

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).

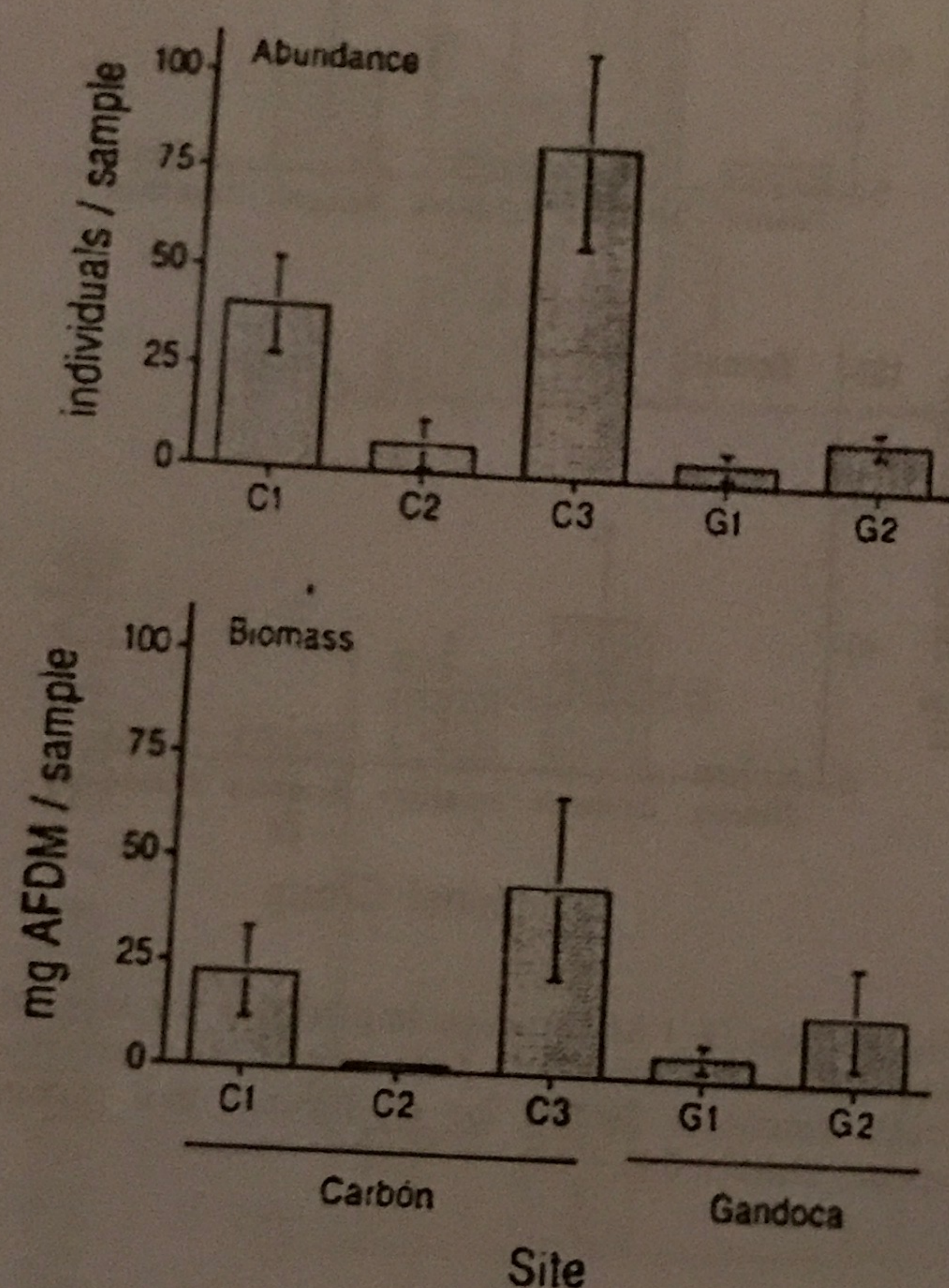


Fig. 5. Mean (± 1 SE) biomass (mg AFDM per sample) and abundance (individuals / sample) of macroinvertebrates at each study site, for all habitats.

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 (Hury & 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*, *Baetis*?), 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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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			
											G1	G2	
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													
Baetis ?	0.31	1.63	0.06	0.13	0.83	2.81							SC
Baetodes	0.00	0.06											
Caenis	0.09	0.38			0.01	0.03	0.01	0.13					
Letophyphes	1.21	6.44	0.05	0.09	1.68	5.25					0.00	0.06	CG
Thraulodes	2.06	9.03	0.11	0.45	2.03	9.72					0.20	0.97	
Traverrella	0.06	0.09			0.10	0.56							
Tricorythodes					1.07	4.31					0.03	0.13	CG
Odonata													
Archaeogomphus											0.00	0.06	P
Argia					0.65	0.31	0.09	0.13					P
Erpetogomphus							2.21	0.13					P
Heteragrion											0.17	0.25	P
Hetaerina					0.02	0.25							P
Libellulidae							0.21	0.56			0.09	0.13	P
Palaemnema							0.92	0.28					P
Phyllocycla			0.94	0.19									P
Progomphus	0.88	0.19					5.87	0.56			0.37	0.19	P
Plecoptera													
Anacroneuria	0.00	0.03									0.02	0.13	P
Hemiptera													
Naucoridae		0.09					0.94				0.00	0.19	P
Megaloptera													
Corydalus			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	
Leptonema					0.05	0.31					0.23	0.25	SH
Wormaldia		0.03	0.01	0.01	0.35	0.50							F
					0.05	0.09							F
Lepidoptera													
Pyrilidae					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

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<i>Psephenidae</i>	0.03	0.13			0.79	1.38						SC
<i>Pikodactilidae</i>	0.01	0.03										CG
Diptera												
<i>Ceratopogonidae</i>					0.01	0.09	0.10	0.56	0.03	0.25		P
<i>Chironomidae</i>	0.19	18.22	0.02	1.18	0.29	28.84	0.02	1.31	0.03	2.21		CG
<i>Simuliidae</i>	0.01	0.13	0.00	0.01								F
<i>Tanypodinae</i>	0.00	0.13			0.01	0.56	0.00	0.38	0.05	0.13		P
<i>Tipulidae</i>	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		