

Effect of habitat type on benthic macroinvertebrates in two lowland tropical streams, Costa Rica

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Abstract: Benthic macroinvertebrate community structure was studied with respect to stream habitat type in two lowland tropical streams. Three reaches along the Carbón river and two within the Gandoca stream were chosen as study sites in Talamanca, Costa Rica. Macroinvertebrates were collected from four habitat types: leaf packs in riffles, cobble in riffles, areas of sand in pools, and areas of gravel in pools. Communities were dominated by insects in the orders Ephemeroptera (*Thraulodes*, *Baetis*?), Diptera (Chironomidae, Tipulidae), Trichoptera (Hydropsychidae, Glossosomatidae, Hydropsilidae, Calamoceratidae), and Odonata (*Progomphus heterina*). Non-insect macroinvertebrates were dominated by shrimps (*Macrobrachium*) and snails (Gastropoda). Functional feeding group composition was dominated by collector-gatherers. In most reaches, both habitat types in riffles supported higher macroinvertebrate abundance and biomass than did habitats in pools. Leaf packs in riffles represent an important habitat that is present year-round in these aseasonal tropical systems. Community composition and diversity were similar to that reported for other areas of Central America.

Key words: Community structure, abundance, diversity, biomass, leaf pack habitats, riffle habitats, Talamanca.

A disproportionate amount of research on benthic community structure in streams has focused on cobble-riffles habitats, compared with other habitat types, although a number of studies in temperate regions have assessed benthic community structure with respect to substrate types (e.g. Egglisshaw 1969, Minshall & Minshall 1977, Rabeni & Minshall 1977, Hawkins *et al.* 1982, Huryn & Wallace 1987). It is now recognized that streams contain a variety of habitats with different physical and chemical conditions (Pringle *et al.* 1988). The availability of habitats and the nature of their faunal assemblages can be expected to change among reaches along a river continuum. For example, Palmer *et al.* (1991) reported that specific macroinvertebrate assemblages were not always associated with habitats in head-

water reaches, but were evident in middle and lower reaches.

The distribution of benthic macroinvertebrates among stream habitats reflects, to some degree, the distribution of benthic resources (e.g. food, oxygen, predators) (Rabeni & Minshall 1977), and provides information about how communities might respond to changes in environmental parameters such as increased sedimentation and changes in flow. Despite its importance, few studies have been published on the distribution of benthic macroinvertebrates among stream habitats for tropical systems (but see Dudgeon 1982, Arunachalam *et al.* 1991).

In this paper, we examined the distribution of benthic macroinvertebrate communities among habitat types in lowland tropical

streams draining the region of Talamanca, Costa Rica. We are not aware of any previous published studies dealing with any aspect of the ecology of stream benthic communities in this region (but see Paaby *et al.* 1998, this issue). The objectives of our study were: (1) to describe the structure of benthic stream communities in Talamanca, and (2) to assess the effect of habitat type on community structure.

MATERIALS AND METHODS

Study area: This study was conducted at the Gandoca-Manzanillo Wildlife Refuge and surrounding areas in southeastern Costa Rica ($82^{\circ}45'N$, $9^{\circ}40'W$) (Fig. 1). The area is located in the tropical wet forest life zone (Holdridge *et al.* 1971). At a nearby meteorological station at Chase (10 km south, 40 m a.s.l.), the mean annual precipitation over a period of 19 years was 2 110 mm. Rain is evenly distributed throughout the year, with no clear seasonality. At the same station, mean annual air temperature ranged from 22 to 27 °C (Herrera 1985).

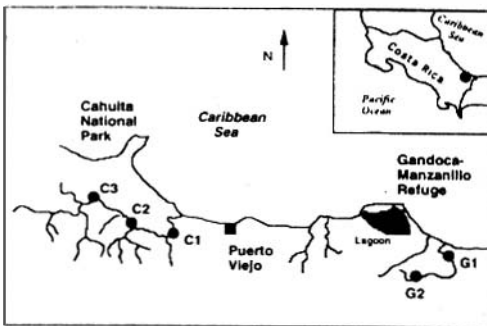


Fig. 1. Location of the study sites in the Caribbean lowlands of Costa Rica.

The Carbón and Gandoca rivers were chosen as study sites. Sampling was done in three reaches in the Carbón and two in the Gandoca river. The main differences among reaches were in stream order and discharge (Table 1). Both rivers have catchments composed of primary and secondary forest, mixed with active pastures and areas of small-scale agriculture. While riparian vegetation was present at all sites, increased sedimentation might be the result of human activities, such as agriculture. A detailed description of sites can be found on

Paaby *et al.* (1998, this issue).

Methods: The five study reaches and all stream habitats were sampled for macroinvertebrates in both December 1995 and May 1996. Stream discharge and water temperature were recorded on both sampling dates (see Paaby *et al.* 1998 this issue). Stream habitat composition was defined as: depositional areas of sand (DS), depositional areas of gravel (DG), cobble substrate in riffle areas (CR), and leaf pack accumulations in riffles (LP). The relative proportion of each habitat was assessed for each site by making a grid (4 m in length by the river width) with 16 sections, and visually surveying the proportion of each habitat inside each division. The mean habitat proportion was used to weight the obtained sample values.

Two random macroinvertebrate samples were collected from each habitat type (DS, DG, CR, LP), at each site on each sampling date. Samples were collected using a kick net (350 μ m mesh), and disturbing an area of near 1 m² of a particular habitat for five consecutive minutes. To prevent build-up of debris and loss of organisms, the net was emptied into a bucket four or five times while sampling and large pieces of wood, stones or leaves were removed. All organisms captured and small debris were preserved in 90% ethanol.

Macroinvertebrates were identified to different taxonomic levels according to available taxonomic information for each group. Non-insects macroinvertebrates were identified only to the class or order level. Among the insects, several groups were identified to genus level using available keys: Ephemeroptera (Flowers 1992), Odonata (Ramirez unpublished information), Trichoptera (Springer unpublished information), and Plecoptera (Baumann 1984). Diptera, Lepidoptera, Hemiptera, and Coleoptera were identified to family level using Roldán (1988) and Merritt & Cummins (1996), and separated into morphotypes. Chironomidae (Diptera) were identified as Tanypodinae and non-Tanypodinae. Functional feeding-groups were assigned to each taxon based on Jackson and Sweeney (1995) and Merritt and Cummins (1996).

