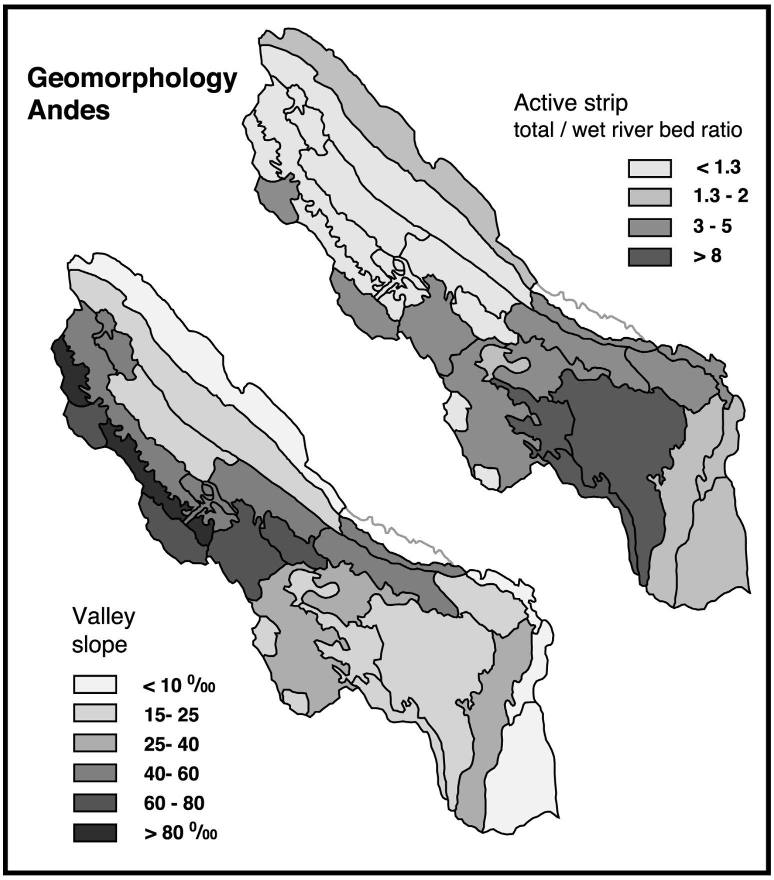

Fig. 5.4 Hydro-ecoregional pattern of the valleys' morphodynamics in the Andean zone: valley bottom slope (m km^{-1}) and active strip ratio (total bed width/wet width). Average values by hydro-ecoregion of the third and fourth order reaches characteristics, calculated from topographic maps; data from Gourdin (1997).

habitat structure; the active strip width reflects the sediment discharge and thus the fluvial dynamics and bed instability during high flow; for lowlands rivers, the sinuosity controls the physical habitat heterogeneity, and the corridor reflects both the dynamics and the connectivity with the terrestrial ecotone. Map layouts are justified by the number of measured (5–30 by HER) reaches and their good spatial distribution.

Andes The valley slopes define a very clear regional structure (Fig. 5.4). On the Amazon facing side of the Cordillera, a regular decrease is observed from the central axis to the subandean zone, and significant differences are noted at the HER-2 level within both Yungean and subandean regions (Ya and Sa). In the Rio Grande basin, facing the Chaco, the structure is different as the Yungean valleys (Yc) are steeper than the more internal semiarid ones (Va). The latter also have much more gentle slopes than the dry valleys of the Rio Beni basin (Vs). For the active strip, the main difference occurs between the humid and dry domains, as the river beds are much more unstable in the latter. But in the humid domain, the eastern Yungean regions (Ya-co, Ya-ce), and the lower subandean ones (Sa-b, Sa-h, Sa-s) also present wider active strips. Thus, if the slope is directly related to the geomorphological structure, the active strip mainly reflects the climatic dichotomy, and secondarily regional differences in rock hardness.

Lowlands The valley slopes (Fig. 5.5) distinguish first the Llanos from the Brazilian shield, and inside this latter the southern regions (Ea) from the northern peneplains and depressions (Eb-ph, Eb-da). This typology is completed using the width of the active corridor and the sinuosity that clearly set apart the Amazonian Llanos (La) from all the Beni

