Use of both benthic and drift sampling techniques to assess tropical stream invertebrate communities along an altitudinal gradient, Costa Rica

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SUMMARY

1. Two sampling techniques were used to characterize invertebrate communities in eight, low-order streams along an altitudinal gradient in Costa Rica that represents the last continuous tract of primary forest spanning such extremes in elevation (i.e. near sea level to 2900 m a.s.l.) along the Caribbean Slope of Central America. A standard Surber sampler was used to sample invertebrates on the stream bottom, and drift sampling nets were used to sample invertebrates drifting in the stream flow.

2. Sites were established at 30, 50, 700, 1800 and 2700 m a.s.l. In one to two streams per site, six Surber samples were collected, and drift was sampled every 3 h over one 24-h period between April and August 1994. All sites were in primary forest, with the exception of the lowest elevation site (30 m) which was located in banana plantations.

3. Both sampling techniques indicated that Diptera (Chironomidae) and Ephemeroptera were the dominant insect groups at all sites. Disturbed streams draining banana plantations were dominated by Chironomidae and had lower taxon richness and diversity than other sites.

4. While data from benthic samples indicated that insects were the major faunal component (> 90%) at all sites, drift samples were dominated by larval shrimps (> 50%) at the 30 m and 50 m sites.

5. Drift periodicity of invertebrates was observed at those sites characterized by predaceous fishes: nocturnal drift densities were higher than diurnal densities at 30, 50 and 700 m a.s.l., however, no periodicity was observed at 1800 and 2700 m a.s.l. where fish were absent.

6. This study shows the importance of measuring invertebrate drift, in addition to directly sampling the benthos. Drift sampling provided data on a major community component (shrimps) of lowland tropical streams, that would have been overlooked using traditional benthic sampling techniques, and in some cases provided additional information on taxon richness.

7. Based on results of the present study, it is recommended that drift sampling be included as a standard complementary tool to benthic sampling in biological assessments (e.g. bioassessment protocols) of tropical streams, which are often characterized by migratory invertebrate species such as shrimps. Drift samples provide critical information on the presence or absence of shrimps and also on the timing and magnitude of their migration which is an important link between many tropical rivers and their estuaries.
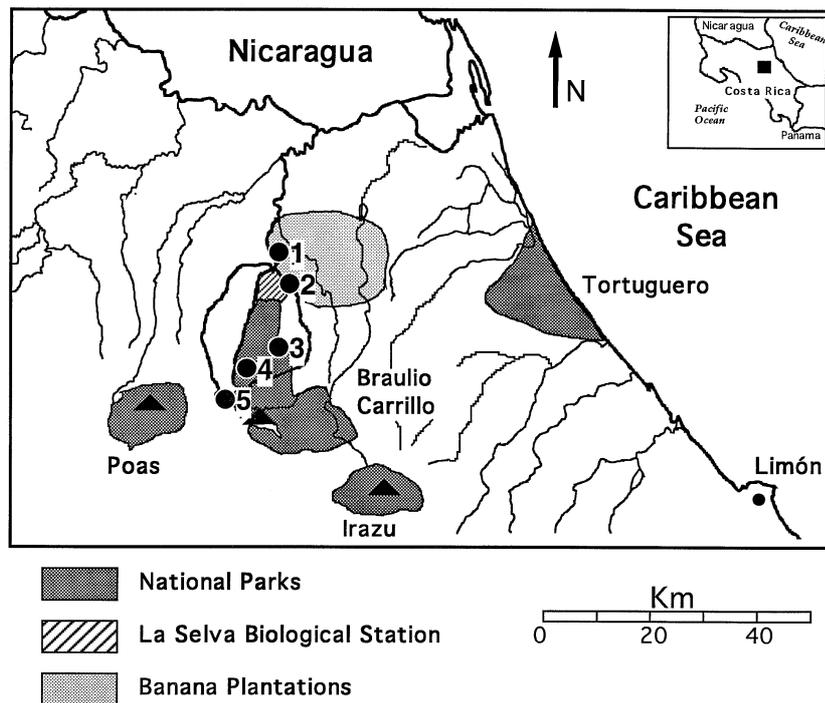
Fig. 1 Study area, showing the location of sampling sites on Costa Rica's Caribbean Slope with respect to Braulio Carrillo National Park, adjacent protected areas (e.g. La Selva Biological Station), and banana plantations. Circled numbers refer to sites: where site 1 = 30 m; site 2 = 50 m; site 3 = 700 m; site 4 = 1800 m; and site 5 = 2700 m.

Introduction

Our understanding of benthic invertebrate communities in streams is complicated by the fact that sampling techniques do not always indicate actual community composition and structure. Most standard techniques for assessment of stream invertebrate communities are insect-based and sample only the stream-bed substrate; for instance, the Surber (Surber, 1937) and Hess (Hess, 1941) samplers are two widely used sampling devices for stream macroinvertebrates (Hauer & Resh, 1996). These samplers are limited to shallow water depths (< 30 cm) and are designed for streams with relatively fine-textured substrata (e.g. gravel and small cobble). While both sampling devices provide quantitative data on the number of invertebrates per given benthic area, some researchers argue that, to obtain a representative picture of benthic community composition, the number of samples that must be collected is prohibitively high (Hess, 1941; Chutter, 1984). Techniques that assess stream communities in less direct ways have not been widely used; for example, while drift samplers have often been employed to study insect behaviour (e.g. Waters, 1972; Smock, 1996), only a few studies have used this method to assess benthic community composition (e.g. Wilson, 1987; Hardwick *et al.*, 1995).

Our understanding of tropical stream invertebrate communities has largely been based on a few studies that have focused on a single site within a watershed (e.g. Stout & Vandermeer, 1975; Turcotte & Harper, 1982; Flowers & Pringle, 1995). More recent investigations, however, have assessed regional and/or altitudinal variations in benthic invertebrates in tropical (Flowers, 1991) and subtropical (Rundle, Jenkins & Ormerod, 1993; Ormerod *et al.*, 1994; Palmer *et al.*, 1994) rivers.

