

Primary Research Paper

Trophic levels and functional feeding groups of macroinvertebrates in neotropical streams

Sylvie Tomanova^{1,2,*}, Edgar Goitia³ & Jan Helešic¹

¹Laboratory of Running Waters Biology, Department of Zoology and Ecology, Masaryk University, Kotlářská 2, 61137, Brno, Czech Republic

²UR 131 Institut de Recherche pour le Développement, ULRA UMSS, Cochabamba, Bolivia

³Unidad de Limnología y Recursos Acuáticos (ULRA), Universidad Mayor de San Simón, Cochabamba, Bolivia

(*Author for correspondence: E-mail: sylvatom@seznam.cz)

Received 7 March 2005; in revised form 16 June 2005; accepted 22 July 2005

Key words: diet, feeding groups, macroinvertebrates, neotropical streams

Abstract

Feeding strategies are typical traits reflecting the adaptation of species to environmental conditions. This concept is currently developed in some water quality systems (e.g. Index of Trophic completeness) and the structure of functional feeding groups (FFGs) could form part of a unified measure across communities differing in taxonomic composition. However, in South America, information about the FFG classification of invertebrates in streams is almost absent and existing studies using FFG structure follows classification from North America. But even taxonomically related species may have different diets in tropical and temperate areas and therefore, studies about FFG structure in neotropics could be biased. For this reason, we determined diet composition, trophic level and FFGs, using gut contents analysis and mouthpart observations of 49 macroinvertebrate taxa (mostly at genus level) from neotropical streams. We observed that practically all macroinvertebrates fed upon fine detritus which indicates the importance of this food resource in neotropical streams. As the assignment to a single FFG does not accurately reflect the functional profile of taxa, we transcribed the affinity of taxa to each FFG using fuzzy codes. Finally, we published the coding of diet composition and FFG of the taxa examined, which could be used in future community analyses of lotic ecosystems in the Neotropical zone.

Introduction

Tropical rivers support a rich but incompletely known biota. Therefore, the principal topic of studies in the Neotropical zone is biodiversity, taxonomic descriptions and the distribution of new species (Jackson & Sweeney, 1995). Besides, an important effort should also be made to develop realistic models of the structure and functioning of natural tropical streams. Since ecological information about tropical species is very scarce, fundamental research on this subject is necessary.

Ecological functions can be described by a multitude of general biological traits that reflect the adaptation of species to environmental conditions (Townsend & Hildrew, 1994). Feeding strategies are typical traits reflecting the adaptation of species and they could form part of a unified measure across communities differing in taxonomic composition (Statzner et al., 2001). Functional feeding classification of aquatic organisms enhances the knowledge of trophic dynamics in streams by simplifying the benthic community into trophic guilds – functional feeding groups (FFGs) (Cummins, 1995). In the temperate

zone, the pattern of FFG distribution has been related to the environmental gradient in the river (River Continuum Concept – Vannote et al., 1980) and is currently used in some water quality systems (e.g. Index of Trophic completeness – Pavluk et al., 2000; Bij de Vaate & Pavluk, 2004). In South America, exact information about the FFGs of aquatic invertebrates is lacking and the existing studies using FFGs are mainly based on the North American classification (e.g. from Merritt & Cummins, 1996). However, the highly flexible life histories and mobility that seem to characterize many neotropical stream taxa may well influence their flexibility in obtaining food resources (Covich, 1988). This can produce significant differences in FFG classification because some neotropical taxa may not feed like the majority of their congeners inhabiting the temperate zone, and therefore should not be placed in the same FFG. Consequently, the resulting FFG structure of neotropical communities based on Merritt and Cummins's FFGs (e.g. Poi de Neiff, 1990; Callisto et al., 2001; Fossati et al., 2001; Buss et al., 2002) could be biased.

In this study, we examined general feeding habits (gut contents) of 49 taxa (mainly identified to genus level) from four neotropical streams in order to determine (1) their trophic levels and (2) their allocation into functional feeding groups. Average diet composition and FFG classification of taxa were completed using existing knowledge from available literature, and resulting information was transcribed to fuzzy codes. The final

results of the present study provide, to our knowledge, the first published database which could be used in future community analyses of lotic ecosystems in the neotropical zone.

Materials and methods

Aquatic insects were collected from four rivers in the foothills of the Bolivian Andes, department of Cochabamba, Bolivia (Navarro & Maldonado, 2002). All streams belong to the Ichilo–Chapare basin, characterized by heavy rainfall of over 1800 mm/year during the dry season, and over 5000 mm/year during the wet season from December to March. All sites are headwater streams and are characterized by steep slopes, fast currents, a dominant coarse substrate and dense riparian vegetation (Table 1).

The benthic macroinvertebrate fauna was sampled during the dry and wet season. For each study site and sampling occasion, qualitative samples (5 min of kicking – net) were taken from riffles and pools (one sample per habitat). The samples were preserved in 4% formaldehyde. In the laboratory, the samples were washed and all macroinvertebrates were sorted under a stereoscopic microscope. The individuals were identified to the lowest possible taxonomic level (mostly genus) using the available keys of Fernández & Domínguez (2001), Roldán (1996), and Merritt & Cummins (1996). Because of the currently limited taxonomic knowledge of neotropical taxa, identification of

Table 1. Characteristics of the sampling sites

	RONCO	LIMA TAMBO	CRISTAL MAYU	AVISPAS
Altitude (m a.s.l.)	1807	1120	494	399
Distance from source (km)	9.7	3.3	4.1	6.0
Slope (%)	12.9	14.4	7.4	9.5
Discharge/dry season (m)	0.5	0.3	0.4	0.5
River width (m)	4–8	4.3–6	3.7–6	5.0
Temperature (°C)	15.6–16.05	17.4–19.8	21.3–21.6	22.2–22.3
Oxygen (mg L ⁻¹)	7.0–8.2	8.2–8.1	8.0–8.8	10.8–9.0
pH	7.6–7.1	6.35–7.1	8.5–8.4	7.12–7.4
Maximum substrate size	Large cobble	Small cobble	Small cobble	Small cobble
First dominant substrate size	Small cobble	Coarse/Very coarse gravel	Coarse gravel	Very coarse gravel
Second dominant substrate size	Very coarse gravel	Medium/Coarse gravel	Medium/Coarse gravel	Medium/Coarse gravel

When two values occur: first – dry season, second – wet season.

larvae to species level is practically impossible. However, previous studies of Dolédec et al. (2000) and Gayraud et al. (2003) showed that the identification to species level was not necessary for studies on functional diversity and therefore, in our case, we considered the genus level as sufficient.