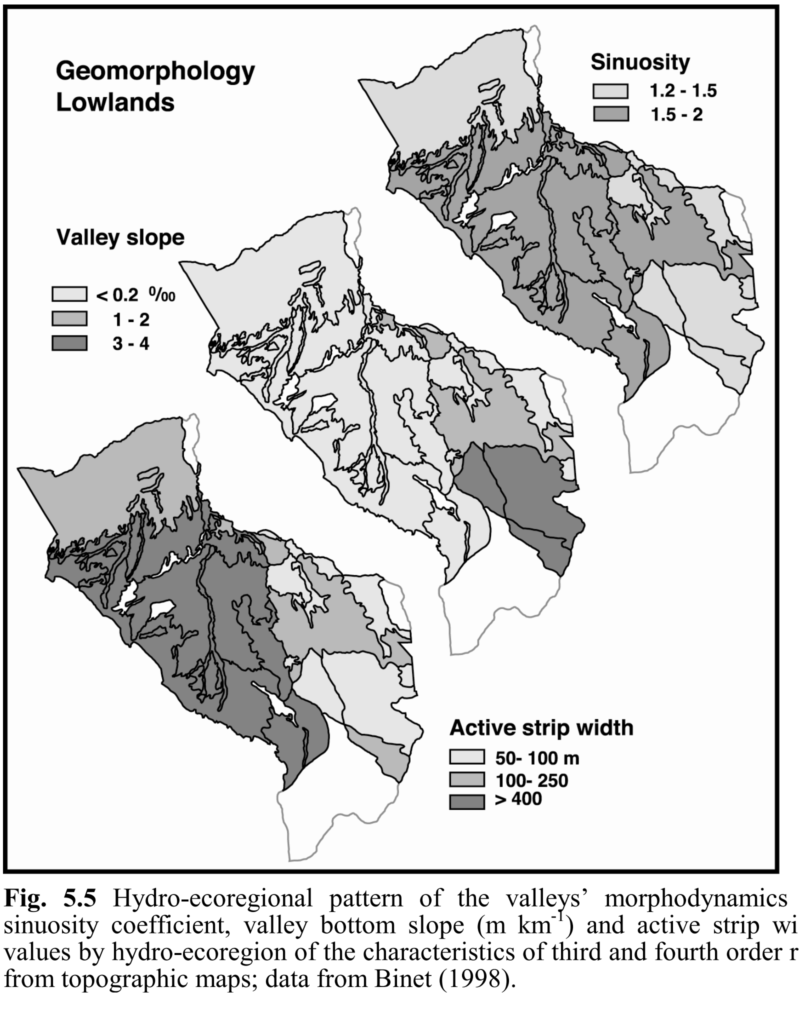

Fig. 5.5 Hydro-ecoregional pattern of the valleys' morphodynamics in the lowlands: sinuosity coefficient, valley bottom slope (m km^{-1}) and active strip width (m). Average values by hydro-ecoregion of the characteristics of third and fourth order reaches, calculated from topographic maps; data from Binet (1998).

Llanos (Lb, Ll, Ls) where dynamics and connectivity are higher, probably because of unconsolidated alluvial formations and intense flooding in these regions. On the Brazilian shield, the rivers of the northern peneplain (Eb-ph) exhibit wider corridors than in the surrounding regions, but the reason for that is unclear. The few rivers of the eastern serranías of the Chaco (Lc-sm) also have active mineral strips that can be related to the general instability of the river beds in the arid regions.

Hydrochemistry

We used the data collected and published by Guyot (1993) during the PHICAB programme, and all corresponding methods and results are available in Guyot's book. The database analysed here includes more than 260 sampling points, with as many as 2400 analyses for some parameters; we used only data from small- or medium-sized basins, generally occurring entirely within a single HER, or in some cases encompassing a maximum of two HERs. The Brazilian shield and the Chaco were excluded from the analysis due to insufficient data. Five parameters were selected for their high biological relevance: conductivity and calcium content for the global productivity, and pH and suspended solids (SS) which may act as limiting factors for aquatic communities; high SS contents are also indicative of river-bed instability affecting benthic assemblages (see Wasson *et al.*, 1998), and we added water colour as an indicator of the dissolved organic matter (DOM) content, another important parameter of the ecological functioning.

The regional differentiation on these five parameters is very clear from the scale of the geoclimatic domains down to the HER-2 level (Fig. 5.6). In the Andes, rivers have generally higher values for conductivity, calcium, pH and SS in the dry domain than in the humid one, and the most salient characteristic is the huge mean SS content of the rivers flowing through the dry (Vs) and lower semiarid valleys (Va-b), suggesting a strong limitation of the biological communities in these regions. These values are fairly reliable for the Vs region, as they are based upon 229 samples from 39 sites, with a mean value of 11.9 $g\ l^{-1}$. For the Va-b region, the data are less reliable for small basins with only 12 analyses for six sites, but our estimate for the region is based upon data collected at the output of the Andes from the main collector of these valleys (the Rio Grande at Abapo, 71 samples over 10 years), leading to a mean SS content of 5.9 $g\ l^{-1}$.

When looked at more closely, almost all HER-2s have their own hydrochemical identity. Some notable examples in the Amazonian Yungas are, the acidic pH of the lower region (Ya-b) due to humic soils (Rivera *et al.*, 1996) and the higher SS in the small semi-humid ones (Ya-s) due to greater erosion caused by aggressive land use for the coca culture. The "Chaco" Yungas (Yc) are also very distinct from the Amazonian ones, and noticeable differences appear at the HER-2 level in the semiarid valleys (Va-b, Va-i) or dry mountains (Ms-a, Ms-m). The factors governing regional hydrochemical characteristics seem to be, in order of importance: climatic conditions, geology, and soils. In the Llanos, the northern region (La) differs from the others for each parameter, thus confirming its particular identity. In the central zone, all the HER-2s present at least one important characteristic, the most obvious being the difference between the acidic waters of the northern savanna region (Ll) and the neutral waters of the central region (Ls-ai), as could be expected on the basis of the soil characteristics that led to their differentiation. Colour is an interesting parameter highlighting the higher DOM content of waters in the savanna regions, which could be related to the higher connectivity of the rivers with the surrounding wetlands and fluvial corridors, as previously assumed on the basis of the geomorphological study. On the humid side of the Andes, with tropical forest cover, the colour increases from the high Yungas to the subandean regions, suggesting a relationship with the mean hillslope gradient of the