This paper examines the composition of stream invertebrate communities along the last remaining continuous transect of tropical forest that spans extremes in elevation, from near sea level to 2900 m a.s.l., on the Caribbean slope of Central America. This unique altitudinal transect is located in Costa Rica, where a northward extension of Braulio Carrillo National Park joins La Selva Biological Station (owned and operated by the Organization for Tropical Studies). The Braulio Carrillo-La Selva land corridor (Fig. 1) protects over 50 000 ha of primary forest, including a large portion of the Sarapiquí River catchment (one of the major river systems in Costa Rica). This protected area provides a unique opportunity to study tropical lotic invertebrate communities along a relatively undisturbed altitudinal continuum of changing forest types, temperature, precipitation and abundance of fish predators. The presence of newly created
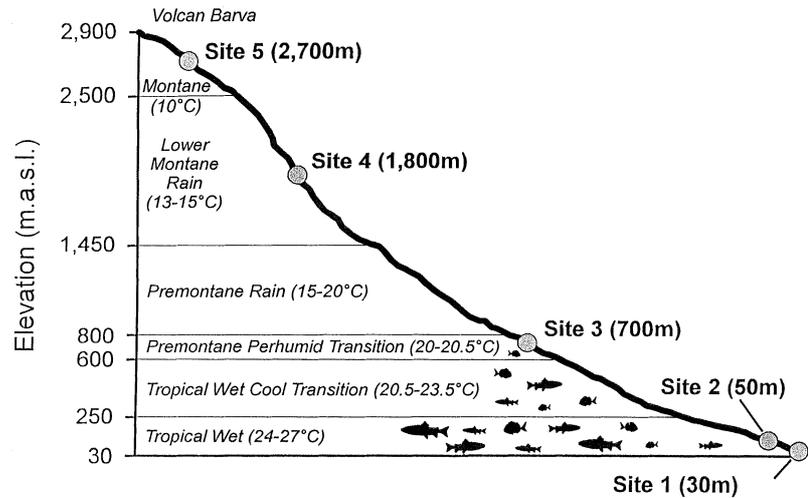
Fig. 2 Schematic representation of the altitudinal gradient, showing site location relative to life zones (Holdridge *et al.*, 1971), water temperature, and changes in fish communities.

banana plantations just north-east of La Selva (Fig. 1) also allowed examination of highly disturbed streams at the lowest elevation along the altitudinal continuum.

The primary objectives of the study were: (i) to examine invertebrate communities along this neotropical altitudinal gradient using two sampling methods: a Surber sampler (which directly samples the stream bottom) and drift nets (which sample the water column); (ii) to evaluate the effectiveness of drift sampling as a complementary tool to benthic sampling for use in 'bioassessment protocols' in tropical streams; and (iii) to begin to place previous studies on benthic invertebrates and community dynamics in lowland streams (e.g. Flowers & Pringle, 1995; Pringle & Hamazaki, 1998) in the context of the regional landscape.

Description of study site

The Braulio Carrillo-La Selva land corridor encompasses four life zones and two transitional zones (Pringle *et al.*, 1984), ranging from tropical wet forest in the lowlands of La Selva to montane forest at the summit of Barva Volcano (2906 m) which is the highest point along the corridor (Figs 1 and 2). While the land corridor spans an altitudinal range of nearly 3000 m over a map distance of about 35 km (resulting in a gradual change in altitude and fairly large middle elevation areas), the underlying lava flows are often abruptly dissected by a multitude of deeply incised streams.

Important ecological changes that occur along the

altitudinal gradient include: (i) a decline in ambient temperatures with increasing elevation (Table 1); (ii) variations in annual rainfall [from 4 m in the lowlands of La Selva to up to 6 m at elevations between 1500 and 1800 m a.s.l., and decreases to near 3 m at higher elevations (i.e. above 2000 m; Hartshorn & Peralta, 1988)]; (iii) a decrease with elevation in both the levels (and spatial variability between streams) of biologically important nutrients such as phosphorus and other elements (e.g. CL, Si, Ca, Mg, SO_4, Pringle, Triska & Browder, 1990); and (iv) a shift in predators, from a high diversity and abundance of fishes in the relatively undisturbed lowlands (forty-five taxa of fish have been recorded in streams of the La Selva area; Bussing, 1994), to fishless streams in the highlands.

Over the last decade, several scientific expeditions have explored the higher elevations of Braulio Carrillo National Park, resulting in a preliminary description of terrestrial plant and animal communities (e.g. Pringle *et al.*, 1984; Almeda & Pringle, 1988 and references therein). However, other than a survey of stream solute chemistry (Pringle *et al.*, 1990, 1993) and fish communities (Burcham, 1984), little is known regarding the streams of high elevation areas, and no information exists on stream invertebrates.

Commercial banana plantations (between 6000 and 8000 ha) were established in the lowlands just north-east of La Selva in 1991 (Fig. 1). Because bananas require extensive drainage, streams draining the plantations have been channelized and re-routed into a network of closely spaced irrigation ditches. Streams that were once sampled for nutrients in 1988 (Pringle *et al.*, 1990) have been completely re-routed and

Table 1 Characteristics of streams along the La Selva-Braulio Carrillo altitudinal gradient

	Banana Plantations		Primary Forest					
	30 m		50 m		70 m		1800 m	2700 m
	a	b	a	b	a	b		
Stream	Cano Negro	Cano San Jose	El Salto	El Sura	Chiquiza	Villalobos	La Legua	Creek at Barva
Stream order	Second	Second	Third	Third	Second	Fourth(?)	Second	First
Life zone	Plantation	Plantation	Wet forest	Wet forest	Premontane forest	Premontane forest	Lower montane forest	Montane forest
Temperature (°C)	26–27	26–27	24–26	24–26	20–21	19–20	16–17	10–11
Bottom substrate	Medium cobble	Medium cobble	Silt and small cobble	Silt and small cobble	Medium cobble	Cobble and rocks	Medium cobble	Medium cobble
No. of fish taxa	± 13	± 13	19–20	19–20	1	1	0	0
Fish references	Burcham (pers.com.)	Burcham (pers.com.)	Burcham (1988)	Burcham (1988)	Authors (pers. ob.)	Authors (pers. ob.)	Authors (pers. ob.)	Authors (pers. ob.)
No. of shrimp taxa	± 8	± 8	± 8	± 8	Unknown	Unknown	0	0
Shrimp references	Pringle (unpubl.data)	Pringle (unpubl.data)	Pringle (unpubl.data)	Pringle (unpubl.data)				
Vegetation cover	Open canopy	Open canopy	Closed canopy	Closed canopy	Closed canopy	Open canopy	Closed canopy	Closed canopy
Sampling date	27 April 94	27 April 94	13 May 94	13 May 94	14 April 94	14 April 94	24 August 94	04 August 94

