

# Spatial and temporal patterns of invertebrate drift in streams draining a Neotropical landscape

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## SUMMARY

1. Invertebrate drift in streams draining a tropical landscape in Costa Rica was studied to assess differences in assemblage composition above and below a major gradient break in geomorphic landform and to assess temporal patterns of drift in lowland reaches below the gradient break. The gradient break (~ 50 m a.s.l.) is the point at which the foothills of the Costa Rican Cordillera Central (piedmont) merge with the Caribbean coastal plain (lowlands).
2. Spatial patterns were assessed along two streams by sampling drift over 24 h once a month for 3 months in both the piedmont (90 m a.s.l.) and lowlands (30 m a.s.l.). Temporal patterns of drift were assessed through monthly diel sampling of three lowland sites over 8–10 months, encompassing both 'dry' (< 400 mm precipitation per month, November to May) and wet (July to October) seasons.
3. Drift composition was insect dominated in piedmont sites and larval shrimp dominated in the lowlands. Percent similarity of assemblages between piedmont and lowland sites was low (range 26–43%) because of high larval shrimp densities in lowland versus piedmont sites.
4. Drift densities were higher during night than day, with peaks at sunset on all dates and at all sites. Diel patterns in drift agree with previous observations for the study area and support the 'risk of predation' hypothesis.
5. Analysis of monthly patterns in lowland sites showed high variability in drift densities; however, all major taxa were found every month. Overall, there was a trend for high invertebrate densities during the 'dry' season but these trends were not significant.
6. Observed changes in drift composition support the concept of river zonation, which predicts a change in community composition along the stream continuum due to geomorphic features. Drift at lowland sites below the gradient break was dominated by shrimps, which are linked to marine environments via their migratory behaviour.

*Keywords:* drift, invertebrates, periodicity, seasonality, tropical streams

## Introduction

Stream communities are expected to change in taxonomic composition from the headwaters to the mouth. Gradual physical changes (e.g. temperature)

and abrupt changes (e.g. waterfalls) are characteristic of many streams and are major factors that influence changes in community composition. Two attempts have been developed to explain such patterns: the river continuum concept and the river zonation concept. While the former focuses on functional changes in stream ecosystems as physical and chemical parameters change downstream (Vannote *et al.*, 1980), the latter deals with changes in community composition and diversity that result from changes in the

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geomorphology of stream systems (e.g. Illies, 1964; Hynes, 1971; Harrison & Rankin, 1975; Covich, 1988). The river zonation concept provides a framework to understand how landscape features affect stream communities, a major challenge for stream ecologists (Angermeier & Karr, 1983). At least two general zones can be recognized as part of the zonation concept: mountain and lowland sites, each characterized by different faunal assemblages and separated by a geomorphic feature in the landscape (Illies, 1964). Within each zone, changes in composition through time reflect the effects of biotic and abiotic factors on benthic communities.

Along the Caribbean slope of Costa Rica, a gradient break in the landscape occurs at about 50 m a.s.l. and represents the point at which the piedmont merges with the lowland coastal plain. Although this gradient break does not represent a major feature for most terrestrial plant communities (e.g. Hartshorn & Hammel, 1994), major changes occur in the physical structure of streams. High gradient piedmont streams are characterized by the presence of boulders and turbulent water flow, while low gradient streams draining the coastal plain have substrate composed of cobble and silt and less turbulent water flow.

Drift sampling is a useful method of assessing benthic community composition, and drift dynamics can provide important information about benthic community regulation. In low-order streams, drift composition often closely reflects the benthic community (e.g. Waters, 1972; Brittain & Eikeland, 1988). Thus, several studies have recommended drift sampling as a technique for assessing benthic community composition (e.g. Wilson & Bright, 1973; Wilson & McGill, 1977; Pringle & Ramírez, 1998). Moreover, in tropical streams drift sampling can reveal the presence of community components (i.e. shrimps) that might be overlooked when only traditional benthic sampling techniques are used (Pringle & Ramírez, 1998).

In this study we assessed invertebrate drift composition in piedmont versus lowland stream sites. In addition, drift patterns were assessed in lowland sites to obtain information on temporal changes in community composition. Fluctuations in drift composition within a day can result from interactions between benthic communities and their predators and competitors (e.g. Flecker, 1992; Allan, 1995) or from abiotic disturbance. In contrast, monthly varia-

tions in drift can indicate responses of benthic communities to seasonal changes in temperature (e.g. Cowell & Carew, 1976; Stoneburner & Smock, 1979), discharge (e.g. O'Hop & Wallace, 1983) or life stages (e.g. Stoneburner & Smock, 1979; Benke, Parsons & Dhars, 1991). Available information from tropical streams remains limited to a few geographic areas, and most studies have been conducted over short periods of time (e.g. Turcotte & Harper, 1982; Flecker, 1992; Füreder, 1994; March *et al.*, 1998; Pringle & Ramírez, 1998; Ramírez & Pringle, 1998a,b).