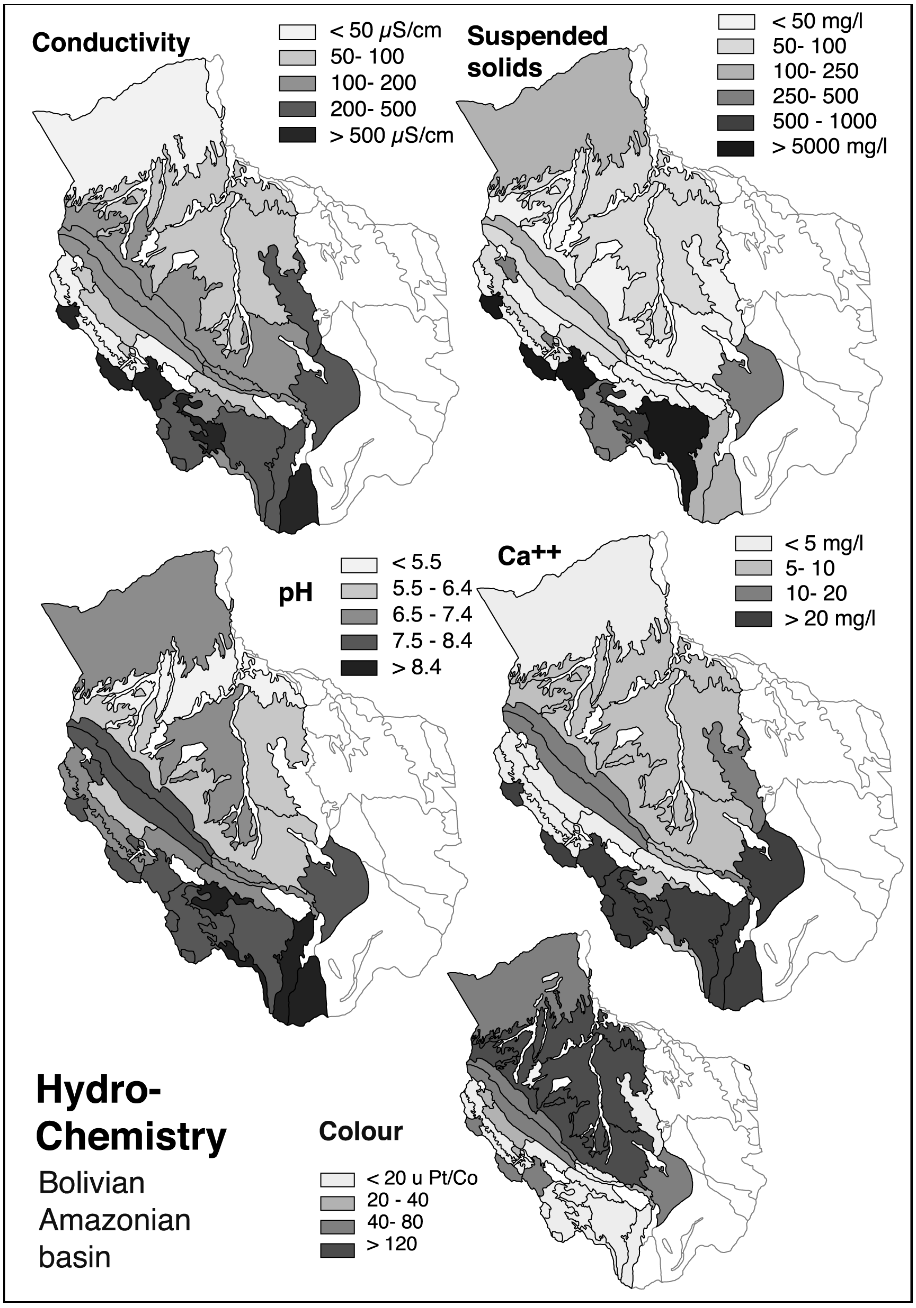

Fig. 5.6 Hydro-ecoregional pattern of river chemistry in the Bolivian Amazonian basin: conductivity (μS cm^{-1}), suspended solids (mg l^{-1}), pH, calcium (mg l^{-1}) and colour (Pt/Co units). Average values by hydro-ecoregion for endogenous basins (see text). Data from Guyot (1993).

different HERs; thus the interaction between the geomorphological structure and the vegetal cover could regulate the DOM content. In a former study of the regional DOC pattern in this basin, Guyot & Wasson (1994) hypothesized about the important role played by the connectivity of the lowlands rivers, but the possible importance of the geomorphological structure in the Andes has been overlooked.