The gut contents of 1–5 individuals of the same genus, were pooled and homogenized, and then studied using the transparency method described in Tierno de Figueroa et al. (1998). The sets of slides were prepared from larvae collected from each sample. The proportion of each food item in the guts was estimated from the relative area of the particles in 10 randomly chosen points on each slide (magnification at 100× or 400×). Eight categories of food resource were recognized (abbreviations in parentheses): sediment particles (S.P), fine detritus < 1 mm (FPOM), coarse detritus > 1 mm (CPOM), microphytes (MiPh), macrophytes (MaPh), dead animals (presumed terrestrial, DA), microinvertebrates (MIIn) and aquatic macroinvertebrates (MAIn). Furthermore, the mouthpart morphology of each taxon was observed and documented.

Since several taxa had very low abundance and/or were absent from some rivers, seasons or habitats, our data were incomplete for performing a between analysis, i.e. analysis of dietary differences between rivers, seasons or habitats. To determine the general feeding habits of each taxon, the proportions of ingested food items for each accessible combination (River * Season * Habitat) were used to compute a mean for each river. Then, we averaged all rivers where the taxon was present. Analysis of diet difference among all taxa was performed using non-centered PCA. Subsequently we applied a cluster ordination to the PCA results in order to determine the groups of taxa with similar dietary habits.

The allocation of each taxon to the FFG depended mainly on the size, type and proportion of food items in gut contents (Cummins, 1973). Our own observations of feeding behavior during sampling and the observations of the mouthpart morphology in the laboratory were also helpful to FFG determination (e.g. presence of brushes of scrapers, fine hair fringes of filterers, or dagger-like teeth on the maxillae of predators; for more details see Palmer et al., 1993b and Wichard et al., 2002). Previous FFG allocations from literature were also

consulted (Merritt & Cummins, 1996; Bello & Cabrera, 2001; Graça et al., 2001; Polegatto & Froehlich, 2003; Molina, 2004) and included in the final results. The FFG affinity as well as the diet composition were transcribed into fuzzy codes because this technique helps to compensate for different types and levels of information (Chevenet et al., 1994). We used a scale from 0 to 3 in the following way: 0 – no affinity of taxon to food item or feeding group, 1 – weak affinity observed or affinity previously mentioned in literature but not observed, 2 – medium affinity observed, and 3 – strong affinity observed. For more details about fuzzy coding methodology of macroinvertebrate traits, see e.g. Tachet et al. (1994), Usseglio-Polatera (1994).

Multivariate analyses and graphical outputs in this paper were computed with R and ADE-4 softwares (Ihaka & Gentleman, 1996; Thioulouse et al., 1997), available free at <http://pbil.univ-lyon1.fr>.

Results

To characterize general feeding habits of studied taxa, the average percentage of each food type was computed for the 49 analyzed taxa (life stage distinguished) (Table 2). However, the low abundance and frequency of some taxa in samples did not allow an accurate analysis. Nevertheless, we published all the results in the furtherance of future complementary studies. Sediment particles, fine detritus and microphytes were the most frequently ingested items for practically all taxa examined. Macroinvertebrates and coarse detritus > 1 mm were less ingested, and finally, macrophytes, dead animals or microinvertebrates were the food items rarely found.

The F1 and F2 axes of PCA, performed on variables listed in Table 2, described respectively 61.82 and 17.89% of total inertia (Fig. 1a). The proportions of macroinvertebrate prey, fine detritus, and sediment particles best explained the discrimination of taxa on the F1 axis (Fig. 1b). On the F2 axis, the proportion of microphytes in the diet was the most discriminating factor. Consequently, we observed a clear separation of predatory taxa on the positive part of the F1 axis, and a separation of Hydroptilidae, which consumed exclusively microphytes, on the positive part of F2 axis (Fig. 1c).