Macroinvertebrate abundance was obtained by counting all individuals per taxon and expressing the results as numbers per sample.

TABLE I

Characteristics of the study sites. Carbon River (C1, C2, C3) and Gandoca stream (G1, G2), Talamanca, Costa Rica

	Carbon River			Gandoca River	
	C1	C2	C3	G1	G2
Stream Order	1	2	3	1	2
Catchment land use	Forest/Pasture	Forest/Pasture	Forest/Pasture	Pasture	Forest
Habitat composition (%)					
Riffle habitats					
Cobble	37.5	45	37.5	0	25
Leaf Packs	12.5	5	25	25	25
Pool habitats					
Sand	37.5	37.5	12.5	75	25
Gravel	12.5	12.5	25	0	25
Mean water					
Temperature (°C)	27	27	26	23	24
Discharge (m ³ /s)	0.93	4.5	3.5	< 1	0.8

Macroinvertebrate biomass was obtained by measuring body length (i.e., head to tip of abdomen) of all individuals of all taxa to the nearest 1 mm using a dissecting microscope, and then applying predetermined regressions of length-to-weight relationships, resulting in mg ash free dry mass (mg AFDM) per sample. Predetermined biomass regressions were selected for each taxon found at the study sites, using known and tested regressions and selecting those for the same taxa or of similar body-shape (Smock 1980, Huryn 1986, A.D. Huryn & J.B. Wallace unpublished data). Equations in dry mass were transformed to AFDM by assuming that 1 g DM = 0.9 g AFDM (Benke 1993).

Where necessary and appropriate, variables were log-transformed ($\log [x+1]$). Macroinvertebrate biomass and abundance were compared both between and within habitats, and between and within reaches using separate one-way analysis of variance (ANOVA) procedures, using GLM procedure in SAS (SAS 1988). Orthogonal contrasts were defined to assess significant differences between habitat abundance and biomass. Diversity was calculated using Fisher's alpha of the log series (Fisher *et al.* 1943) since it is independent of sample size and does not give excessive weight to common species (Wolda 1981, Flowers 1991). It also allow us to compare with other studies in Central America (e.g., Flowers 1991, Pringle & Ramirez 1998).

RESULTS

Physical parameters: Habitat composition was found to be different among sites. The proportion of habitats in each site is shown in Table I. Although, some variation was observed, DS and CR were dominant in most sites. Discharge ranged from less than 1 m³ s⁻¹ in first-order sites to more than 4 m³ s⁻¹ in third-order sites. Water temperature varied around 26°C in Carbón and 25°C in Gandoca rivers (Table 1).

Benthic community composition: Benthic macroinvertebrate communities at all sites were dominated by only a few groups of insects: mayflies (Ephemeroptera) and true flies (Diptera), and non-insect macroinvertebrates: shrimps (Decapoda) and snails (Gastropoda).

Thraulodes (Leptophlebiidae) was the dominant mayfly genera representing more than 10% of total abundance and biomass in the Carbón river (Table 2). *Leptohyphes* (Leptohyphidae) and *Baetis?* (Baetidae) were also collected in smaller proportions in the Carbón river (Table 2). Mayflies were less abundant in Gandoca (Table 2). Chironomidae and Tipulidae were the most common dipterans in both streams. Percent abundance of Chironomidae was greater than 10% at all sites, and represented 56% of all insects collected at C2. However, Chironomidae biomass was never higher than 2% at a single site (Table 2). Larval Tipulidae were found in low

TABLE 2

Percentage contribution of the main taxa to total habitat-weighted biomass (B) and abundance (A) (>2%) in the Caribón (C1, C2, C3) and Gandoca rivers (G1, G2), Talamanca, Costa Rica

Taxa	C1		C2		C3		G1		G2	
	A	B	A	B	A	B	A	B	A	B
Collector-Filterers										
Hydropsychidae	1.3	0.8	0.0	0.0	8.1	7.8	0.0	0.0	0.6	0.2
Collector-Gatherers										
<i>Baetis</i> ?	3.9	1.5	6.3	4.6	3.0	1.6	0.0	0.0	0.0	0.0
Chironomidae	43.2	1.0	56.5	2.0	30.7	0.5	11.3	0.2	14.7	0.2
Decapoda	3.3	65.5	0.0	0.0	4.0	44.5	0.0	0.0	5.6	73.0
<i>Leptohyphes</i>	15.3	6.0	4.1	4.4	5.6	3.2	0.0	0.0	1.1	6.1
<i>Tricorythodes</i>	0.0	0.0	0.0	0.0	4.6	2.0	0.0	0.0	1.1	6.1
Predators										
Ceratopogonidae	0.0	0.0	0.0	0.0	0.1	0.0	4.9	0.9	1.1	0.2
<i>Corydalis</i>	0.0	0.0	0.6	1.1	0.1	11.8	0.0	0.0	0.0	0.0
Erpetogomphus	0.0	0.0	0.0	0.0	0.0	0.0	1.0	19.4	0.0	0.0
<i>Phyllocycla</i>	0.0	0.0	9.0	76.7	0.0	0.0	0.0	0.0	0.0	0.0
<i>Progomphus</i>	0.4	4.3	0.0	0.0	0.6	11.0	0.0	0.0	1.7	2.4
Tipulidae	0.8	8.8	0.0	0.0	0.5	3.4	0.0	0.0	2.2	3.4
Scrapers										
Gastropoda	0.0	0.0	0.0	0.0	0.0	0.0	69.2	74.9	18.3	2.5
Glossomatidae	0.4	0.1	0.0	0.0	13.9	1.2	0.0	0.0	0.0	0.0
<i>Thraulodes</i>	21.4	10.2	21.7	9.3	10.3	3.8	0.0	0.0	8.6	1.3
Shredders										
Calamoceratidae	0.0	0.0	0.0	0.0	0.1	0.1	0.0	0.0	10.0	1.4
Pyralidae	0.0	0.0	0.0	0.0	2.5	2.4	0.0	0.0	0.0	0.0
Total	93.1	99.6	99.2	99.7	89.3	98.7	99.9	100.0	84.5	100.0