Stream ecosystem structures

Ecological data were collected for 25 stream sites (24 sites for fish) representative of eight HER-2s of the Andean zone. As the purpose was to evaluate the relevance of the regional framework, independent sites (i.e. situated in different basins without any upstream–downstream relationship) were chosen having similar width (20–50 m at bankfull discharge) to avoid the effect of longitudinal variations. All the streams are undisturbed at the local scale (without direct contamination or physical alteration), but we cannot avoid completely the effects of traditional agriculture, which include water abstraction for irrigation in the driest region (Va-b). As sampling is almost impossible during high flow, the sites were sampled during the dry seasons (1997–1999) and data are representative of low flow conditions. The basins of the studied sites are generally limited to a single HER-2, or in some cases partially encompass an adjacent HER-2 belonging to the same HER-1; these sites were grouped for analysis according to the HER-2 in which they lie. But four stream sites of the Amazonian Yungas (Ya-a), whose basins come from the glacial Cordillera (Cg), were grouped separately for the analysis (Ya+Cg) to evaluate the possible differences between endogenous and heterogeneous streams. At each site data were taken on physical and chemical parameters, fish and invertebrates. Physical parameters are stream slope, proportion of lentic units, global stability evaluated by the Pfankuch index (Collier, 1992; Pfankuch, 1975), substrate characteristics (granulometry, porosity and mobility), and water temperature. Chemical parameters include conductivity, suspended solids (SS), pH, alkalinity, calcium and potassium. Fish communities were sampled at each site by electrofishing (15 sampling points per site), a battery of nets (from 10 to 110 mm mesh size), and ichtyotoxic (rotenone) when possible. For the benthic invertebrates, six Surber samples (0.1 m^2) representative of the main habitats were collected at each site. The detailed methodology for abiotic parameters and invertebrates, together with the results obtained at 13 sites are published in Rocabado & Wasson (1999) and Rocabado *et al.* (2001). All the multivariate analyses were performed with ADE-4 software (Chessel & Dolédec, 1996). We present below the first results of the regional differences of these 25 sites based upon physical and chemical parameters and some salient examples of the characteristics of the fish and invertebrates communities.

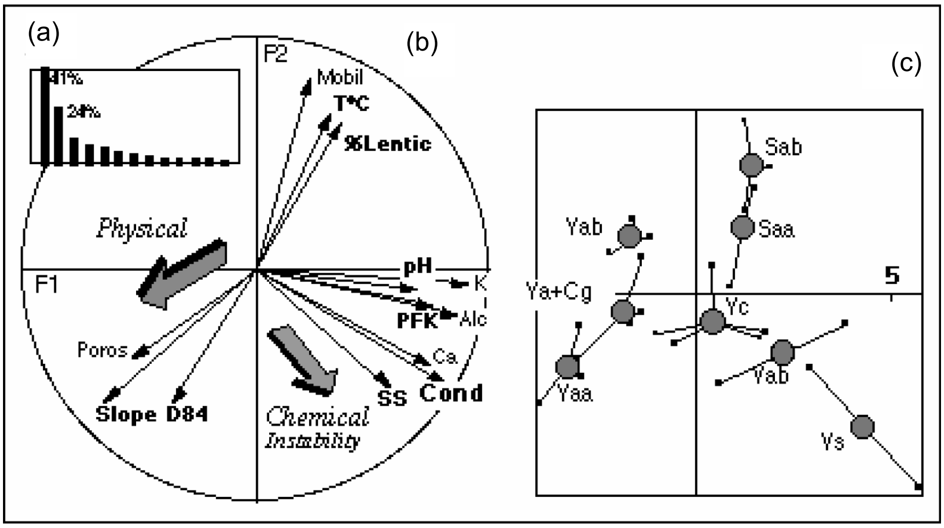

Fig. 5.7 Abiotic structure of the 25 stream sites sampled in the Andean zone: normalized principal component analysis (nPCA) of 13 physical and chemical parameters. (a) Relative contribution of the axis (eigenvalues). (b) Factorial map of the first two axis; Alc: alkalinity, Ca: calcium (mg l^{-1}), Cond: conductivity (µS cm^{-1}), D84: diameter (phi units) of the superficial granulometry 84th percentile, K: potassium (mg l^{-1}), %Lentic: proportion of lentic morphological units (pools), Mobil: ranking of substrate elements potential mobility, PFK: Pfankuch index, Poros: porosity of the substratum (%), Slope: stream slope (m km^{-1}), SS: suspended solids (mg l^{-1}), T°C: temperature in degrees Celsius. (c) site map of the first two axis; each star represents the sites (squares) grouped by hydro-ecoregions (circles projected at the barycentre of the related sites); see Table 5.1 and text for region codes.