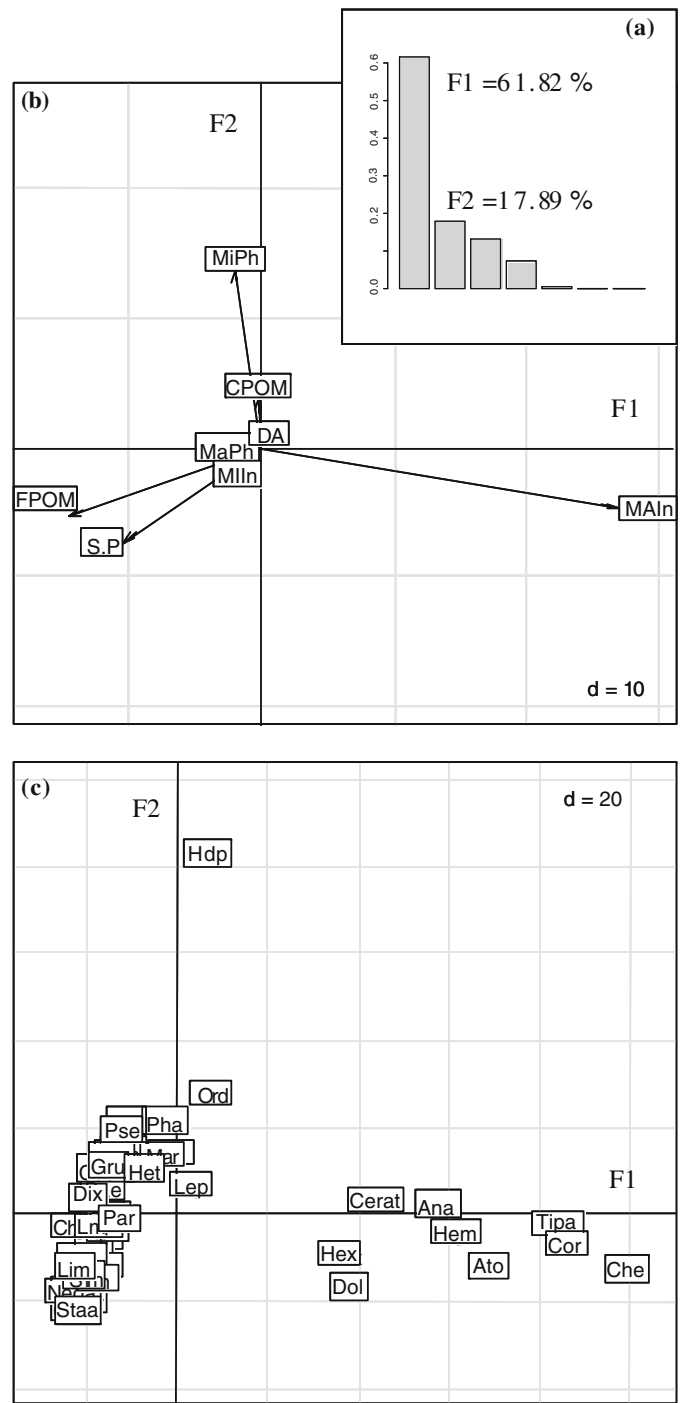


Figure 1. Principal correspondence analysis (PCA) of diet composition of the 49 analyzed neotropical taxa. (a) Histogram of eigenvalues, (b) position of food items at the F1 and F2 axes, (c) distribution of neotropical taxa at the F1 and F2 axes (see Table 2 for food items and taxa labels).

Since the majority of taxa showed a great affinity to fine detritus and sediment particles, they were grouped together on the negative part of the F1 axis. The cluster ordination depicted in Figure 2 shows a clearer separation of those taxa. We can distinguish three principal groups (I–III) and eight subgroups. Group I is composed of taxa with a high affinity to macroinvertebrate prey. The proportion of this food item in the guts was > 80, 80–50 and < 50% in the I.A, I.B and I.C subgroups, respectively. Group II includes most of the taxa, which are separated into three subgroups, all characterized by a high affinity to fine detritus. Taxa of the II.A subgroup did not usually ingest microphytes. The taxa of the II.B subgroup ingested between 0 and 10% of microphytes, and finally, this food resource represented about 10–20%

of the diet of the II.C subgroup. The third group presents the highest within-group variability in terms of food proportions in the diet. The separation of Hydroptilidae is explained by their food specialization (about 90% of microphytes). Despite this, we included the Hydroptilidae in the III.A subgroup with taxa whose diets were composed of > 25% of microphytes. The last subgroup, III.B, is mainly constituted of taxa with a high affinity to particulate organic matter, and three genera of this subgroup (*Leptonema*, *Smicridea* and *Marilia*) also showed some affinity to macroinvertebrate prey.

A brief summary of the taxa affinity to trophic levels is represented in the right part of Figure 3. We state that omnivory, broadly defined as feeding on more than one trophic level, is a common feature of most taxa. In the left part of Figure 3, we

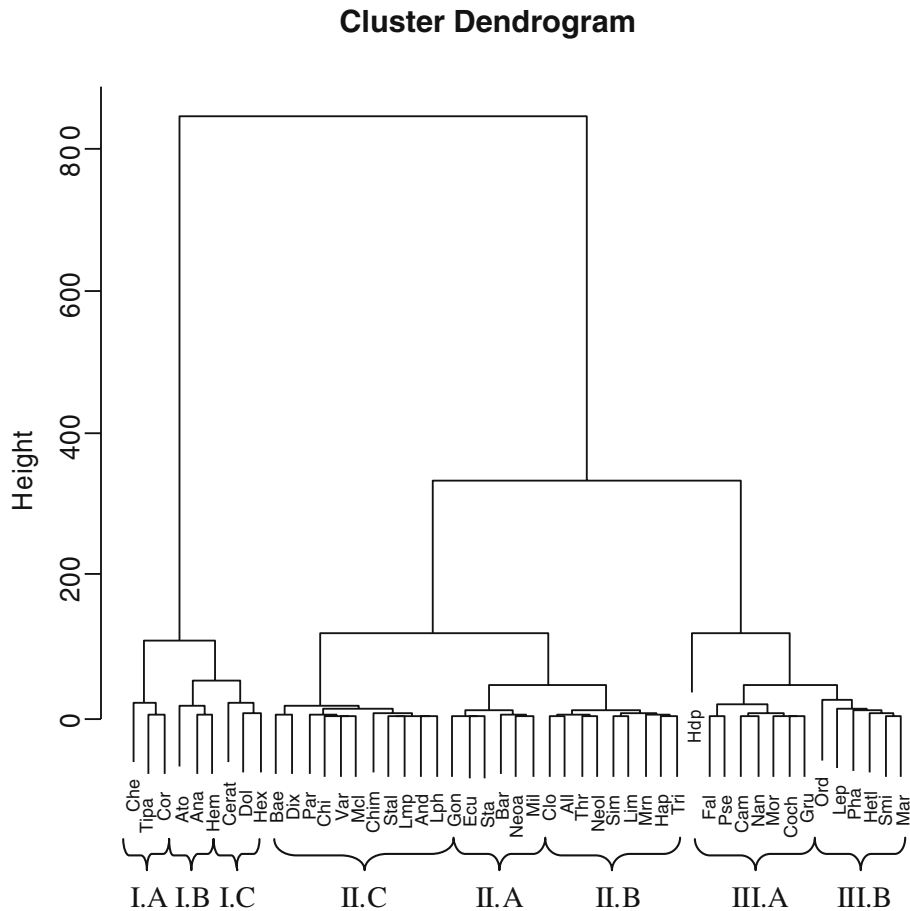


Figure 2. Cluster ordination of taxa based on the PCA results of their diet composition (see Table 2 for taxa labels). For more descriptions, see text.