numbers (<2%) but their biomass varied from 3% to 9% at sites C1, C3, and G2. Caddisflies (Trichoptera) were found at all sites in low numbers. Hydropsychidae were abundant only at site C3, where they composed nearly 8% of the total biomass and abundance. Other families were represented only at one or two sites. For instance, the Calamoceratidae reached high abundance and biomass only at site G2 (Table 2). Odonata were always present in low numbers, and never reached high abundance in any site. However, some large Odonata make a large part of the biomass at some sites. For example, *Phyllocycla* (Gomphidae) make 77% of the total biomass at site C2, but only 9% of the abundance (Table 2).

Among non-insect macroinvertebrates, shrimps (mainly *Macrobrachium*) were dominant, comprising less than 10% of the total abundance. However, large bodied shrimps were collected at some of the sites, where their

biomass increased to more than 40% of the total. Snails were abundant only in the Gandoca river; at G1 snails comprised 69% of the abundance and 75% of the biomass of the benthic community (Table 2).

Effect of habitat type: Different stream habitats supported different benthic community compositions. LP habitats had a fauna composed mainly of collector-gatherers (Chironomidae, Decapoda, Leptohyphidae), filterers (Hydropsychidae), predators (Odonata), and at site G2 by shredders (Calamoceratidae) (Figs. 2 and 3). The fauna in DS habitats contained mainly collector-gatherers (Chironomidae, Decapoda), predators (*Progomphus*) and some scrapers (Gastropoda) (Figs. 2 and 3). DG habitats supported several groups of equal representation, among them filterers (Trichoptera), collector-gatherers (Chironomidae, Decapoda) and predators

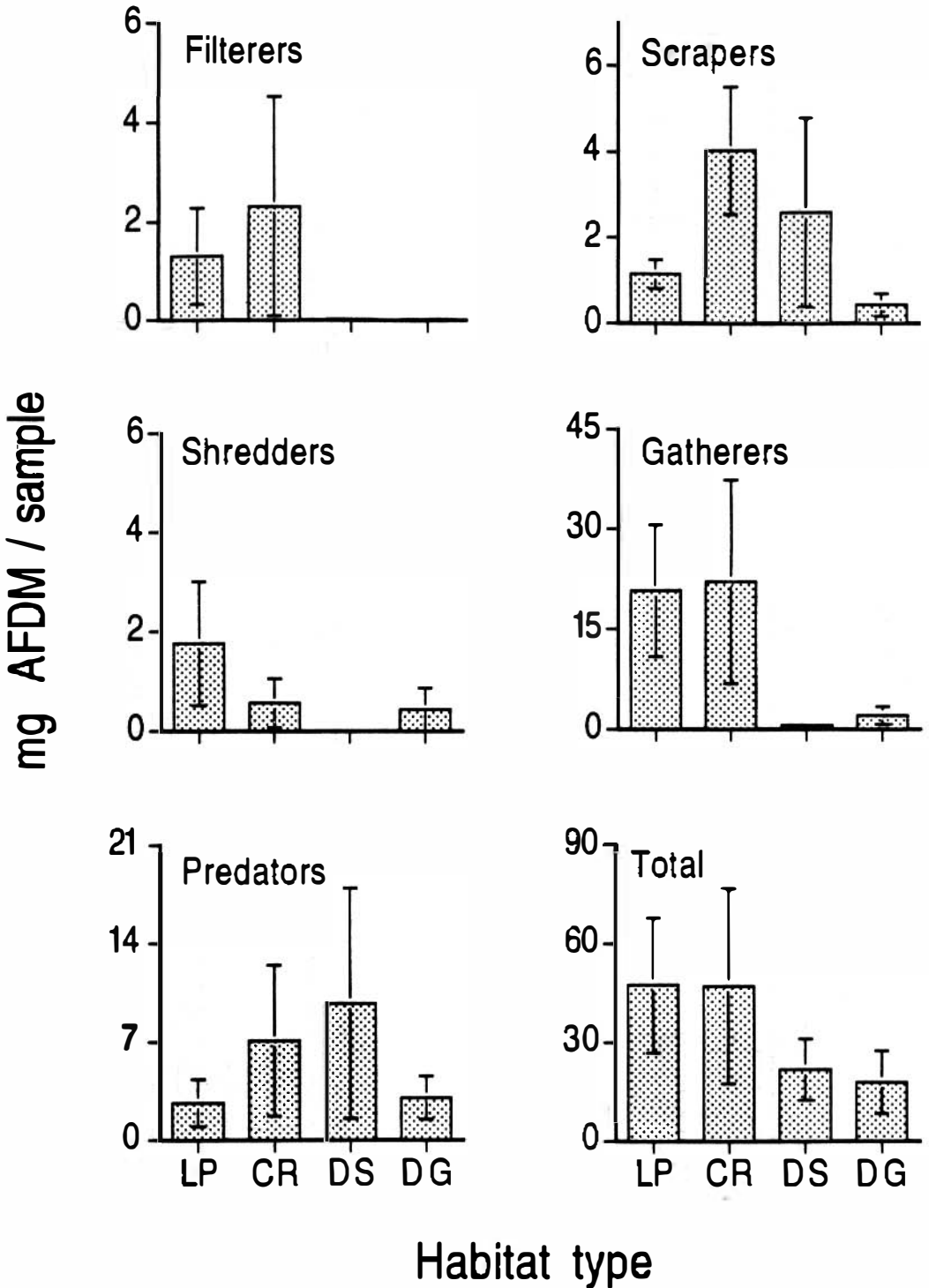


Fig. 2. Mean (± 1 SE) biomass of macroinvertebrates functional feeding group (mg AFDM / sample) in four habitat types (LP, leaf packs; CR, cobble-riffle; DS, depositional sand; DG, depositional gravel) for all reaches combined (n = 5). Note the different scales in the vertical (y) axis.