Abiotic structure A normalized principal component analysis (nPCA) was performed for 13 physical and chemical parameters. The first two axes of the nPCA account for 65% of the total variance (Fig. 5.7(a)). The factorial map (Fig. 5.7(b)) indicates that the streams are grouped according to two independent (orthogonal) axes; the first opposing slope, granulometry and porosity with temperature, substrate instability and percentage of lentic units, is clearly related to a gradient of physical conditions; the second corresponds to the chemical characteristics and the Pfankuch index. The pattern of the sites grouped by HER-2 (Fig. 5.7(c)) reveals a satisfactory discrimination of the different regions on the basis of the abiotic characteristics of the streams. Regions are spread out over the physical axis, from the high Amazonian Yungas (Ya-a) to the subandean regions (Sa-a, Sa-b), according to a gradient of physical conditions mainly governed by the stream slope. The chemical axis clearly separates the dry and arid valleys (Vs, Va-b) with high conductivity and SS, from all the humid regions, among which the low Amazonian Yungas (Ya-b) lies apart due to a significantly lower pH. The pattern of stream instability is also interesting: the substrate mobility, estimated on the basis of size and form of the elements, is inversely correlated to the slope and thus higher in the subandean regions. But the Pfankuch index, which measures a global morphological instability, is correlated to the chemical parameters and not to the physical ones, thus indicating highly unstable river beds in the dry regions due to high sediment transport. The main conclusion here is that the abiotic conditions observed at the local scale are clearly consistent with the hydro-ecoregional structure: the physical and chemical axis of the nPCA correspond respectively to the geomorphological and climatic determinants used for the HER construction.

Biological communities: quantitative metrics The fish and invertebrate data set is still under analysis, but some consistent regional trends in diversity and density are already recognizable (Fig. 5.8). There is evidence of a very distinctive pattern between the humid and dry domains.

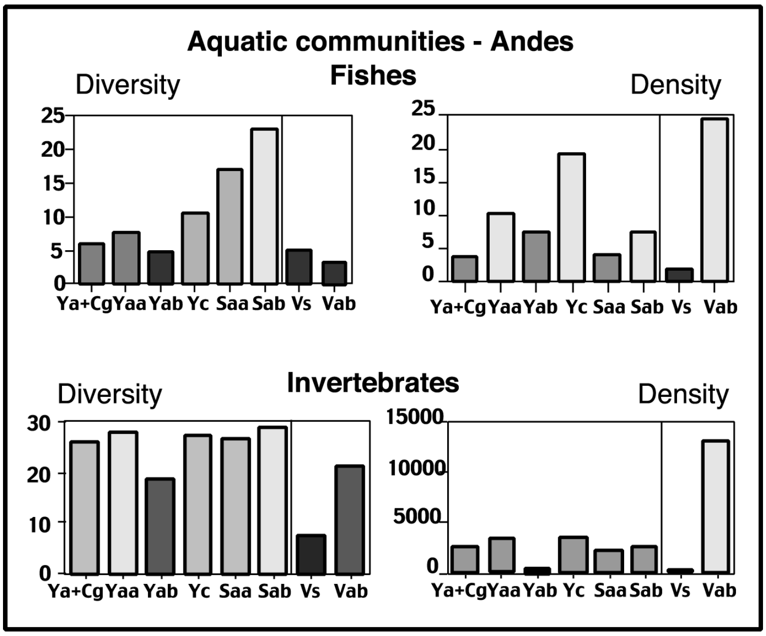

Fig. 5.8 Aquatic communities quantitative structure in the Andean hydro-ecoregions: mean values by hydro-ecoregion for four metrics measured at the stream sites. Bars with different fill colours are significantly different ($P < 0.05$) on the basis of nonparametric tests (Mann-Whitney) performed at the sample level. *Fishes*: 24 stream sites, quantitative data from 15 electrofishing points by site; diversity: number of genera; density: number of individuals 10 m^{-2} min^{-1}. ***Invertebrates*****:** 25 stream sites, six Surber samples (0.1 m^2) by site; diversity: number of families; density: number of individuals m^{-2}. See Table 5.1 and text for region codes.

In the humid domain, the most salient feature is the progressive diversification of the fish community (number of genera) from the high Yungas (Ya-a) to the low subandean regions (Sa-b), which can be directly related to the decrease in the geomorphological gradient (lower slope, higher proportion of lentic units, see Fig. 5.7). Conversely, the invertebrate diversity pattern (number of families) is fairly homogeneous, with only a slight increase in both high Yungas and low subandean. A noticeable deviation to this pattern appears in the low Yungas region (Ya-b) that presents for both communities a significantly lower taxonomic richness related to the limiting effect of the acidic pH. When looking at fish density, the regional pattern is unclear, also reflecting high variability at the local scale; the low densities observed in different HERs cannot be related to the same limiting factor, and this is not explained. The pattern of invertebrates' density is homogeneous, with the same exception of the low Yungas region where densities are lowest because of acidic pH. However, for Ephemeroptera, a positive relationship has been observed between the geomorphological gradient and the densities, confirmed by a significant correlation with the stream slope (Rocabado *et al.*, 2001).

In the dry domain, the consistent figure for both fish and invertebrates is a low biodiversity and a strong contrast between the lowest densities observed in the dry valleys (Vs) and the highest densities in the arid valleys (Va-b). These biotic structures illuminate a common limiting factor for both regions but also an important difference in terms of temporal variability of aquatic ecosystem functioning. In both regions, during high flow, the river bed instability and huge SS contents act as strong limiting factors, but during low flow the hydrological conditions are very distinct. In the dry valleys (Vs), the main water courses fed by the high cordillera maintain a sustained baseflow during the dry season, and because of their high slope, the waters are permanently turbid and river beds unstable. Conversely, rivers in the arid valleys (Va-b) have lower slopes, and during the dry season the discharge drops to a few litres per second, which is just sufficient to feed extensive pools where some species can proliferate. Thus the biological data reflect the important difference in stream ecosystem functioning, with a marked seasonality in the one case (Va-b), and permanently adverse conditions in the other (Vs).