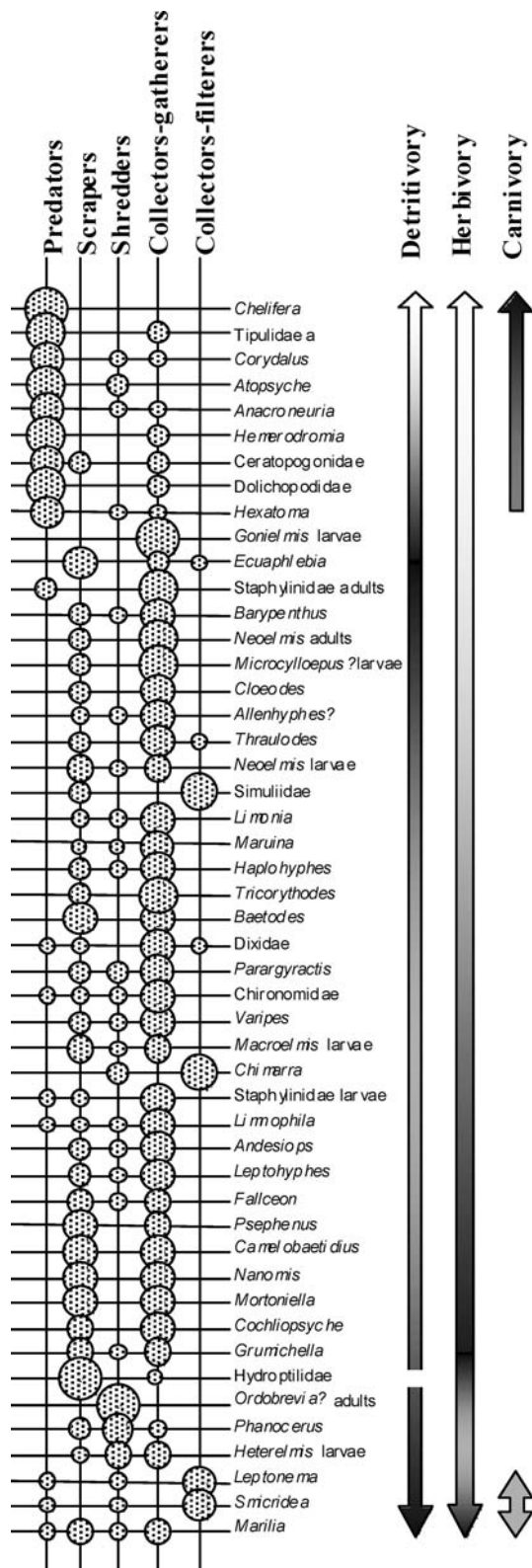


Figure 3. Brief summary of taxa affinity to different trophic levels (right part: black color – high affinity, white color – no affinity); and the allocation of taxa to functional feeding groups (FFGs) (left part: the larger size of point, the higher affinity to the FFG).

present the affinity of each taxon to functional feeding groups. This is the final result, combining our analysis and the available information of FFG from the literature (see Materials and methods). Most taxa were assigned to more than one FFG. Collectors-gatherers and scrapers were the most frequent groups. Approximately 1/4 of the taxa were determined as predators (engulfers or piercers) with a slight affinity to collector-gathering feeding activity. Some taxa had a slight affinity to the shredder feeding group. Collectors-filterers were rarely assigned but often with a high affinity. The numerical outputs of Figures 2 and 3 are presented in the form of fuzzy codes (as in Tachet et al., 1994 and Usseglio-Polatera, 1994) in Appendix 1. Despite its omnipresence in gut contents (Table 2), sediment particles were not coded as food resource for the majority of taxa (P. Usseglio-Polatera, pers. communication).

Discussion

The studies reviewed in Covich (1988) suggest that neotropical food webs in small streams are dominated by generalist consumers. Our study showed that the majority of examined taxa are able to occupy at least two trophic levels. The relative flexibility in trophic levels could reduce niche overlap among and within species and therefore, decrease the inter- and intraspecific competition (Woodward & Hildrew, 2002). Moreover, in unpredictably disturbed streams in terms of discharge, the supply and persistence of a particular food item is very variable. Hence the ability to exploit changing resources may potentially maintain population stability against natural fluctuations (Hart & Robinson, 1990). Indeed, the generalist feeding habit in the tropics is not surprising because it is considered as common strategy among lotic macroinvertebrates (various citations in Mihuc, 1997). Probably, this diet flexibility might contribute to an increase in the survival ability, and may have facilitated the

spatial colonization of aquatic insect species throughout the world.

In accord with Palmer et al. (1993a), we observed a common affinity of taxa to fine detritus, indicating the importance of this food resource and a collector-gatherer activity of organisms in neotropical freshwater ecosystems. A community dominated by taxa with high affinity to the same food resource implies less inter-specific competition for the resource, and hence a relatively high resource availability. Leaf decomposition to fine detritus in warm tropical streams is fast (Dudgeon, 1982 in Covich, 1988; Mathuriau & Chauvet 2002; Dobson et al. 2003) and continuous throughout the year. Consequently, fine detritus should be omnipresent and abundant in neotropical freshwater ecosystems. This indicates that the occurrence of this food item in the guts is principally due to its high availability in the habitat (Allan, 1982; Allan et al., 1987; Henriques-Oliveira et al., 2003) rather than to feeding specialization. However, the high consumption of fine detritus may be also explained by other factors related to the collector-gatherer strategy. All streams studied in this paper are subjected to high hydraulic stress, especially during the wet season when the discharge (related to rainfall) changes unpredictably. Following the River Habitat Templet concept (Townsend & Hildrew, 1994), the macroinvertebrates inhabiting this environment should develop the specific energy-saving adaptations (behavioral, morphological, etc.) that increase their probability of survival and reproduction. The feeding strategies of scrapers, predators and shredders involve a higher mobility (active searching for food) or visiting unstable substrates (shredders in settled leaf litter), and thus higher exposure to the flow and finally higher risk of drift. We suggest that these strategies could be unsuitable for invertebrates living in frequently and unpredictably disturbed streams. In contrast, organisms may adapt a collector-gatherer feeding strategy in order to avoid the constraints of fast currents, as predicted by Lamouroux et al. (2004). In addition, Wallace et al. (1999) have demonstrated that fauna of bedrock streams with storm discharge shows a stronger relation to fine benthic organic matter than to leaf litter.