Objectives of the present study were to: (i) examine invertebrate drift composition in both piedmont and lowland sites of two different streams; and (ii) assess both diel and monthly patterns in drift composition and density in lowland sites of three streams.

## Methods

This study took place at La Selva Biological Station (10°26'N, 84°01'W), owned and operated by the Organization for Tropical Studies. La Selva is located on the Caribbean slope of Costa Rica, near sea level (35–100 m a.s.l.), in the transition zone between the coastal plain and the foothills of the Cordillera Central. The study catchments are within the protected areas of La Selva and the adjacent Braulio Carrillo National Park. Mean annual rainfall at La Selva averages 4 m. A 'dry' season, with precipitation of less than 400 mm month<sup>-1</sup>, occurs from December to May (Sanford *et al.*, 1994). Diverse assemblages of macroconsumers (i.e. fishes and shrimps) characterize the streams of La Selva. The fish assemblage is composed of over 43 diurnally-active species (Bussing, 1994), which are mostly omnivorous, feeding on algae, detritus, seeds, and both terrestrial and aquatic insects (Burcham, 1988; Bussing, 1993). The shrimp assemblage includes at least eight nocturnally active species, which are largely omnivorous (Pringle & Hamazaki, 1998).

Although the entire area has been classified as tropical wet forest (Holdridge *et al.*, 1971), a gradient break located at about 50 m in elevation divides the streams at La Selva into two types: piedmont and lowland (Fig. 1). Piedmont streams have a relatively steep gradient with large boulders intermixed with smaller cobble substrata, turbulent water flow and low concentrations of phosphorus in the water (<20 µg L<sup>-1</sup> SRP, Pringle *et al.*, 1993). Below the

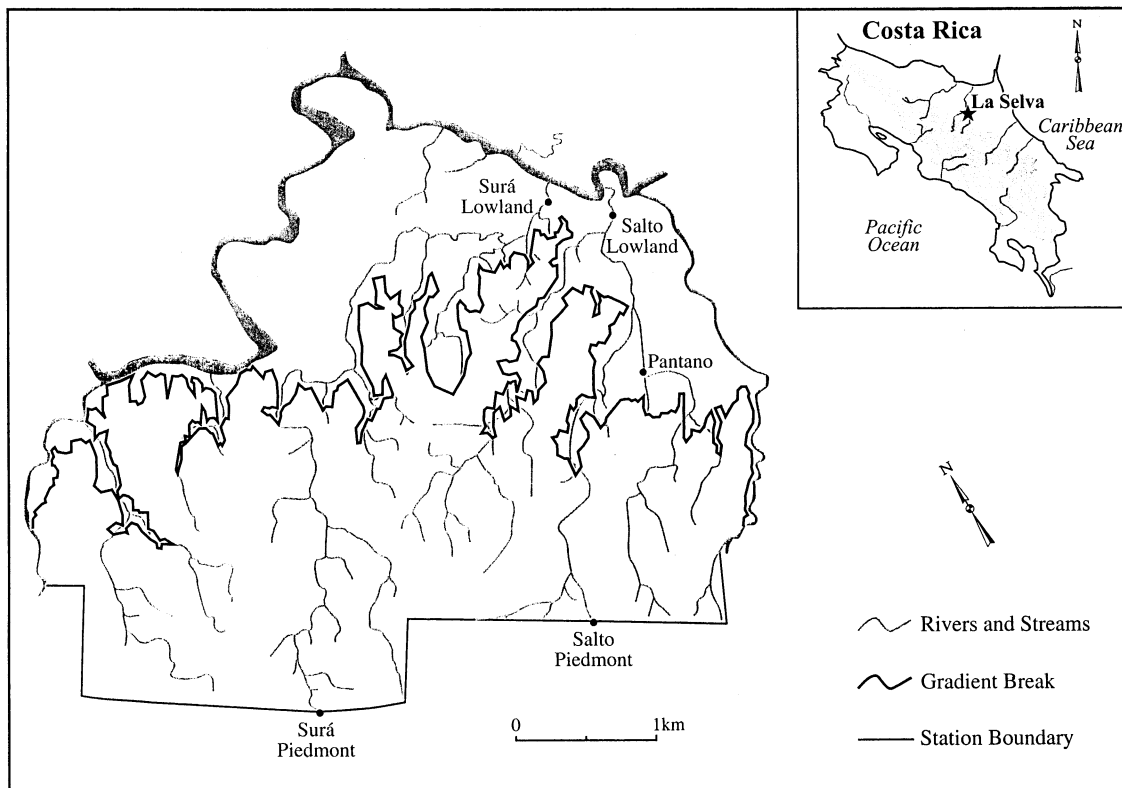
gradient break, lowland streams drain a flatter terrain, substrata are composed of silt and cobble, water flow is less turbulent and phosphorus concentrations can be relatively high (up to  $400 \mu\text{g L}^{-1}$  SRP, Pringle *et al.*, 1993) as a result of phosphorus-rich springs that discharge into streams at the gradient break. In addition, lowland streams contain deep pools and runs that are habitat to a variety of macroconsumers, such as *Macrobrachium* shrimps and large fishes (e.g. *Brycon*, *Cichlasoma*). These large pools and runs are absent in piedmont reaches. Lowland reaches also drain swampy areas that contain large amounts of organic matter.