Biological communities: qualitative structure The composition of the communities was first examined by means of correspondence analysis, and the strength of the partition assessed by discriminant analysis with a Monte-Carlo simulation test. For fish, the regional structures are very well discriminated at the HER-1 level, but the HER-2 does not show a much clearer partition. For invertebrates, the figure is more blurred. However, for both

Table 5.2 Discrimination strength of various classification factors for fish and invertebrate communities in the Andean sites: results of discriminant analysis performed over a correspondence analysis (see text). Fish—semi-quantitative data from electrofishing and net samples; invertebrates—log transformed densities from six Surber samples. % Inertia—total inertia explained by each classification. *P*—significance level (Monte-Carlo simulation) fixed at 0.05 (*), 0.01 (**), 0.001 (***), or not significant (n.s.).

Factors	No. of classes for each factor	Fish: % Inertia	*P*	Invertebrates: % Inertia	*P*
Catchment	2	11.3	***	6.6	*
Altitude	3	17.2	***	12.3	*
Altitude	6	-	n.s.	-	n.s.
Slope	3	20.5	***	12.2	*
Slope	6	32.7	**	26.1	*
Domains	3	21.2	***	15.9	**
HER-1	6	39.5	***	29.4	**
HER-2	8	46.4	***	38.3	**

communities, any regional classification (domain, HER-1 or HER-2) explains significantly more of the total inertia than any classification based on a single factor such as slope, altitude or basin, with the same number of classes (Table 5.2). Among these factors, the clear basin effect (Rio Beni *vs* Rio Grande) observed for fish is mainly a biogeographical effect, as at present these two basins are connected near the Brazilian border, at a distance of about 1000 km from the Andean piedmont. Sarmiento & Barrera (1997) have reported noticeable dissimilarities in fish fauna between the Andean basins of the Rio Beni and Rio Mamore, to which pertains the Rio Grande, and such biogeographical dissimilarities interfere with the regional effect. Conversely, to explain the regional differences in the community composition, slope is a factor much more powerful and significant than altitude which allows only the lowest sites to be distinguished from the others, as partition into six classes does not give a significant result. Thus, we can infer that the geomorphological structure used as a primary determinant for HER delineation also plays a major role in explaining faunistic patterns.

Correspondences between hydro-ecoregions and biological structures Fish and invertebrate communities present clear, and sometimes strong regional differences when taking into account a combination of density, diversity, and taxonomic composition. The distinction is good at the HER-1 level and still relevant for HER-2, at least with the quantitative metrics (density and diversity). Regional faunistic patterns are stronger for fish than for invertebrates, a result consistent with similar studies in the USA (Rabeni & Doisy, 2000; Whittier *et al.*, 1988). However, the distinction based upon the endogenous *vs* heterogeneous basins (Ya-a *vs* Ya+Cg) did not lead to a decisive differentiation at the site scale, perhaps because in the studied case the particular characteristics of the upstream HER (glacial cordillera), mainly related to stream slope, temperature and hydrological regime, is not likely to have a strong effect on the downstream characteristics. The figure would probably be more contrasted in the case of a drier upstream region, expected to strongly influence the water chemistry and sediment transport downstream.

A rather surprising result here is the low level of differentiation in the composition of the invertebrate community when compared to the strong differences observed in the abiotic structures: why does the invertebrate fauna not respond more clearly? The answer should be sought in three directions: (a) the influence of local *vs* regional factors upon invertebrate communities, (b) the taxonomic resolution and (c) the seasonal variability. For (a), a rapid survey of existing papers reveals some conflicting conclusions. Some authors found a good or fair agreement between various ecoregional classifications and invertebrate communities (Feminella, 2000; Gerritsen & Barbour, 2000; Ivol, 1998; Rabeni & Doisy, 2000; Sandin & Johnson, 2000), but in many cases the fit is poor (Hawkins & Vinson, 2000; Quinn & Hickey, 1990; Waite *et al.*, 2000; Whittier *et al.*, 1988; and see review in Rabeni & Doisy 2000). All authors emphasize the importance of local factors in structuring benthic communities. Ecoregional discrimination is significantly higher when streams of similar size are compared between ecoregions (Waite *et al.*, 2000), and obvious differences are generally noted between mountains and plains; in our study, the first condition is observed, but not the second. Nevertheless, when comparing the range of geographical variations encompassed in the Andes, the regional discrimination of the benthic communities is somewhat weaker than expected, and we suspect that other factors could have reduced the fit. For taxonomy, all the studies comparing ecoregional discrimination at different taxonomic levels concluded that the genus/species level generally improves the discrimination, although not strongly, when compared to the family level (Feminella, 2000; Hawkins & Vinson, 2000; Ivol, 1998; Waite *et al.*, 2000). But these works deal with northern countries where the fauna is well known, and it remains questionable whether the present knowledge of neotropical fauna, where many genera and species are currently awaiting detailed description, leads to the same degree of comparability of different taxonomic levels (family/genus/species) as in temperate countries. In other words, does the family level give the same degree of discrimination for fauna in North and South America? The identification at genus level, presently in progress, will help answer this question. Finally, another important bias possibly specific to the humid tropics is the high inter-seasonal variability of the stream fauna, following dry/wet climate alternations. For the few specialists of the Yungas regions, the wet and dry seasons are two distinct "faunistic worlds" (E. Dominguez, personal communication). Because sampling is impossible at most sites during high flow, we might have captured only a limited part of the invertebrate fauna, perhaps the most resilient and widespread, thus reducing its ability to discriminate hydro-ecoregional differences.