Authors who have studied the FFG structure have normally assigned taxa to a single category of FFG (e.g. Poi de Neiff, 1990; Wallace et al., 1999;

Callisto et al., 2001; Buss et al., 2002; Miserendino & Pizzolón, 2004). Following this methodology, several authors have suggested that shredder species are practically absent in tropical streams (citations in Dudgeon, 2000; Buss et al., 2002; Dobson et al., 2002). However, Dudgeon (2000) has proposed that this may reflect trophic flexibility and hence FFG misclassification. For example, Molina (2004) has examined the diet of *Andesiops* (Baetidae) in cold rivers from Bolivian high mountains and stated that particulate organic matter represents an important part of its diet. However, during this study we did not find particulate organic matter in the diet of *Andesiops*. Actually, the role of physical fragmentation and microbial activity in our rivers should be more important than in high mountain rivers, and consequently the litter breakdown process should be faster (Irons et al., 1994; Mathuriau & Chauvet, 2002; Dobson et al., 2003). This may decrease the availability of CPOM, and increase the availability of FPOM to such an extent that it is preferable for *Andesiops* to behave as collectors-gatherers and not as shredders. Then, the same taxon, with the same mouthpart morphology, can behave as shredder or collector-gatherer depending on different environmental circumstances, and therefore a misclassification of FFG is possible.

Many studies using FFG structure of neotropical communities (e.g. Poi de Neiff, 1990; Callisto et al., 2001; Fossati et al., 2001; Buss et al., 2002) are based on trophic information from North America, i.e. from Merritt & Cummins (1996). Of the 49 taxa studied here, only 24 could be assigned to one or two feeding groups according to the Merritt & Cummins's key (Appendix 1). We found that the assignment of 5 of these 24 taxa differed from our results. In the diet of Staphylinidae (adults and larvae) and *Limnophila* (Tipulidae), previously assigned as predators, we found no macroinvertebrate remains. Furthermore, *Marilia* (Odontoceridae) and *Limonia* (Tipulidae) have been previously determined as shredders, but particulate organic matter did not occur in their gut contents. As mentioned before, this could be simply the result of local environmental conditions. As the purpose of this work is to determine general FFG affinity of taxa, we completed our data with currently available information. We even retained the information from North

America, and expressed it as a minor affinity of the taxa, representing a potential feeding behavior rather than a confirmed reality (Fig. 3, Appendix 1). Nonetheless, we suggest that future studies on feeding habits of these and other taxa from the neotropical zone are needed to complement our results and clarify the observed differences.

Palmer et al. (1993a, b) stated that FFG affinity cannot be distinguished on the basis of gut contents, and that mouthpart morphology and feeding behavior are better indicators of FFG. In contrast, we are convinced that the FFG determination based mainly on the mouthpart morphology can yield erroneous results. If the mouthpart morphology is quite similar within a family, taxa of this family, although inhabiting different climatic zones, would be classified in the same FFG. However, as discussed before, taxa assigned to a particular FFG in the temperate zone may behave differently under tropical environmental conditions because of different energetic advantages. We consider that gut content analysis is very important for accurately determining the role of taxa in ecosystem functioning, such as their FFG affiliation. Alternatively, the direct analyses of invertebrate diets could better indicate the river functioning (e.g. the importance of some energy sources) than simple FFG analysis of macroinvertebrate communities (see Plaque et al., 1998; Rosi-Marshall & Wallace, 2002).

Chevenet et al. (1994) suggested that the assignment of a taxon to a single functional category can lead to inaccurate characterization of biological/ecological taxa profiles. As a function of availability of food resource, it is evident that diet composition can vary between rivers, seasons and habitats (e.g. Sedlák, 1983; Palmer et al., 1993a; Teslenko, 1997; Plaque et al., 1998; Díaz Villanueva & Albariño, 1999; Albariño, 2001 etc.). Macroinvertebrate taxa seem to have a quite flexible feeding behavior, and their grouping into a single FFG can be idealistic. In this case, the technique of fuzzy coding can be more appropriate. This procedure has commonly been accepted for coding numerous species traits in the temperate zone, such as 'food composition' and 'feeding habits' among others, which have already been used to compare the aquatic communities at a large scale (e.g. Charvet et al., 2000; Gayraud et al., 2003; Lamouroux et al., 2004; Statzner et al.,

2004). Thereby, in Appendix 1, we describe the general profiles of taxa which could be used to analyze the functional aspect of communities in neotropical rivers (see Chevenet et al., 1994). As we used the same methodology of coding as the authors from France, the study on FFG organization between tropical and temperate rivers should be possible. However, the present fuzzy coding is the first published version, and can change in the light of new studies in the neotropical zone.

Acknowledgements

We are grateful to Pablo Tedesco, Thierry Oberdorff and two anonymous reviewers for comments that significantly improved the manuscript; to Marinely Bustamante, Nadezhda I. Guevara and Krisna B. Carrasco for helpful work in the laboratory. This paper is an outcome of the financial and scientific collaboration between the Masaryk University from Czech Republic, the Universidad Mayor de San Simón from Bolivia and the Institut de Recherche pour le Développement (IRD) from France. The final version of this paper was supported by project MSM 0021622416 and Grant No. 206/02/0902 from the Czech Grant Agency.