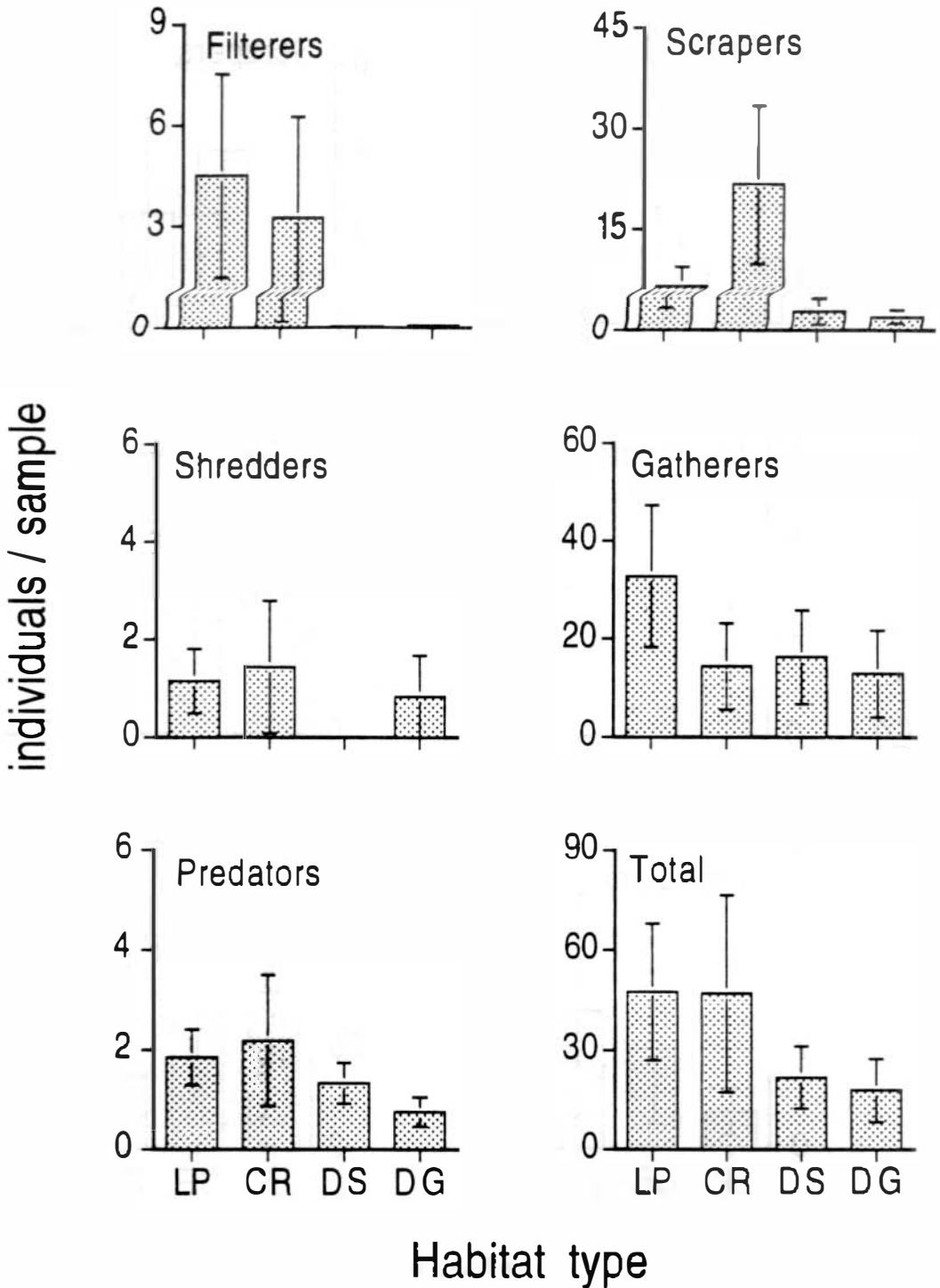


Fig. 3. Mean (± 1 SE) abundance of macroinvertebrates functional feeding group (individuals / sample) in four habitat types (LP, leaf packs; CR, cobble-riffle; DS, depositional sand; DG, depositional gravel) for all reaches combined ($n = 5$). Note the different scales in the vertical (y) axis.

(Tipulidae) (Figs. 2 and 3). CR habitats were composed by large numbers of collector-gatherers (Chironomidae, Leptohiphidae), predators (Odonata) and scrapers (*Thraulodes*, Gastropoda, Helicopsychoidea) (Figs. 2 and 3).

Total abundance and biomass of macroinvertebrates differed among habitats within a site. At the Carbón river both riffle habitats had significantly higher biomass than the two pool habitats, however, abundance was not significantly different among habitats at C1 and C3 (Table 3), in contrast C2 had significantly higher abundance of macroinvertebrates in LP (Table 3). Biomass and abundance in Gandoca stream were not significantly different among habitats, however, only two habitats were found at G1 (Table 3).

TABLE 3

Mean abundance (individuals / sample) and biomass (mg AFDM / sample) for each stream habitat sampled at each site

Site	Habitat	Abundance	S.E.	Biomass	S.E.
C1	LP	1.93	0.09 a	1.78	0.14 a
	CR	1.45	0.46 a	1.39	0.41 a
	DG	0.81	0.41 a	0.76	0.39 b
	DS	1.31	0.66 a	0.43	0.30 b
C2	LP	1.48	0.17 a	0.69	0.09 a
	CR	0.46	0.24 b	0.14	0.10 b
	DG	0.00	0.00	0.00	0.00
	DS	0.16	0.16 c	0.35	0.35 c
C3	LP	1.91	0.43 a	1.35	0.25 a
	CR	2.25	0.09 a	1.91	0.23 a
	DG	1.66	0.25 a	0.69	0.42 b
	DS	1.25	0.63 a	0.87	0.69 b
G1	LP	0.38	0.38 a	0.63	0.63 a
	CR	0.00	0.00	0.00	0.00
	DG	0.00	0.00	0.00	0.00
	DS	1.13	0.22 a	1.11	0.22 a
G2	LP	1.38	0.17 a	1.29	0.67 a
	CR	1.06	0.07 a	0.90	0.17 a
	DG	0.80	0.42 a	0.54	0.33 a
	DS	0.77	0.15 a	0.78	0.38 a

When data for functional groups were grouped for all habitats, collector-gatherers and scrapers showed the highest abundance (Fig. 4). Collector-gatherers and predators were highest in terms of biomass.