DISCUSSION AND PERSPECTIVES

We shall briefly broach four questions.

(a) Is the hydro-ecoregion approach an ecohydrological question?
(b) Does it work?
(c) What are the scientific perspectives?
(d) What is the practical interest?

Ecohydrological questions

This point refers to the specificity of running water ecosystems: water flowing in a bed, i.e. physically driven, linear, oriented, dynamic. When Hynes stated in 1975 "the valley rules the stream", the concept was rapidly raised to the basin control level by "applied" scientists of the Corvallis (Oregon) US Environment Protection Agency team (Frissell *et al.*, 1986; Lotspeich, 1980). These authors focused their approach upon the geomorphological control of running water ecosystems by nesting the physical factors in a hierarchical scheme from the basin to the instream habitat level. From here arose the idea of using an ecoregional framework to classify running waters, first developed by Omernick (1987). This approach was also advocated and developed in France in an "applied" research institute, CEMAGREF (Wasson, 1989, 1996; Wasson *et al.*, 1993). But the undiscriminating use of the term "ecoregion" (without the qualifier "aquatic" initially used by Omernick) might have blurred the concept, as in its original meaning this word referred to terrestrial ecological units principally characterized by their vegetation. In this sense, climate is seen as the main controlling factor, and physiography only as a secondary one modifying the climate (Bailey, 1996). Even if mountains and landforms are finally taken into account respectively at the third ("provinces") and fourth level ("sections") of Bailey's classification, i.e. the levels generally used to compare aquatic ecosystems, Bailey's and Omernick's ecoregions do not correspond to one another because they do not refer to the same hierarchy of controlling factors. For the same reasons, our regionalization does not coincide with the geographical classification of the "aquatic and swampy systems of Bolivia" proposed by Navarro (1999), which was mainly based upon bioclimatic factors and vegetation features.

Following the concepts of the Corvallis team, we advocate that for running waters the geophysical factors (geomorphology, geology) must be raised *at least* to the same hierarchical level as the climatic ones. For instance, we expect more similarity between mountainous running water systems over a broad climatic range than between mountain and plain systems under the same climate. This conceptual difference is strong enough to justify a specific approach exclusively dedicated to the regionalization of running waters, for which we prefer the term “hydro-ecoregion”. In this perspective, the hydro-ecoregion approach is not a mere (or one more) classification system, but relies on real ecohydrological questions dealing with the hierarchy of ecosystem controlling factors. This comes to investigating the degree of dependence between a running water ecosystem and its basin. The central questions refer less to the accuracy of the classification than to “how much” and “by means of what factors” regional features explain ecological functioning. Another important difference is that in the terrestrial approach, the vegetation itself serves as a basis to delineate ecoregions: i.e. we classify objects we can see. The figure is completely different for running waters. The regions are not based on aquatic biota but upon their potential determinants. Thus hydro-ecoregions are an hypothesis, whose validation is made *a posteriori* and independently with the challenge to relate assumed causes to observed effects. In this view, the regional framework cannot be seen as definitively fixed, and like any scientific hypothesis it might be improved by taking into account the results of the validation process.

Another misleading point is to consider the ecoregional approach as an alternative to the classical longitudinal “zonation” or “continuum” concepts to classify ecosystems and predict their biological features. In reality, the longitudinal position of a site in the hydrographic network, i.e. its size, has been recognized for half a century as the first factor governing the physical structure and biotic pattern of running waters (see review by Wasson 1989). No regional characteristic is expected to erase or even override this structure. Thus, as pointed out by many authors, a regionalization must be seen as complementary to any longitudinal classification and not as an alternative as it is sometimes depicted in the literature (Van Sickle & Hughes, 2000). The right way to assess the validity of a regionalization is to compare either sites of similar size, or the longitudinal evolution patterns between different regions. And its usefulness must be evaluated on the basis of “how much” the prediction of ecological features at a site of a given size is improved.

Does it work?