diverted, to the extent that it was not possible to relocate old sampling sites. Massive amounts of fertilizers, insecticides, herbicides and fungicides are applied to the banana plantations (Hernandez & Witter, 1996) and large fish kills in the Rio San Juan on the border of Nicaragua and Costa Rica have been attributed to pesticide runoff (see Vargas, 1995 and references therein).

In contrast to the lack of information on streams draining high elevation areas in Braulio Carrillo National Park, and those draining banana plantations in the lowlands, information exists for the undisturbed lowland streams of La Selva Biological Station on: solute chemistry (Pringle & Triska, 1991); algae (Paaby & Goldman, 1992); benthic insects (Stout & Vandermeer, 1975; Flowers & Pringle, 1995); fish distribution and ecology (Burcham, 1988; Bussing, 1994); and community dynamics (Pringle & Hamazaki, 1997; Pringle & Hamazaki, 1998).

Materials and methods

Low-order streams were selected at five different points along the altitudinal gradient ranging from 30 to 2700 m a.s.l. (Table 1). All stream sites were first- to third-order and located within the Puerto Viejo–Sarapiquí–San Juan drainage which empties into the Caribbean Sea (Fig. 1). Stream sites along the altitudinal gradient exhibited a range of fish taxa from nineteen to twenty at the 50 m site to no fishes at the 1800 and 2700 m sites. Study sites located above 800 m were selected, in part, based on accessibility; sampling sites were accessed by hiking into this densely forested and deeply incised terrain from remote roadheads on the national park's western boundary. Water temperatures were measured at all sites using a maximum-minimum thermometer placed in the stream for 24 h (Table 1).

At the lowest elevation site (30 m) two streams (Caño Negro and Caño San Jose) that drained banana plantations on the alluvial coastal plain were sampled. These streams lacked riparian vegetation, were partially channelized, and water temperatures were the highest recorded along the altitudinal gradient (26–27 °C vs. 10 °C at the 2700 m site; Fig. 2). A 50 m site was established at La Selva Biological Station, where two study streams (El Salto and El Surá) drained dense tropical wet forest. Two study streams at the 700 m site (Chiquiza and Villalobos) were bordered by

primary tropical premontane forest and were sampled within a biological reserve (Rara Avis) adjacent to the Braulio Carrillo Park's eastern boundary. It was only possible to access and sample one study stream at each of the highest elevation sites, which were in dense primary forest: La Legua at 1800 m in lower montane forest and Barva at 2700 m in montane forest.

Streams at all study sites were sampled once between April and August 1994. All samples were collected at base flow, during first to third lunar quarters. No precipitation occurred during sampling periods, except at the highest elevation site, where heavy rain fell after the first diel sample was taken resulting in increased discharge for 1 h. Normal base flow was re-established soon after.

The benthic invertebrate composition of the stream bottom was assessed using a standard Surber sampler (area: 0.09 m^2; mesh size: 363 μm). At each site, six samples were collected: three from riffles and three from pools. Riffle environments were selected in relatively shallow turbulent areas (< 30 cm deep) where the water flow was high (usually > 0.40 m s^{-1}). Pools (> 40 cm deep) with low flow (< 0.20 m s^{-1}) were selected. All samples were collected by disturbing the substrate manually to a depth of 5 cm for a 1-min period. Invertebrate samples were preserved using 10% formalin and later sorted and placed into 70% ethanol.

The taxonomic composition and diel periodicity of drifting invertebrates was evaluated by sampling sites within the main stem of each study stream ($n = 8$) every 3 h over a 24-h period. Drift sampling was conducted 5 m upstream of the benthic sampling area at the downstream end of a riffle. During each sampling period, two Wildco® drift nets (mouth: 0.1 m^2; length: 1.5 m; mesh size: 363 μm) were placed in the water column for 10–30 min. The duration of the drift sampling period varied among sites and was adjusted to avoid clogging of the net by debris. Samples were preserved as described above for benthic samples. Benthic densities were expressed as numbers per m^2 of stream bottom and invertebrate drift density (number per 100 m^3) was calculated by dividing the total number of invertebrates per sample by the volume of water sampled. Drift nets were typically only partially submerged and water volume was calculated based on the submerged cross-sectional area of the drift net, current velocity at the net mouth, and

sampling time. Current velocity was measured with a Marsh McBirney® current meter.

All invertebrates were identified to the lowest taxonomic level possible using available literature (e.g. Roldán, 1988; Flowers, 1992). Among the insects, Ephemeroptera, Odonata and Plecoptera were identified to genus. Trichoptera, Diptera, Hemiptera and Coleoptera were identified to family level and separated into morphotypes. Taxonomic identification below family level was difficult for some families of Trichoptera, especially the Hydroptilidae, since most of the larvae were separated from their cases, which are useful for identification to genus level (Wiggins, 1977).

Invertebrate diversity was calculated using the Fisher alpha of the log series (Fisher, Corbet & Williams, 1943; Wolda, 1981). This diversity measure was used because it is not biased by sample size and allows comparison of data with other studies (e.g. Flowers, 1991). Day-to-night drift ratio was estimated as the mean drift density during the day divided by the mean night-time density. A non-parametric Kruskal–Wallis test was used to compare the day-to-night drift ratio among the sites. An index of percentage similarity of invertebrate taxonomic composition was calculated in both the presence and absence of shrimps to compare the similarity between sampling techniques at each stream site along the gradient. Similarity was calculated using the relative proportion of each invertebrate taxon collected with respect to the total density at a site (Smith, 1990).