Biomass and abundance data were also

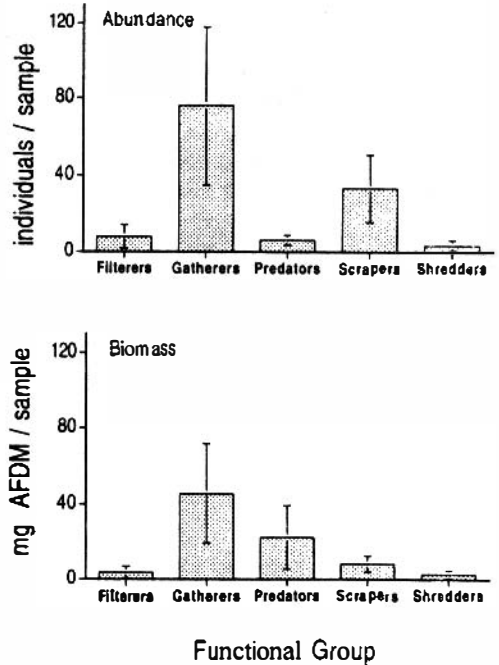


Fig. 4. Mean (± 1 SE) biomass (mg AFDM per sample) and abundance (individuals / sample) of macroinvertebrates functional feeding for all habitats and groups reaches combined (n = 20).

TABLE 4

Species (S) and alpha diversity for the study sites in Talamanca

Site	S	N	Diversity alpha	SE	
Carbon River	C1	21	162	12.7	3.8
	C2	11	19	-	-
	C3	32	331	8.9	0.9
Gandoca River	G1	9	23	5.4	1.8
	G2	22	55	13.5	2.9

S=richness, N=number of individuals

weighted by habitat composition at each site to compare different reaches. Significant differences among reaches were found, with sites C1 and C3 showing higher abundance and biomass (abundance: ANOVA, $P < 0.05$; biomass: ANOVA, $P < 0.05$) than sites C2, G1, and G2, which were similar among themselves (Fig. 5). Comparisons of the reaches showed

that species richness was highest at site C3, similar between sites C1 and G2, and lowest at site G1. Alpha diversity was different among reaches, being higher at site C1 and G2, and lowest at site C2 (Table 4).

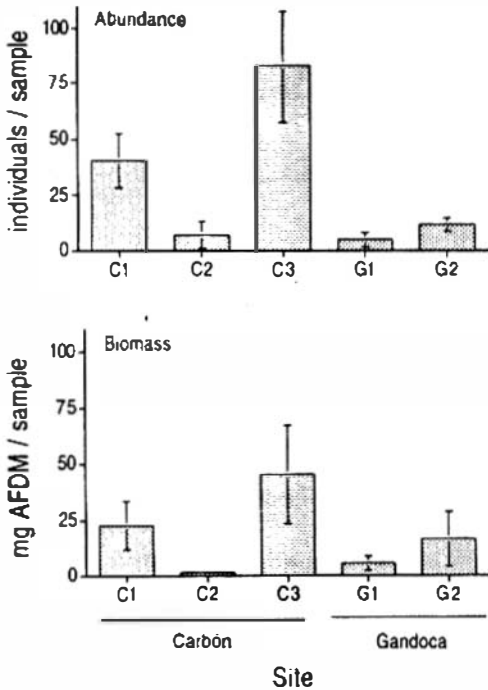


Fig. 5. Mean (± 1 SE) biomass (mg AFDM per sample) and abundance (individuals / sample) of macroinvertebrates at each study site, for all habitats.

DISCUSSION

Prior to this study and that of Paaby *et al.* (1998, this issue), to our knowledge published studies of stream benthic macroinvertebrate community structure exist for only two other regions in the Caribbean of Central America: La Selva Biological Station in Costa Rica and the northern side of the Caribbean slope of Panamá (Flowers 1991, Flowers & Pringle 1995, Pringle & Ramírez 1998, Ramírez & Pringle in review). While specific taxonomic studies exist for Central America (often based on adults) (e.g., Hurlbert & Villalobos-Figueroa 1982, Flowers 1992, Spangler & Santiago-Fragoso 1992), the community structure of stream-dwelling larval macroin-

vertebrates has received little attention. Taxonomic composition of macroinvertebrate communities in Talamanca streams was found to be similar to that reported for La Selva and Panamá, with single reaches often containing up to 30 taxa. Diversity in our study reaches was also similar, although sometimes lower, than stream reaches at the same elevation in Panamá (Flowers 1991), and higher than reaches at similar elevations at La Selva Biological Station (Pringle & Ramírez 1998). The major difference in community structure between previous studies and ours was the greater proportion of non-insect macroinvertebrates in Talamanca (Table 2). For example, shrimps are a main component of the benthic community at La Selva Biological Station (Pringle & Hamazaki 1998), but nocturnal adults are rarely collected using benthic samplers, such as Surbers or kick nets (Pringle & Ramírez 1998). In Panamá shrimps were not reported at all (Flowers 1991). In contrast, adult shrimps and snails were an important component of the benthic community of some reaches in Talamanca (e.g., C1, C3, and G2).