References

- Albariño, R. J., 2001. The food habits and mouthpart morphology of a South Andes population of *Klapopteryx kuscheli* (Plecoptera: Austroperlidae). *Aquatic Insects* 23: 171–181.
- Allan, J. D., 1982. Feeding habits and prey consumption of three setipalpiid stoneflies (Plecoptera) in a mountain stream. *Ecology* 63: 26–34.
- Allan, J. D., A. S. Flecker & N. L. McClintock, 1987. Prey preference of stoneflies: sedentary vs mobile prey. *Oikos* 49: 323–331.
- Bello, C. L. C. & M. I. F. Cabrera, 2001. Alimentación ninfal de Leptophlebiidae (Insecta: Ephemeroptera) en el Cano Paso del Diablo, Venezuela. *Revista de Biología Tropical* 49: 999–1003.
- Buss, D. F., D. F. Baptista, M. P. Silveira, J. L. Nessimian & L. F. M. Dorville, 2002. Influence of water chemistry and environmental degradation on macroinvertebrate assemblages in a river basin in south-east Brazil. *Hydrobiologia* 481: 125–136.
- Callisto, M., C. E. Moreno & F. A. R. Barbosa, 2001. Habitat diversity and benthic functional trophic groups at Serra do Cipo, southeast Brazil. *Revista Brasileira de Biologia* 61: 259–266.

- Charvet, S., B. Statzner, P. Usseglio-Polatera & B. Dumont, 2000. Traits of benthic macroinvertebrates in semi-natural French streams: an initial application to biomonitoring in Europe. *Freshwater Biology* 43: 277–296.
- Chevenet, F., S. Dolédec & D. Chessel, 1994. A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology* 31: 295–309.
- Covich, A. P., 1988. Geographical and historical comparisons of neotropical streams: biotic diversity and detrital processing in highly variable habitats. *Journal of the North American Benthological Society* 7: 361–386.
- Cummins, K. W., 1973. Trophic relations of aquatic insects. *Annual Review of Entomology* 18: 183–206.
- Cummins, K. W., 1995. Invertebrates. In Calow, P. & G. E. Petts (eds), *The Rivers Handbook*. Blackwell Scientific, Oxford: 234–250.
- Díaz Villanueva, V. & R. J. Albariño, 1999. Feeding habit of *Notoperla archiplatae* (Plecoptera) larvae in a North Patagonian Andean stream, Argentina. *Hydrobiologia* 412: 43–52.
- Dobson, M., A. Magana, J. M. Mathooko & F. K. Ndegwa, 2002. Detritivores in Kenya highland streams: more evidence for the paucity of shredders in the tropics? *Freshwater Biology* 47: 909–919.
- Dobson, M., J. M. Mathooko, F. K. Ndegwa & C. M’Erimba, 2003. Leaf litter processing rates in a Kenyan highland stream, the Njoro River. *Hydrobiologia* 519: 207–210.
- Dolédec, S., J. M. Olivier & B. Statzner, 2000. Accurate description of the abundance of taxa and their biological traits in stream invertebrate communities: effects of taxonomic and spatial resolution. *Archiv für Hydrobiologie* 148: 25–43.
- Dudgeon, D., 1982. An investigation of physical and biotic processing of two species of leaf litter in Tai Po Kau Forest stream, New Territories, Hong Kong. *Archiv für Hydrobiologie* 96: 1–32.
- Dudgeon, D., 2000. The ecology of tropical Asian rivers and streams in relation to biodiversity conservation. *Annual Review of Ecology and Systematics* 31: 239–263.
- Fernández H. R., Domínguez E., 2001. Guía para la determinación de los artrópodos bentónicos sudamericanos Universidad Nacional de Tucuman, Tucuman.
- de Figueroa Tierno, J. M., J. M. Luzon-Ortega & A. Sanchez-Ortega, 1998. Imaginal biology of the stonefly *Hemimelaena flaviventris* (Pictet, 1841) (Plecoptera: Perlodidae). *Annales Zoologici Fennici* 35: 225–230.
- Fossati, O., J. G. Wasson, C. Hery, G. Salinas & R. Marin, 2001. Impact of sediment releases on water chemistry and macroinvertebrate communities in clear water Andean streams (Bolivia.). *Archiv für Hydrobiologie* 151: 33–50.
- Gayraud, S., B. Statzner, P. Bady, A. Haybachp, F. Scholl, P. Usseglio-Polatera & M. Bacchi, 2003. Invertebrate traits for the biomonitoring of large European rivers: an initial assessment of alternative metrics. *Freshwater Biology* 48: 1–20.
- Graça, M. A. S., C. Cressa, M. O. Gessner, M. J. Feio, K. A. Callies & C. Barrios, 2001. Food quality, feeding preferences, survival and growth of shredders from temperate and tropical streams. *Freshwater Biology* 46: 947–957.
- Hart, D. D. & C. T. Robinson, 1990. Resource limitation in a stream community: phosphorus enrichment effects on periphyton and grazers. *Ecology* 71: 1494–1502.
- Henriques-Oliveira, A. L., J. L. Nessimian & L. F. M. Dorville, 2003. Feeding habits of chironomid larvae (Insecta: Diptera) from a stream in the Floresta da Tijuca, Rio de Janeiro, Brazil. *Revista Brasileira de Biologia* 63: 269–281.
- Ihaka, R. & R. Gentleman, 1996. R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics* 5: 299–314.
- Irons, J. G., M. W. Oswood, R. J. Stout & C. M. Pringle, 1994. Latitudinal patterns in leaf litter breakdown: is temperature really important? *Freshwater Biology* 32: 401–411.
- Jackson, J. K. & B. W. Sweeney, 1995. Research in tropical streams and rivers: introduction to a series of papers. *Journal of the North American Benthological Society* 14: 2–4.
- Lamouroux, N., S. Dolédec & S. Gayraud, 2004. Biological traits of stream macroinvertebrate communities: effects of microhabitat, reach, and basin filters. *Journal of the North American Benthological Society* 23: 449–466.
- Mathuriau, C. & E. Chauvet, 2002. Breakdown of leaf litter in a neotropical stream. *Journal of the North America Benthological Society* 21: 384–396.
- Merritt, R. W. & K. W. Cummins, 1996. *An Introduction to the Aquatic Insects of North America*. Kendall/Hunt, Dubuque, Iowa.
- Mihuc, T. B., 1997. The functional trophic role of lotic primary consumers: generalist versus specialist strategies. *Freshwater Biology* 37: 455–462.
- Miserendino, M. L. & L. A. Pizzolón, 2004. Interactive effects of basin features and land-use change on macroinvertebrate communities of headwater stream in the Patagonian Andes. *River Research and Applications* 20: 1–17.
- Molina, C. I. A., 2004. Estudios de los rasgos biológicos y ecológicos en poblaciones de los ordenes: Ephemeroptera, Plecoptera y Trichoptera (clase Insecta), en un río al pie del glaciar Mururata. Tesis de Licenciatura, Universidad Mayor de San Andres, La Paz, Bolivia.
- Navarro G., Maldonado M., 2002. *Geografía Ecológica de Bolivia, Vegetación y Ambientes Acuáticos*. Centro de Ecología Simon I. Patino - Departamento de Difusión, Cochabamba, Bolivia.
- de Neiff Poi, A., 1990. Categorización funcional de los invertebrados en ríos de Llanura del Chaco oriental (Argentina). *Revista Brasileira de Biologia* 50: 875–882.
- Palmer, C., J. O’Keeffe, A. Palmer, T. Dunne & S. Radloff, 1993a. Macroinvertebrate functional feeding groups in the middle and lower reaches of the Buffalo River eastern Cape, South Africa. I. Dietary variability. *Freshwater Biology* 29: 441–453.
- Palmer, C., J. O’Keeffe & A. Palmer, 1993b. Macroinvertebrate functional feeding groups in the middle and lower reaches of the Buffalo River eastern Cape, South Africa. II. Functional morphology and behaviour. *Freshwater Biology* 29: 455–462.
- Pavluk, T. I., A. de Bij Vaate & H. A. Leslie, 2000. Development of an index of trophic completeness for benthic macroinvertebrate communities in flowing waters. *Hydrobiologia* 427: 135–141.