Results

A major difference between results obtained from the two different sampling techniques was the presence of abundant larval shrimps in drift vs. benthic samples at lowland sites (see Fig. 3 and Appendix). Larval shrimp densities in drift reached up to 700 larvae per 100 m^3 of water sampled, at the 30 and 50 m sites. In contrast, larval shrimps were never present in Surber samples, except at very low densities (0.8 larvae m^{-2}) in one Surber sample at the 50 m site (Appendix). The presence of shrimps in drift but not benthic samples contributed to the low percentage similarity in invertebrate taxonomic composition between sampling techniques at low elevation sites (13–40% similarity), as indicated by the enhanced similarity (26–74%) when shrimps were excluded (Table 2). Nonetheless, the
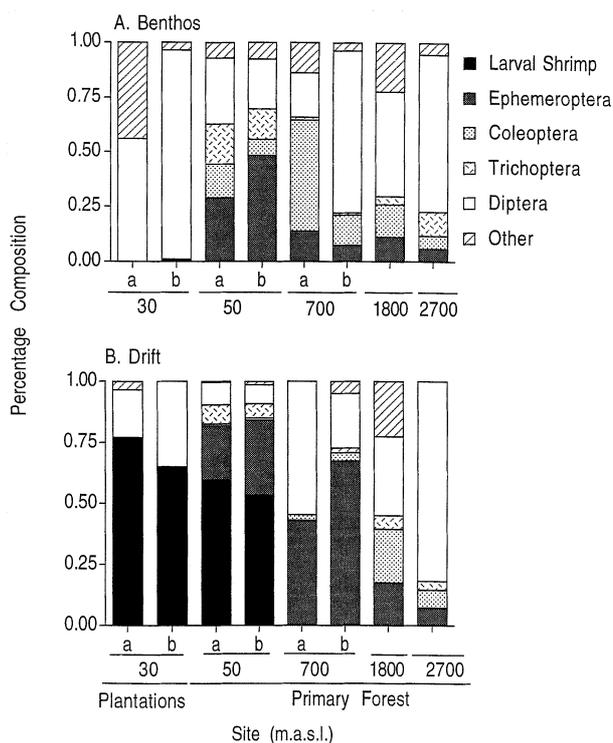

Fig. 3 Proportion of major invertebrate groups along the altitudinal gradient in: (a) benthic Surber samples; and (b) drift samples. Note: If more than two streams were sampled at a given site, they are denoted on the x-axis as 'a' and 'b.' Please see Table 1 for stream name and associated characteristics.

percentage similarity between sampling techniques was highly variable when calculated in both the presence and absence of shrimps (Table 2).

Benthic invertebrate community composition (as sampled with the Surber sampler) varied along the altitudinal gradient and was dominated by insects (Fig. 3a and Appendix). Diptera and Ephemeroptera were dominant at all sites, followed by other insect groups (e.g. Coleoptera, Trichoptera). When benthic and drift samples were considered for each site, disturbed streams draining banana plantations exhibited lower taxon richness and diversity than undisturbed sites at higher elevations (Table 2).

At the disturbed banana plantation site (30 m a.s.l.), benthic invertebrate densities were significantly lower than at the undisturbed 50 m site at La Selva (Fig. 3). Communities were dominated by relatively few groups including larval shrimps and Chironomidae, followed by lower densities of Ceratopogonidae and Elmidae. Some species of Odonata and Hemiptera

Table 2 Number of morphotypes (S), and alpha diversity (D) ± SE of invertebrates in drift (*n* = 16) and Surber samples (*n* = 6) at the study sites along Costa Rica's Caribbean slope. The number of invertebrate specimens (*n*) collected is in parentheses after S values. Percentage similarity in invertebrate taxonomic composition between sampling techniques is also shown in both the presence and absence of larval shrimp

Site		S (*n*)				D ± SE		% Similarity in taxonomic composition	
		Drift		Surber		Drift	Surber	With shrimps	Without shrimps
Banana Plantations									
30 m	a	8	(595)	11	(556)	1.31 ± 0.19	1.96 ± 0.25	13	26
30 m	b	11	(1311)	11	(141)	1.69 ± 0.20	2.86 ± 0.48	35	54
Primary Forest									
50 m	a	19	(1236)	18	(934)	3.22 ± 0.30	3.21 ± 0.32	40	74
50 m	b	36	(2758)	27	(1167)	5.91 ± 0.40	5.02 ± 0.42	36	61
700 m	a	18	(201)	22	(112)	4.81 ± 0.64	19.38 ± 10.90	32	32
700 m	b	7	(35)	17	(67)	2.72 ± 0.77	3.44 ± 0.36	17	17
1800 m		19	(54)	8	(53)	10.33 ± 2.23	2.63 ± 0.61	55	55
2700 m		18	(100)	14	(148)	6.49 ± 1.08	3.84 ± 0.60	64	64

were also present in comparatively low densities and very few larvae of Ephemeroptera and Trichoptera were collected (Fig. 4 and Appendix).