The composition of functional feeding groups showed that benthic macroinvertebrate communities were dominated by collector-gatherers. Collector-gatherers are the most abundant macroinvertebrates in many stream systems; they feed on fine particulate organic matter (FPOM) that accumulates on the substrate and are responsible for the processing and resuspension of those particles (Benke *et al.* 1984, Wallace & Webster 1996). The streams of Talamanca contain levels of nutrients sufficiently high to be considered eutrophic (see Paaby *et al.* 1998, this issue), favoring higher bacterial biomass and/or production (Weyers & Suberkropp 1996). Therefore, enhancing food resources for collector-gatherers that can obtain nutrients from bacteria while feeding on FPOM (Fisher & Gray 1983). Despite of their importance, collector-gatherers are one of the least studied groups of macroinvertebrates (Wallace & Webster 1996).

Previous studies in subtropical and tropical systems showed evidence that some stream habitats are often responsible for sustaining a large part of the benthic community. For example, in lowland subtropical streams woody debris represent an important habitat for benthic communities, even though it represents a

small percentage of the total habitat available in the river (Benke *et al.* 1984, Benke *et al.* 1985). In our study sites, benthic macroinvertebrates were clearly segregated among habitats in a particular and consistent way, suggesting that resources may also be patchily distributed. Both riffle habitats (LP and CR) were found to support highest abundance and biomass of macroinvertebrates.

Riffle habitats in Talamanca streams were composed of leaf packs and cobble areas. Leaf pack and their associated microflora play important roles as a source of energy for benthic communities (Reice 1980). Although leaf packs may be less stable than areas of cobble, they have been found to affect macroinvertebrate distribution (Drake 1984). For example, in temperate streams accumulations of leaves on the stream bottom were found to support higher diversity and abundance of macroinvertebrates than other stream habitats, although leaves are present in the stream only part of the year (Mackay & Kalff 1969, Allan 1995). In contrast, in tropical aseasonal systems, leaves are present year round (Stout 1980, Pfeiffer 1996). In these streams, both shredders and collector-gatherers appear to benefit directly from the presence of leaf accumulations. Studies on leaf decomposition in tropical systems have found that, while shredders are rare, collector-gatherers are the dominant feeding group in leaf packs (Benstead 1996, Rosemond *et al.* 1998), and microbes are suggested as responsible for leaves decay (Irons *et al.* 1994). Rosemond *et al.* (1998) suggest that macroinvertebrates in lowland tropical streams use leaf packs as a refuge against predation from fishes and adult shrimps.

Cobble-riffles are perhaps the most well studied stream habitat. A combination of factors such as stable substrate, constant flow of water, nutrients and oxygen, and higher availability of refuges from predation (Stout & Vandermeer 1975), make riffles a suitable habitat for aquatic macroinvertebrates. Our results coincide with previous studies at La Selva Biological Station, where cobble-riffles were found to support higher biomass and abundance than depositional-pool habitats (Ramírez & Pringle in review). Results also support the fact that pool habitats are a comparatively less important habitat for benthic mac-

roinvertebrates (Huryñ & Wallace 1987, Wohl *et al.* 1995). Pool habitats in tropical streams can be subject to higher predation or disturbance by fishes and shrimps (Pringle 1996). In contrast, areas of pools that contain sufficient substrate that functions as a refuge, can support a higher abundance of macroinvertebrates than pools lacking such refugia (Arunachalam *et al.* 1991).

Further research is needed to properly assess parameters affecting benthic community structure and function in streams of Talamanca, and to assess how those parameters will change with variations in catchment land use. Although the study streams are relatively disturbed, diversity levels (as alpha index) were as high as those found in other areas of the Caribbean (e.g., streams running through primary forest at La Selva Biological Station; Pringle & Ramírez 1998). In addition, differences in biomass and abundance among sites can be explained by the presence or absence of some taxa, such as shrimps and snails, in some of the sites. However, the present study was not design to assess the effects of landuse on aquatic macroinvertebrate communities. Therefore, they can be potentially useful as reference streams for the restoration of other streams in the area of Gandoca-Manzanillo.

In conclusion, stream macroinvertebrate communities in Talamanca are dominated by insects, with shrimps and snails as dominant groups only in some reaches. Riffles habitats supported the highest abundance and biomass of macroinvertebrates. Although leaf packs were abundant, few insect shredders were collected, and functional feeding groups were dominated by collector-gatherers.

RESUMEN

La estructura de las comunidades de macroinvertebrados bénticos fue estudiada en relación con el tipo de hábitat riverino presente en quebradas tropicales. Se trabajó en cinco tramos localizados en dos quebradas en Talamanca, Costa Rica. Los macroinvertebrados fueron recolectados de cuatro tipos de hábitats: "paquetes" de hojas y áreas de piedras en rápidos, y arenales y grava en pozas. Las comunidades de macroinvertebrados fueron dominadas por insectos de los órdenes Ephemeroptera (*Thraulodes*, *Bae&s?*), Diptera

(Chironomidae, Tipulidae), Trichoptera (Hydropsychidae, Glossosomatidae, Hydroptilidae, Calamoceratidae), y Odonata (*Progomphus*, *Hetaerina*). Además de los insectos, otros grupos dominantes fueron camarones (*Macrobrachium*) y caracoles (Gastropoda). La composición de grupos funcionales fue dominada por recolectores. En la mayoría de los tramos, los dos tipos de hábitats en rápidos presentaron mayor abundancia y biomasa de macroinvertebrados, en comparación a los hábitats en áreas de pozas. Rápidos y "paquetes" de hojas fueron los tipos de hábitats más importantes para las comunidades bénticas. La importancia de las hojas es resaltado por el hecho de que en sistemas tropicales estos se encuentran presentes todo el año. La composición de la comunidad y la diversidad fue similar a la reportada en otros sitios de América Central.