- Plague, G. R., J. B. Wallace & J. W. Grubaugh, 1998. Linkages between trophic variability and distribution of *Pteronarcys* spp. (Plecoptera: Pteronarcyidae) along a stream continuum. *American Midland Naturalist* 139: 224–234.
- Polegatto, C. M. & C. G. Froehlich, 2003. Feeding strategies in Atalophlebiinae (Ephemeroptera: Leptophlebiidae), with considerations on scraping and filtering. In Gaino, E. (ed.), *Research Update on Ephemeroptera & Plecoptera*. University of Perugia, Perugia: 55–61.
- Roldán, G. P., 1996. Guía para el estudio de los macroinvertebrados acuáticos del Departamento de Antioquia. Fondo Fen Colombia/Colciencias/Universidad de Antioquia, Bogota.
- Rosi-Marshall, E. J. & J. B. Wallace, 2002. Invertebrate food webs along a stream resource gradient. *Freshwater Biology* 47: 129–141.
- Sedlák, E., 1983. Feeding habits of some caddis larvae. *Scripta facultatis Scientiarum Naturalium Universitatis Purkynianae Brunensis* 13: 33–42.
- Statzner, B., S. Dolédec & B. Hugueny, 2004. Biological trait composition of European stream invertebrate communities: assessing the effects of various trait filter types. *Ecography* 27: 470–488.
- Statzner, B., A. G. Hildrew & V. H. Resh, 2001. Species traits and environmental constraints: Entomological research and the history of ecological theory. *Annual Review of Entomology* 46: 291–316.
- Tachet, H., P. Usseglio-Polatera & C. Roux, 1994. Theoretical habitat templates, species traits, and species richness: Trichoptera in the Upper Rhône River and its floodplain. *Freshwater Biology* 31: 397–416.
- Teslenko, V. A., 1997. Feeding habits of the predaceous stoneflies in a salmon stream of the Russian far east. In Landolt, P. & M. Sartori (eds), *Ephemeroptera & Plecoptera Biology–Ecology–Systematics*. MTL, Fribourg: 73–78.
- Thioulouse, J., D. Chessel, S. Dolédec & J. M. Olivier, 1997. ADE-4: a multivariate analysis and graphical display software. *Statistics and Computing* 7: 75–83.
- Townsend, C. R. & A. G. Hildrew, 1994. Species traits in relation to habitat templet for river systems. *Freshwater Biology* 31: 265–275.
- Usseglio-Polatera, P., 1994. Theoretical habitat templates, species traits, and species richness: aquatic insects in the Upper Rhône River and its floodplain. *Freshwater Biology* 31: 417–437.
- de Vaate Bij, A. & T. I. Pavluk, 2004. Practicability of the Index of Trophic Completeness for running waters. *Hydrobiologia* 519: 49–60.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell & C. E. Cushing, 1980. The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* 37: 130–137.
- Wallace, J. B., S. L. Eggert, J. L. Meyer & J. R. Webster, 1999. Effects of resource limitation on a detrital-based ecosystem. *Ecological Monographs* 69: 409–442.
- Wichard, W., W. Arens & G. Eisenbeis, 2002. *Biological Atlas of Aquatic Insects*. Apollo Books, Stenstrup.
- Woodward, G. & A. G. Hildrew, 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. *Journal of Animal Ecology* 71: 1063–1074.