Among the undisturbed sites, benthic and drift densities generally decreased with increasing elevation. Drift densities at both low elevation sites (30 and 50 m) were highest, with larval shrimps representing more than 50% of the total invertebrate density (Figs 3 and 4). The wet forest site at La Selva (50 m) had significantly higher densities of benthic invertebrates than all other sites and was taxonomically very rich (Table 2). The insect fauna was composed of high numbers of Ephemeroptera, with an abundance of larvae belonging to *Tricorythodes*, *Leptohyphes* (Leptohyphidae), *Baetis*(?) (Baetidae) and *Thraulodes* (Leptophlebiidae; see Appendix). Within the Coleoptera, adult and larval Elmidae were abundant, followed by Staphylinidae and Hydrocasphidae. Pyralidae (Lepidoptera) were collected in low numbers. Of the caddisflies (Trichoptera), two families (Hydropsychidae and Hydroptilidae) were very abundant, while Philopotamidae was represented by low numbers of *Wormaldia*. Chironomidae were by far the most abundant of the dipterans, but densities were lower than those found at the disturbed banana plantation site (Appendix). In contrast, Simuliidae were present at high densities. At the premontane forest site (700 m), the benthic community was dominated by Ephemeroptera in the genera *Thraulodes* (Leptophlebiidae), *Baetis*(?), and
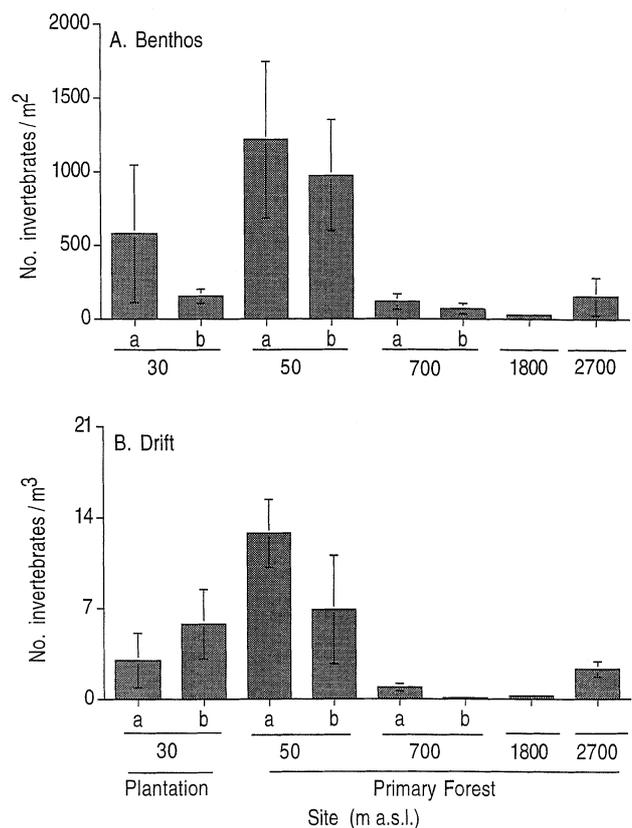

Fig. 4 Total invertebrate densities along the altitudinal gradient in: (a) benthic Surber samples; and (b) drift samples. Note: If more than two streams were sampled at a given site, they are denoted on the *x*-axis as 'a' and 'b.' Please see Table 1 for stream name and associated characteristics.

Baetodes (Baetidae). Chironomidae and Simuliidae also occurred at high densities. Coleoptera were primarily represented by Elmidae and Psephenidae. Trichoptera were poorly represented by the families Hydroptilidae and Leptoceridae. Relatively low numbers of *Argia* (Coenagrionidae: Odonata) were also collected (Appendix). The lower montane (1800 m) and montane (2700 m) forest sites had the lowest densities of benthic insects (Fig. 4). Invertebrate communities were dominated by Diptera (Tipulidae, Simuliidae and Chironomidae). At the 2700 m site, Trichoptera was represented by two groups found only at this site: *Atopsyche* (Hydrobiosidae) and an unidentified genus in the Polycentropodidae (Fig. 3 and Appendix).

Diel drift periodicity of benthic invertebrates showed different patterns along the altitudinal gradient. Numbers of invertebrates drifting during the night were higher than those drifting during the day at the 30, 50 and 700 m sites (Fig. 5). At the 30 and 50 m sites, the predominance of larval shrimps in postdusk drift enhanced night-time peaks (Figs 3b and 5a,b). Maximum drift densities generally occurred at sunset (18.00 h), sometimes with a peak around 03.00 h (Fig. 5a). Comparison of day-to-night drift ratios between sites indicated that the three lowermost sites were not significantly different ($P = 0.802$), however, the two high elevation sites had significantly ($P = 0.0392$) higher ratios than lower sites (Fig. 6). At higher elevation, fishless sites (1800 and 2700 m a.s.l.), drift patterns did not show any clear peak during the night (Fig. 5d). At 30, 50 and 700 m sites, all major insect groups (i.e. Ephemeroptera, most Diptera and Trichoptera) were night drifters with the exception of larval Chironomidae which showed no diel periodicity.

Discussion

Previous studies conducted in tropical regions have demonstrated that invertebrates respond in different ways to changes in elevation, with no clear relationship between altitude and diversity. Wolda (1987) found that diversity of terrestrial groups decreased at higher altitudes, while Boon, Jupp & Lee (1986) found the opposite in a study of stream invertebrates in the Blue Mountains of Jamaica. Janzen (1987) found that terrestrial invertebrate diversity increased incrementally with elevation until a threshold or plateau was reached at mid-elevations. In the present study
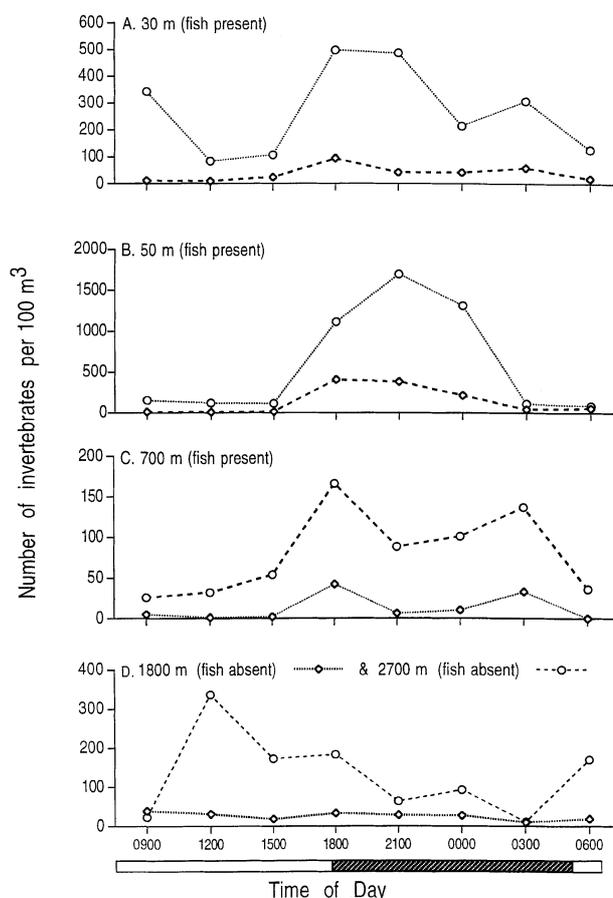

Fig. 5 Invertebrate drift patterns in study streams along the altitudinal gradient: (a) 30 m a.s.l., Cano Negro (dashed line) and Cano San Jose (dotted line); (b) 50 m a.s.l., Salto (dashed) and Sura (dotted); (c) 700 m a.s.l., Villalobos (dashed) and Chiquiza (dotted); (d) 1800 m a.s.l., La Legua and 2700 m a.s.l., Barva Creek.

no relationship was found between altitude and either insect diversity or taxon richness. Flowers (1991) also found no relationship between these parameters in his study of Panamanian streams.