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REFERENCES

- Allan, J.D. 1995. Stream ecology. Chapman & Hall, London.
- Arunachalam, M., K.C. Madhusoodanan Nair, J. Vijverberg, K. Kortmulder & H. Suriyanarayanans. 1991. Substrate selection and seasonal variation in densities of invertebrates in stream pools of a tropical river. *Hydrobiologia* 213: 141-148.
- Baumann, R.W. 1984. Plecoptera. P: 215-239. In S.H. Hurlbert & A. Villalobos-Figueroa (eds.), Aquatic Biota of Mexico, Central America and the West Indies. San Diego State University, San Diego, California.
- Benke, A. C. 1993. Concepts and patterns of invertebrate production in running waters. *Verh. Internat. Verein. Limnol.* 25: 15-38.
- Benke, A.C., T.C. Van Arsdall Jr., D.M. Gillespie & F.K. Parrish. 1984. Invertebrate productivity in a subtropical blackwater river: the importance of habitat and life history. *Ecol. Monog.* 54: 25-63.
- Benke, A.C., R.L. Henry, D.M. Gillespie, R.J. Hunter. 1985. Importance of snag habitat for animal production in Southeastern streams. *Fisheries* 10: 8-13.
- Benstead, J.P. 1996. Macroinvertebrates and the processing of leaf litter in a tropical stream. *Biotropica* 28: 367-375.
- Drake, J.A. 1984. Species aggregation: the influence of detritus in a benthic invertebrate community. *Hydrobiologia* 112: 109-115.
- Dudgeon, D. 1982. Aspects of the microdistribution of insect macrobenthos in a forest stream in Hong Kong. *Arch. Hydrobiol. Suppl.* 64: 221-239.
- Egglishaw, H.J. 1969. The distribution of benthic macroinvertebrates on substrate in fast flowing streams. *J. Anim. Ecol.* 38: 19-33.
- Fisher, R.A., A.S. Corbet & C.B. Williams. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. *J. Anim. Ecol.* 12: 42-58.
- Fisher, S.G. & L.J. Gray. 1983. Secondary production and organic matter processing by collector macroinvertebrates in a desert stream. *Ecology* 64: 1217-1224.
- Flowers, R.W. 1991. Diversity of stream-living insects in northwestern Panamá. *J.N. Am. Benthol. Soc.* 10: 322-334.
- Flowers, R.W. 1992. Review of the genera of Mayflies of Panamá, with a checklist of Panamanian and Costa Rican species (Ephemeroptera). 692 p. In: Quintero, D. & A. Aiello (eds.). *Insects of Panama and Mesoamerica: selected studies*. Oxford University, Oxford.
- Flowers, R.W. & C.M. Pringle. 1995. Yearly fluctuations in the mayfly community of a tropical stream draining lowland pasture in Costa Rica. p: 131-150. In L.D. Corkum & J.J.H. Ciborowski (eds.). *Current Directions in Research on Ephemeroptera*. Canadian Scholars, Toronto.
- Hawkins, C.P., M.L. Murphy, N.H. Anderson. 1982. Effects of canopy, substrate composition and gradient on the structure of macroinvertebrate communities in Cascade range streams of Oregon. *Ecology* 63: 1840-1856.
- Herrera, W. 1985. Clima de Costa Rica. In *Vegetación y clima de Costa Rica*. L. D. Gómez (ed.). Universidad Estatal a Distancia, San José, Costa Rica.

- Holdridge, L.R., W.C. Grenke, W.H. Hatheway, T. Liang & J.A. Tosi Jr. 1971. Forest environments in tropical life zones: A pilot study. Pergamon, Oxford, England.
- Hurlbert, S.H. & A. Villalobos-Figueroa. 1982. Aquatic Biota of Mexico, Central America and the West Indies. San Diego State University, San Diego, California.
- Huryn, A.D. 1986. Secondary production of the macroinvertebrate community of a high-elevation stream in the southern Appalachian mountains. Ph.D. Dissertation. University of Georgia, Athens, Georgia.
- Huryn, A.D. & J.B. Wallace. 1987. Local geomorphology as a determinant of macrofaunal production in a mountain stream. *Ecology* 68: 1932-1942.
- Irons, J.G. III, Oswood M.W., Stout R.J. & Pringle C.M. 1994. Latitudinal patterns in leaf litter breakdown: is temperature really important? *Fresh. Biol.* 32: 401-411.
- Jackson, J.K., & B.W. Sweeney. 1995. Egg and larval development times for 35 species of tropical stream insects from Costa Rica. *J. N. Am. Benthol. Soc.* 14: 115-130.
- Mackay, R.J. & J. Kalf. 1969. Seasonal variation in standing crop and species diversity of insects communities in a small Quebec stream. *Ecology* 50: 101-109.
- Merritt, R.W. & K.W. Cummins. 1996. An introduction to the aquatic insects of North America. Kendall/Hunt.
- Minshall, G.W. & J.N. Minshall. 1977. Microdistribution of benthic invertebrates in a rocky mountain stream. *Hydrobiologia* 55: 231-249.
- Paaby, P., A. Ramírez & C.M. Pringle. 1998. The benthic macroinvertebrate community in Caribbean Cost Rican streams and the effect of two sampling methods. *Rev. Biol. Trop.* 46. Supl. 6: 185-199.
- Palmer, C.G., J.H. O'Koeffe, & A.R. Palmer. 1991. Are macroinvertebrate assemblages in the Buffalo River, southern Africa, associated with particular biotopes? *J. N. Am. Benthol. Soc.* 10: 349-357.
- Pfeiffer, W.J. 1996. Litter invertebrates. 137-182. In: D.P. Reagan & R.B. Waide (eds.). *The food web of a tropical rain forest*. University of Chicago, Chicago.
- Pringle, C.M. 1996. Atyid shrimps (Decapoda: Atyidae) influence the spatial heterogeneity of algal communities over different scales in tropical montane streams, Puerto Rico. *Freshwater Biol.* 35: 125-140.
- Pringle, C.M. & T. Hamazaki. 1998. The role of omnivory in a neotropical stream: separating diurnal and nocturnal effects. *Ecology* 79: 269-280.
- Pringle, C.M. & A. Ramírez. 1998. Use of both benthic and drift sampling techniques to assess tropical stream invertebrate communities along an altitudinal gradient, Costa Rica. *Fresh. Biol.* 39: 359-373.
- Pringle, C.M., R.J. Naiman, G. Bretschko, J.R. Karr, M.W. Oswood, J.R. Webster, R.L. Welcomme & M.J. Winterbourn. 1988. Patch dynamics in lotic streams: the stream as a mosaic. *J. N. Am. Benthol. Soc.* 7: 503-524.
- Rabeni, C.F. & G.W. Minshall. 1977. Factors affecting micro-distribution of stream benthic insects. *Oikos* 29: 33-43.
- Reice, S.R. 1980. The role of substratum in benthic macroinvertebrate microdistribution and litter decomposition in a woodland stream. *Ecology* 61: 580-590.
- Roldán, G. 1988. Guía para el estudio de los macroinvertebrados del departamento de Antioquia. Colombia. Presencia, Bogotá. 217 p.
- Rosemond, A.D., C.M. Pringle & A. Ramirez. 1998. Macroconsumer effects on insect detritivores and detrital processing in a tropical stream food web. *Fresh. Biol.* 39: 515-523.
- SAS Institute. 1988. SAS/STAT User's guide. Release 6.04. SAS Institute, Cary, North Carolina.
- Smock, L.A. 1980. Relationships between body size and biomass of aquatic insects. *Freshwater Biol.* 10: 375-383.
- Spangler, P.J. & S. Santiago-Fragoso. 1992. The aquatic beetle subfamily Larainae (Coleoptera: Elmidae) in México, Central America, and the West Indies. *Smith. Cont. Zoo.* 528.
- Stout, J. 1980. Leaf decomposition rates in Costa Rican lowland tropical rain forest streams. *Biotropica* 12: 264-272.
- Stout, J. & J.H. Vandermeer. 1975. Comparison of species richness for stream-inhabiting insects in tropical and mid-latitude streams. *Am. Nat.* 109: 263-280.
- Wallace, J.B. & J.R. Webster. 1996. The role of macroinvertebrates in stream ecosystem function. *Ann. Rev. Entomol.* 41: 115-139.
- Weyers, H.S. & K. Suberkropp. 1996. Fungal and bacterial production during the breakdown of yellow poplar leaves in 2 streams. *J. N. Am. Benthol. Soc.* 15: 408-420.
- Wohl, D.L., J.B. Wallace & J.L. Meyer. 1995. Benthic macroinvertebrate community structure, function and production with respect to habitat type, reach and drainage basin in the southern Appalachians (U.S.A.). *Freshwater Biol.* 34: 447-464.
- Wolda, H.S. 1981. Similarity Indices, sample size and diversity. *Oecologia* 50: 296-302.