Appendix

Appendix 1. Diet composition (see Table 2 for labels), functional feeding group (FFG) affinity transcribed to fuzzy codes (0 – no affinity to a category, 3 – high affinity), and FFG classification after Merritt & Cummins (1996) of 49 neotropical taxa (ND – FFG of taxa is not defined at genus level; FFG in boldface italic does not agree with our results)

	S.P.	FPOM	CPOM	MiPh	MaPh	DA	MIIn	MAIn	Predators (engulfers, piercer)	Scrapers	Shredders	Collectors- Gatherers	Collectors- Filterers	Collectors- Filterers	FFG (after Merritt & Cummins, 1996)
Ephemeroptera															
Baetidae															
<i>Andesiops</i>	1	3	1	1	0	0	0	0	0	2	1	3	0	0	ND
<i>Baetodes</i>	0	2	0	1	0	0	0	0	0	3	0	3	0	0	scrapers
<i>Camelobaetidius</i>	1	2	0	2	0	0	0	0	0	3	0	3	0	0	ND
<i>Cloodes</i>	1	3	0	1	0	0	0	0	0	1	0	2	0	0	collectors-gatherers
<i>Fallcon</i>	0	3	1	2	0	0	0	0	0	3	1	3	0	0	ND
<i>Nanomis</i>	1	2	0	2	0	0	0	0	0	3	0	3	0	0	ND
<i>Varipes</i>	1	3	1	2	0	0	0	0	0	2	1	3	0	0	ND
Leptophlebiidae															
<i>Allenhyphes?</i>	1	3	1	1	0	0	0	0	0	1	1	3	0	0	ND
<i>Haplohyphes</i>	1	3	1	1	0	0	0	0	0	2	1	3	0	0	ND
<i>Leptohyphes</i>	1	3	1	1	0	0	0	0	0	2	1	3	0	0	ND
<i>Tricorythodes</i>	1	3	0	1	1	0	0	0	0	1	0	3	0	0	collectors-gatherers
Leptophlebiidae															
<i>Ecuaphlebia</i>	1	3	0	1	0	0	0	0	0	3	0	2	1	0	ND
<i>Thraulodes</i>	1	3	0	1	0	0	1	0	0	2	0	3	1	0	ND
Plecoptera															
Perlidae															
<i>Anacronetaria</i>	0	1	0	1	0	0	0	3	3	0	1	1	0	0	ND
Trichoptera															
Glossosomatidae															
<i>Mortoniella</i>	0	3	0	2	0	0	0	0	0	3	0	3	0	0	ND
Helicopsychidae															
<i>Cochitopsyche</i>	0	2	0	1	0	0	0	0	0	2	0	3	0	0	ND
Hydrobiosidae															
<i>Atopsyche</i>	0	1	0	1	0	0	0	3	3	0	1	0	0	0	predators
Hydropsychidae															
<i>Leptonema</i>	0	3	2	2	1	0	0	2	1	0	1	0	3	0	collectors-filterers
<i>Smicridea</i>	0	3	2	2	1	0	0	1	1	0	1	0	3	0	collectors-filterers
Hydroptilidae															
<i>Hydroptilidae</i>	0	1	0	3	0	0	0	0	0	3	0	1	0	0	scrapers, collectors-gatherers
Leptoceceridae															
<i>Grunichella</i>	0	3	1	2	0	0	0	0	0	2	1	2	0	0	ND
Odontoceridae															
<i>Barypenthus</i>	1	3	0	1	0	0	0	0	0	2	1	3	0	0	ND
<i>Marilia</i>	0	3	1	2	0	0	0	2	1	3	1	3	0	0	<i>shredders</i>
Philopotamidae															
<i>Chimarra</i>	0	3	0	1	0	0	0	0	0	0	1	0	3	0	collectors-filterers
Elmidae															
<i>Gonielmis</i> larvae	0	3	0	0	0	0	0	0	0	0	0	3	0	0	ND
<i>Heterelmis</i> larvae	0	3	2	1	0	0	0	0	0	1	3	3	0	0	ND
<i>Macroelmis</i> larvae	0	3	1	1	0	0	0	0	0	2	1	2	0	0	ND

Continued on p. 264

	S.P	FPOM	CPOM	MiPh	MaPh	DA	MIIn	MAIn	Predators (engulfers, piercer)	Scrapers	Shredders	Collectors- Gatherers	Collectors- Filterers	FFG (after Merritt & Cummins, 1996)
<i>Microcyloepus?</i> larvae	0	3	0	1	0	0	0	0	0	1	0	3	0	ND
<i>Neocleminis</i> larvae	0	3	1	1	0	0	0	0	0	2	1	2	0	ND
<i>Neocleminis</i> adults	0	3	0	1	0	0	0	0	0	1	0	3	0	ND
<i>Ordobrevia?</i> adults	0	1	3	1	0	0	0	0	0	0	3	0	0	ND
<i>Phanocerus</i>	0	3	3	2	0	0	0	0	0	2	3	1	0	ND
<i>Psephenus</i>	0	3	0	2	0	0	0	0	0	3	0	2	0	scrapers
Staphylinidae larvae	0	3	0	1	0	0	0	1	1	1	0	3	0	<i>predators</i>
adults	1	3	0	0	0	0	0	1	1	0	0	3	0	<i>predators</i>
Ceratopogonidae	0	1	0	1	0	0	0	3	2	1	0	1	0	generally predators, collectors-gatherers
Chironomidae	1	3	1	1	0	0	0	1	1	1	1	3	0	collectors-gatherers and filterers, predators
Dixidae	0	3	0	1	0	0	0	1	1	1	0	3	1	collectors-gatherers and filterers
Dolichopodidae <i>Aphrosylus?</i>	0	1	0	0	0	0	0	2	3	0	0	1	0	predators
Empididae <i>Chelifera</i>	0	0	0	0	0	0	0	3	2	0	0	0	0	ND
<i>Hemerodromia</i>	0	1	0	1	0	0	0	3	2	0	0	1	0	predators, collectors-gatherers
Psychodidae <i>Maruina</i>	1	3	1	0	0	0	0	0	0	1	1	3	0	<i>scrapers</i> , collectors-gatherers
Simuliidae Tipulidae <i>Hexatoma</i>	0	3	1	1	0	0	0	0	0	1	0	0	3	collectors-gatherers collectors-filterers
<i>Limnophila</i>	1	3	1	1	0	0	0	0	1	1	1	1	0	predators
<i>Limonia</i>	1	3	0	1	0	0	0	0	0	1	1	3	0	<i>predators</i>
<i>a</i>	1	1	0	1	0	0	0	3	3	0	0	1	0	<i>shredders</i>
Megaloptera Corydalidae <i>Corydalus</i>	0	1	1	1	0	0	0	3	3	0	1	1	0	ND
Lepidoptera Pyrallidae <i>Parargyactis</i>	0	2	1	1	1	0	0	0	0	1	1	2	0	predators scrapers