Taxon richness values reported here are similar to those reported for other sites in Central America. Panamanian streams located at elevations below 50 m a.s.l. had around twenty to thirty-four taxa of insects (Flowers, 1991), a range that matches the undisturbed lowland site at La Selva (nineteen to thirty-six morphotypes), but which is higher than that found in disturbed streams draining banana plantations (thirteen taxa). Mid-elevation sites along the La Selva-Braulio Carrillo corridor were as diverse as these same elevations in Panama (Flowers, 1991).

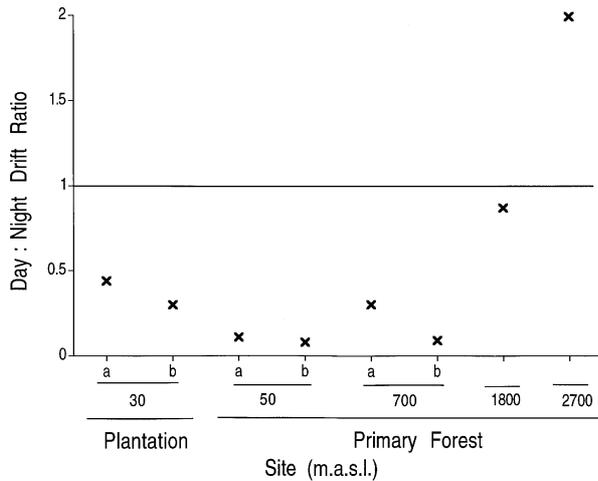While banana plantations have been shown to cause

Fig. 6 Day-to-night drift ratios of invertebrates in streams along the altitudinal gradient.

increased sedimentation and eutrophication, and also pesticide loading that results in toxic effects on invertebrates and fishes (e.g. Salame, 1993; Hernandez & Witter, 1996; Castillo, de la Cruz & Ruepert, 1997; Henriques *et al.*, 1997), much of the literature on effects in freshwater systems is anecdotal in nature and few scientific studies have actually quantified these impacts; for example, it was not possible to find any published studies that documented invertebrate communities in low-order streams draining banana plantations to which results obtained by the present study could be compared. While the highly disturbed nature of streams draining banana plantations undoubtedly contributed to the low taxonomic diversity that was observed at this site relative to other sites, interpretation is confounded by differences between sites and a paucity of relatively undisturbed 'reference' sites; for example, while the forested catchments of La Selva Biological Station are also located in the lowland, tropical, wet forest life zone (Fig. 2), they are underlain by relatively recent Pleistocene lava with shallow alluvial deposits, and streams draining the area are fed by phosphorus-rich springs (Pringle & Triska, 1991). In contrast, banana plantations are characterized by deep alluvium and streams in this region are lower gradient with an absence of phosphorus-rich springs (Pringle *et al.*, 1990). As most of the alluvial plain surrounding the banana plantations has been deforested and is under pasture or secondary forest, there are few suitable reference sites.

Drift periodicity

Periodicity in benthic invertebrate drift is a well known phenomenon reported in a wide variety of lotic systems throughout the world (see reviews by Waters, 1972; Allan, 1995). Strong nocturnal drift activity has been hypothesized to be related to the presence of predators; for example, visual predators such as fish represent a major source of mortality for benthic insects that enter the water column during the day (Flecker, 1992; Brewin & Ormerod, 1994). A complementary hypothesis is that the nocturnal activity of invertebrate predators and night-feeding fish results in an increase in entrance rates of benthic invertebrate prey into the drift as they attempt to escape predation or avoid competition (e.g. Hildrew & Townsend, 1980; McIntosh & Townsend, 1994). As pointed out by Brewin & Ormerod (1994), however, while the 'predation risk hypothesis' is attractive, other variables along the altitudinal gradient (e.g. temperature and hydrological factors) may also influence temporal drift patterns.

In this study, drift was strongly nocturnal in the presence of diurnally feeding fish. The lowermost sites (30, 50 and 700 m) were characterized by nocturnal drift densities that were several times higher than diurnal densities. At these locations, predator communities were dominated by diurnally active fish and nocturnally active omnivorous shrimps (*Macrobrachium* spp.) (Table 1). With the exception of the nocturnal taxon *Gymnotus cylindricus* La Monte [which has been collected at the 50 m site and is quite rare (W. Bussing, Universidad de Costa Rica, personal communication)], all fish taxa are diurnally active. At the 30 and 50 m site, the most abundant fish fall into three different families (Characidae, Cichlidae and Poeciliidae), which include many species that are trophic generalists, feeding on aquatic and terrestrial insects, detritus, seeds and algae (Burcham, 1988; Bussing, 1994). The one fish taxon that was observed at the 700 m site (Table 1) was the poeciliid, *Priapichthys annectens* (Regan), which consumes both aquatic and terrestrial insects (Bussing, 1994).

At the two high elevation sites (1800 and 2700 m), where no fish were present, aperiodicity in drift was observed (Figs 5 and 6), despite the presence of invertebrate predators [i.e. *Atopsyche* sp. (Hydrobiosidae, Trichoptera), a cool water predator (Wiggins, 1977), and larvae of the family Polycentropodidae, which

has two of its three Costa Rican species reported as predators (Wiggins, 1977; Holzenthal, 1988)].