APPENDIX

(CG), filterer (F), predator (P), scraper (SC), and shredder (SH) Biomass (B, mg AFDM / sample) and abundance (A, individuals / sample) of macroinvertebrate collected in study sites, in Talamanca, Costa Rica. Functional feeding groups (FFG) as follows: collector-gatherer

TAXON	C1		Carbón		River		C3		Gandoca		Stream		FFG
	B	A	B	A	B	A	B	A	B	A	B	A	
Gastropoda									8.52	8.00	0.38	2.05	SC
Decapoda	13.21	1.41			23.76	3.81					11.34	0.63	CG
Ephemeroptera													
<i>Baetis</i> ?	0.31	1.63	0.06	0.13	0.83	2.81							SC
<i>Baetodes</i>	0.00	0.06											
<i>Caenis</i> '	0.09	0.38			0.01	0.03	0.01	0.13					
<i>Letophyphes</i>	1.21	6.44	0.05	0.09	1.68	5.25					0.00	0.06	CG
<i>Thraulodes</i>	2.06	9.03	0.11	0.45	2.03	9.72					0.20	0.97	
<i>Traverrella</i>	0.06	0.09			0.10	0.56							
<i>Tricorythodes</i>					1.07	4.31					0.03	0.13	CG
Odonata													
<i>Archaeogomphus</i>											0.00	0.06	P
<i>Argia</i>					0.65	0.31	0.09	0.13					P
<i>Erpetogomphus</i>							2.21	0.13					P
<i>Heteragrion</i>											0.17	0.25	P
<i>Hetaerina</i>					0.02	0.25							P
Libellulidae							0.21	0.56			0.09	0.13	P
<i>Palaemnema</i>					0.92	0.28							P
<i>Phyllocyca</i>			0.94	0.19									P
<i>Progomphus</i>	0.88	0.19			5.87	0.56					0.37	0.19	P
Plecoptera													
<i>Anaconeuria</i>	0.00	0.03									0.02	0.13	P
Hemiptera													
Naucoridae		0.09					0.94				0.00	0.19	P
Megaloptera													
<i>Corydalus</i>			0.01	0.01	6.29	0.09							P
Trichoptera													
Calamoceratidae					0.03	0.06					1.77	1.13	SH
Glossosomatidae	0.02	0.19			0.63	13.09							SC
Helicopsychidae							0.22	0.38			0.33	1.52	SC
Hydroptilidae	0.15	0.56			4.17	7.59					0.03	0.06	F
Leptoceridae	0.00	0.38			0.01	1.31					0.01	0.38	
<i>Leptonema</i>					0.05	0.31					0.23	0.25	SH
<i>Wormaldia</i>		0.03	0.01	0.01	0.35	0.50							F
					0.05	0.09							F
Lepidoptera													
Pyralidae					1.26	2.38							SC
Coleoptera													
Elmidae larvae	0.12	0.59	0.01	0.01	0.12	1.00					0.76	0.21	SC
Elmidae adult	0.00	0.03	0.00	0.00	0.01	0.09					0.01	0.06	SC

Psephenidae	0.03	0.13			0.79	1.38						SC
Plecoptera	0.01	0.03										CG
Diptera												
Ceratopogonidae					0.01	0.09	0.10	0.56	0.03	0.25		P
Chironomidae	0.19	18.22	0.02	1.18	0.29	28.84	0.02	1.31	0.03	2.21		CG
Simuliidae	0.01	0.13	0.00	0.01								F
Tanypodinae	0.00	0.13			0.01	0.56	0.00	0.38	0.05	0.13		P
Tipulidae	1.77	0.34			1.82	0.50			0.52	0.25		P
Total	6.95	40.78	1.23	2.08	29.62	90.19	2.86	3.56	3.71	8.53		