In summarizing the preceding results and comparing them to the literature referenced above, three important conclusions can be drawn. First, HERs provide a valid framework to regionalize ecologically important abiotic characteristics of running water ecosystems. In the Bolivian Amazon basin, morphodynamic and hydrochemical parameters measured at the reach scale are consistent with the geomorphological and climatic regional features. In the Andes, regions are well discriminated by the abiotic structures observed at the site scale. The predictive capacity of the HER approach is not yet evaluated but is expected to be good for a limited set of abiotic parameters. Secondly, for aquatic biota, the regional pattern is stronger for fishes than for invertebrates. This can be related to the spatio-temporal scale of the physical habitat required by each community. Fish have a greater life span, a larger body size and a greater mobility than invertebrates, so they are more dependent on the bi-dimensional (longitudinal and transversal) morphological structures and on the seasonal dynamics of habitat availability. We can infer that fish react to the inter-annual morphodynamic characteristics at the reach scale, while invertebrates react seasonally to micro-habitat structure and stability. We thus formulate the hypothesis that the broader the spatio-temporal habitat exploited by a community, the higher its dependence on large-scale physical factors. This could explain the weaker regional patterns observed for invertebrates, and we expect on this basis even weaker structures for communities of micro-organisms, as observed in the Loire basin (see Ivol, 1998). Third, we can validate the hypothesis that among the primary determinants, geophysical factors are *at least* as important as climatic factors. In the study of Andean sites, the main discrimination is given by the physical structure governed by the site gradient, even though the study area comprises two major global-scale climatic domains (Bailey, 1996), but does not encompass the major physical border between mountainous and lowland zones. In fact, we could hypothesize a higher importance of geophysical factors, but this must be validated with more biological data. However, we can note that river-bed instability, acting as a major physical control factor at the reach scale, is mainly related to the aridity, i.e. a climatic determinant.

Scientific perspectives

The first improvement of the approach would be to shift from a mere classification based upon structural parameters to a regional typology expressing the ecological functioning in relation to the controlling factors. As an example, we could combine only six abiotic and biotic functional traits to characterize the seven HERs studied in the Andes. These traits refer to physical harshness (due to slope, current velocity), chemical harshness (due to conductivity, pH, SS), instability (mainly morphological), global biological productivity, and fish and invertebrate biodiversity. Each trait can be ranked and seasonally differentiated (Table 5.3), highlighting the opposition between favourable milieus with high biological potential (Sa-a, Sa-b) and harsh systems with poor aquatic communities (Ya-b, Vs, Va-b). We emphasize the *tentative* nature of this typology, due to the limitation and incomplete treatment of the data set, but it gives an idea of what could be achieved.

A second perspective is the extension of the regionalization to surrounding basins. By its geographical position, the Bolivian Amazonian basin comprises samples of most ecoregions encountered in the inter-tropical range of the eastern side of the Andes, from northern Argentina to Venezuela; so a spatial extrapolation would be relatively easy without increasing excessively the number of HERs, at least at the first level. The methodology is solid and the only limitation concerns the geographical data availability. Such a regional framework should greatly favour the comparison of hydro-ecological studies in this zone.

Further developments concern the possibility of linking the basin and reach scales by the construction of hydro-ecoregional models. The basis for this approach derived from the conceptual scheme (Fig. 5.1) is the following: regionalization simplifies the geographical space by dividing it into homogeneous areas where some dominant physical processes are expected to govern ecosystem structure and dynamics. This stabilizes many fundamental "input parameters" for modelling, including geology and geomorphology (and thus sediment input rates), precipitation regime (and hydrological variability), hydrochemistry

Table 5.3 Hydro-ecoregional typology of running water ecosystems (*tentative*). Abiotic and biotic functional traits are ranked from very low (+) to very high (+++++); S indicates a high seasonal variation of the trait.

HER-2	Ya-a	Ya-b	Yc	Sa-a	Sa-b	Vs	Va-b
Physical harshness	++++	+++	+++	++	+	+++	+++
Chemical harshness	++	++++	+	+	+	+++++	S +++++
Morphological instability	+	+	++	++	++	+++++	S +++++
Biological productivity	++	+	+++	++	++	+	S ++
Biodiversity of invertebrates	++++	++	+++	+++	++++	+	S ++
Biodiversity of fish	++	+	+++	++++	+++++	+	+

(controlling biological productivity), etc. Thus, in each region a limited set of parameters mainly related to longitudinal variation (slope, drainage area) can emerge as powerful control variables, leading to robust statistical models allowing the prediction of the physical and chemical characteristics at the reach scale (see Cohen *et al.*, 1998). Then, the development of functional models, coupling the biological responses to the physical and chemical habitat characteristics, might enable the prediction of important biotic community features at the reach scale (Lamouroux *et al.*, 1999). This approach is still under development but could lead to integrated modelling across spatial scales.

Practical interest

The "ecoregional" approach of running waters was first developed in the USA with the aim of establishing realistic quality standards based upon regional reference conditions, and to define regionally coherent management policies (Hughes *et al.*, 1990). These objectives apply now to the European Community with the recent "Water Framework Directive" in which a similar approach is recommended. This remains the main practical application of the hydro-ecoregions. However, with our experience in Bolivia, we can point out two major outcomes for developing countries. First, the top-down approach may save time and money in achieving a preliminary description of the characteristics and potential of poorly known ecosystems. A limited panel of sampling sites representative of the main HERs might give a fairly good preview of the existing conditions, allowing further spatial extrapolation by means of hydro-ecoregional modelling. Secondly, cartographic representation of the results is a powerful communication tool for national decision makers. An attendant regionalization of anthropogenic activities and colonization dynamics, presently in progress, will reveal rising "water problems" related to both resource management and ecosystem conservation. We hope that this integrated approach will help Bolivian leaders in establishing sustainable development policies taking into account the regional potentialities and vulnerabilities of aquatic ecosystems.

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