Benthic vs. drift sampling techniques

Both sampling techniques provided important and often complementary information on stream invertebrates. The drift sampler was effective in sampling shrimp larvae, which were common at the 30 and 50 m sites, while few to no shrimp larvae were collected with the benthic sampler. At some sites the drift sampler was more effective in collecting rare taxa, while at other sites the benthic sampler was more effective. This is a function, in part, of the total number of invertebrate specimens collected with each technique, because the chances of encountering a rare taxon are greater with a larger sample size (e.g. Pielou, 1966). Storey, Edward & Gazey (1991) found the Surber sampler to be more effective than other sampling techniques such as kick nets in detecting rare species. Kirk & Perry (1994) recommended the combination of several samplers (such as multiplate artificial substrates and gravel baskets) to obtain more reliable results than those obtained when using only one sampling device. The results obtained by the present study and those discussed above illustrate that ecological sampling methods are subject to bias and should be checked with independent methods when possible.

In the study reported here, if benthic community composition had only been examined using traditional benthic sampling techniques (e.g. kick nets, Surber samplers), the presence of freshwater shrimps would have been overlooked. The two most common shrimp genera found in the study area were omnivorous *Macrobrachium* (Palaeomonidae) and *Atya* (Atyidae, Pringle & Hamazaki, 1998). In tropical streams characterized by abundant fish (e.g. lowland streams of La Selva), adult shrimps hide during the day (Pringle & Hamazaki, 1998) under rocks, boulders, wood and within stream banks. Because of difficulties in sampling adults using traditional benthic sampling methods, previous studies have often sampled them using non-quantitative techniques, such as baited or un-baited minnow traps set during the night (e.g. Covich, 1988). As illustrated by the present study and others (Fureder, 1994; J. G. March *et al.*, unpublished observations; J. P. Benstead *et al.*, unpublished observations), drift sampling of the larval life stage also serves

as an effective means of determining whether shrimp are present in a system. Freshwater shrimp are typically amphidromous: larvae released from adult females drift downstream to the estuary, where they spend part of their life cycle, and juveniles subsequently migrate back upstream to freshwater environments. It is not clear what part of the stream environment larval shrimps inhabit during the day because they were rarely collected using benthic samplers (J. G. March *et al.*, unpublished observations).

Variations in proportions of specific taxa obtained with drift vs. benthic sampling techniques can be explained, in part, by behavioural and life history differences between invertebrate taxa; for example, Baetidae were more abundant in drift than in Surber samples because of the behavioural propensity of this group to enter the water column during the night while grazing and drift for relatively short distances (e.g. Kohler, 1985), while other taxa such as late instars of net-spinning caddisflies are often less likely to enter the drift (e.g. O'Hop & Wallace, 1983). In contrast, larval shrimps were collected primarily in drift samples at night during their long-distance migration to the estuary. J. G. March *et al.* found that the magnitude of larval shrimp drift increased in a downstream direction in a detailed study conducted within two catchments in Puerto Rico (unpublished observations). There was a significant, positive, exponential relationship between shrimp drift with length of stream channel above each of three study sites located in the two catchments. Thus, in the case of migratory shrimps, drift provides an integrated sample reflective of the total upstream catchment rather than a given study site or stream reach. Likewise, drift sampling also detects allochthonous contributions from outside of the stream channel within the catchment. This can include large microcrustacean volumes contributed by wet rice terraces and other lentic habitats that drain into rivers – in addition to terrestrial insects (Brewin & Ormerod, 1994).

The use of drift sampling in bioassessment protocols in tropical streams

We propose that drift sampling be used as a standard complementary tool to benthic sampling in assessments of water quality and invertebrate community composition in tropical streams, 'where invertebrate

species with migratory life cycles are common and often major faunal components (e.g. shrimps)'.

While the choice of sampling methods is obviously dependent on the question(s) being addressed, several aspects of drift sampling enhance its value as a complementary tool to benthic sampling. First, while drift samplers are biased towards collection of those organisms that enter the water column (as discussed above) and they do not provide a quantitative estimate of benthic invertebrates per area of stream bottom, they represent an integrated sample of invertebrates from a variety of habitats. While it is acknowledged that drift sampling alone may not provide data representative of some systems (e.g. those characterized by oligochaetes, molluscs, and/or heavy-cased Trichoptera), it can serve as an effective complementary tool to direct sampling of one or a few habitats using traditional benthic sampling. Second, drift samples are fairly 'clean' (i.e. invertebrates are not mixed with substrate from the stream bottom, as frequently occurs in Surber samples), making the sorting process easier and faster. Third, drift sampling is non-destructive (i.e. it does not disturb the bottom substrate as do benthic sampling techniques).

Combined drift and benthic sampling have been used effectively in studies of fish feeding and prey selection in lotic systems (e.g. Dahl & Greenberg, 1996). Brewin & Ormerod (1994) found a significant correlation between the percentage abundance of taxa in benthic samples collected in kick nets across all habitat types and drift composition in their study of macroinvertebrate drift along an altitudinal gradient in Nepal. The potential value of drift sampling in assessing species composition and monitoring water quality has also been illustrated in studies of larval Chironomidae (e.g. Wilson & McGill, 1977; McGill, Wilson & Bright, 1973; Wilson, 1987).

Biological monitoring of riverine systems to assess water quality is a common practice in temperate zones (e.g. Plafkin *et al.*, 1989; Southerland & Stribling, 1995); for example, rapid bioassessment protocols (RBPs) have been designed to establish guidelines for water quality monitoring throughout the U.S.A. Such RBPs are often based on assessment of the relative abundances of benthic macroinvertebrates (e.g. Lenat, 1993; Barbour, Stribling & Karr, 1995; Wallace, Grubaugh & Whiles, 1996).

In the present study, the *combined* use of both drift and benthic sampling techniques met those criteria

that are considered to be most important in choosing a sampling technique for RBPs: (i) ability to provide data representative of the study site; and (ii) ease and facility of use. To improve its facility of use (e.g. in *rapid* bioassessment protocols), drift sampling can be conducted during postdusk intervals between 18.00 and 21.00 h in order to capture potential peaks in invertebrate drift density (J.P. Benstead *et al.*, unpublished information).

The use of drift sampling as a standard technique in bioassessment protocols in tropical rivers promises to provide critical information on the presence or absence of migratory components of the invertebrate community and also on the timing and magnitude of their migration. This is important, as migratory biota such as freshwater shrimps are a major energetic link between tropical rivers and their estuaries. The ecological impact of human activities (e.g. land-use, water abstraction, damming) that disrupt this migratory connection is becoming increasingly understood in tropical streams (e.g. Pringle, 1997; Pringle & Scatena, in press; J. P. Benstead *et al.*, unpublished information); for instance, Benstead *et al.* found that water abstraction associated with a dam on one of the main rivers draining Puerto Rico's Caribbean National Forest disrupted stream connectivity by causing direct mortality of over 50% of migratory shrimp larvae, which were entrained into water intakes for municipal water supplies.

In conclusion, the use of both benthic and drift sampling techniques provided important and often complementary information on stream invertebrate communities along an altitudinal gradient extending from near sea level to 2700 m a.s.l. on Costa Rica's Caribbean Slope. While data from benthic samples indicated that insects (Chironomidae and Ephemeroptera) were the major invertebrate faunal component at all sites, drift samples indicated that shrimps were also a dominant component at lower elevations (i.e. 30 and 50 m sites). It is recommended that drift sampling be included as a standard technique and complementary tool to benthic sampling in biological assessments in tropical streams which are often characterized by migratory invertebrate taxa such as shrimps.

Acknowledgments

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Appendix 1

Total percent contribution of each taxon in drift (D) and Surber (S) samples in streams (a and b) along the La Selva-Braulio Carrillo altitudinal gradient (see Table 1 for stream name associated with 'a' and 'b')

	Banana Plantations				Primary Forest											
	30 m				50 m				700 m				1800 m		2700 m	
	a		b		a		b		a		b					
Taxa	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S
Larval shrimp	50.06		64.68		53.24	0.84	59.52									
Acari	0.42						0.20						0.95		6.35	3.90
Amphipoda		16.55														1.30
Gastropoda		2.76					1.93	0.04	5.05							
Ephemeroptera															6.35	
Baetis? sp			0.17	0.18	10.06	2.63	12.09	12.55	25.59	8.56	46.81		6.67		1.59	5.41
Baetodes sp					0.38	1.23	0.69	0.11	13.96		11.91		3.81			0.68
Caenis sp	0.08			0.36												
Campylocia sp												0.96				
Epeorus sp											1.11					
Ephemeridae					0.02											
Leptohyphes sp					20.28	41.88	8.73	15.45	2.33	2.85	6.92			11.57		
Moribaetis sp																
Stenonema sp					0.02	0.18	0.08									
Thraulodes sp						1.93	0.61	0.86	2.33	2.85	3.05	5.73			4.76	
Traverella sp					0.38	0.35										
Tricorythodes sp													7.62			
Ulmeritus sp			0.18								0.96					

	Banana Plantations				Primary Forest											
	30 m				50 m				700 m				1800 m		2700 m	
	a		b		a		b		a		b					
Taxa	D	S	D	S	D	S	D	S	D	S	D	S	D	S	D	S
Plecoptera																
Anacroneuria sp							0.11				1.38		0.95			
Hemiptera																
Gerridae	0.08				0.05						0.28					
Mesoveloidea sp											0.28					
Naucoridae	0.76				0.04	0.53			2.85		0.28	0.96		3.86		
Notonectidae									1.43							
Veliidae				1.26	0.04	0.26			1.43				0.95			
Odonata			0.34													
Argia sp									2.85				0.95	3.86		
Brechmorhoga sp					0.15	0.35			1.43		0.55	0.96	0.95	3.86		
Gomphidae		0.72			0.02							0.96				
Heteragrion sp				1.98	0.04	0.35										
H. erythrogastrum					0.15		0.04									
Hetaerina sp					0.09		0.08	0.11					1.90			
Protoneuridae			0.18													
Coleoptera																
Curculionidae											0.96				1.59	
Dytiscidae									1.43		0.28	0.96	0.95			
Elmidae	0.17			0.36	0.73	6.75	0.81	13.73	2.33	44.24	1.66	9.56	1.90	7.72		
Gyrinidae							0.04									
Hydrocasphidae						0.61		1.61								
Lampirydae					0.07											
Psephenidae									5.71		0.28	2.87				
Ptilodactylidae					0.02						0.28					
Staphylinidae	0.08				0.05								2.86		1.59	2.71
Other Coleoptera					0.07						1.11		16.98	7.72	3.17	3.38
Lepidoptera																
Pyralidae	0.17				0.40	3.07		1.72			0.28		11.43	7.72		
Megaloptera																
Corydalus sp									1.43							
Trichoptera																
Calamoceratidae					0.02		0.04				0.28					
Glossosomatidae						0.18		0.11								
Hydrobiosidae																10.82
Hydropsychidae					3.47	7.01	4.77	2.15			0.83		4.74	3.86		
Hydroptilidae					2.04	5.61	2.63	16.09	1.43		0.55					
Leptoceridae											0.28	0.96	0.95			
Polycentropodidae															3.17	
Wormaldia sp					0.31	1.31	0.36									
Diptera																
Chiron. adults	35.46															
Chironomidae	12.62	77.59	34.81	93.71	1.92	4.99	4.89	20.17	16.30	15.70	9.42	70.72	3.83	19.29	33.33	24.35
Culicidae					0.07		0.16									
Forcipomyiinae					0.05		0.08								1.59	
Hexatoma sp		0.72							1.43				0.95			1.35
Muscidae															4.76	
Probezzia? sp	0.08	1.44		1.80	0.02	0.26	0.04	2.15	4.28			2.87			3.17	0.68
Simuliidae					5.74	17.78	4.08	8.05	39.54		13.57	0.96	16.19	19.29	19.05	19.62
Tipulidae					0.07											
Other Diptera													12.38	11.57	9.52	25.70