In this study, we assessed spatial patterns of drift composition with respect to the gradient break. Piedmont and lowland sites were sampled along the main stems of the Sura and Salto (Fig. 1). An additional lowland tributary of the Salto was sampled (the Pantano) to increase our sample size for lowland sites (Fig. 1). Each site was sampled three times between August and December 1993. To assess temporal patterns in drift density and periodicity, the three low-

land sites were sampled monthly for a total of 8–10 months. Drift sampling took place between July 1993 and September 1994 in the Sura and Salto and between November 1993 and August 1994 in the Pantano.

Drift samples were collected using Wildco® (Saginaw, MI, U.S.A.) drift nets (mouth:  $0.1 \text{ m}^2$ ; length: 1.5 m; mesh size:  $363 \mu\text{m}$ ). On each date, samples were collected every 3 h over 24 h using two nets located in the main stream channel. Samples were collected by leaving the nets in the water for 10–20 min, usually sampling the entire height of the water column. Current velocity was measured with a Marsh McBirney® (Frederick, MD, U.S.A.) current meter. Invertebrate drift density was calculated by dividing the number of invertebrates in a sample by the volume of water sampled. Water volume was calculated by multiplying submerged net area, current velocity at the net mouth and sampling time.

All samples were preserved in 5–10% formalin. Invertebrates were later sorted from debris and placed in 70% ethanol. Aquatic insects were identified



**Fig. 1** Location of the five sampling sites along the Sura, Salto and Pantano streams and location of the gradient break at La Selva Biological Station, Costa Rica.

**Table 1** Mean drift densities (No. m<sup>-3</sup>) at each study site over the entire sampling period

Taxa	Lowlands			Piedmont	
	Sura	Salto	Pantano	Sura	Salto
<i>Sampling dates</i>	10	10	8	3	3
<i>Non-insects</i>					
Larval shrimps	1.91	2.05	0.27	0.00	0.00
<i>Ephemeroptera</i>					
Baetidae	0.49	0.70	0.63	0.02	0.15
<i>Leptohyphes</i>	0.61	0.40	0.30	0.00	0.12
<i>Tricorythodes</i>	0.07	0.09	0.10	0.01	0.05
<i>Odonata</i>					
Libellulidae	0.01	0.01	0.02	0.01	0.01
<i>Hetaerina</i>	0.01	0.01	0.01	0.01	0.01
<i>Coleoptera</i>					
Elmidae larvae	0.02	0.08	0.07	0.00	0.05
Elmidae adults	0.00	0.02	0.01	0.06	0.03
<i>Trichoptera</i>					
Hydropsychidae	0.10	0.32	0.16	0.04	0.04
Hydroptilidae	0.04	0.09	0.03	0.01	0.01
<i>Diptera</i>					
Simuliidae	0.15	0.58	0.05	0.11	0.39
Chironomidae	0.08	0.37	0.37	0.05	0.09
Total	3.58	3.70	1.88	0.36	1.08

**Table 2** Percent similarity in invertebrate taxonomic composition among study sites\*

	Lowlands			Piedmont	
	Sura	Salto	Pantano	Sura	Salto
<i>Lowlands</i>					
Sura	—				
Salto	77 (71)	—			
Pantano	42 (65)	58 (75)	—		
<i>Piedmont</i>					
Sura	26 (42)	28 (40)	43 (44)	—	
Salto	39 (54)	43 (56)	47 (48)	60 (60)	—

\* The number in parenthesis represents the percent similarity in absence of larval shrimps. For this comparison only two to three dates were used. For Salto and Sura in lowlands August–October, for Salto and Sura in piedmont September–November, and for Pantano November–December.

to genus whenever possible. Keys to genera were available for Ephemeroptera (Flowers, 1992), Odonata (Ramírez, 1996, 1997, unpublished data) and Trichoptera (M. Springer, unpublished data). Remaining taxa were identified to family using keys by Roldán

(1988) and Merritt & Cummins (1996) and later separated into morphotypes.

An index of percent similarity among sites was calculated using the relative proportion of each invertebrate taxon collected with respect to total density at a site (Wolda, 1983). Due to the lack of normality in the data, differences in drift densities between day and night and 'dry' and wet seasons were tested using a Wilcoxon test. Differences in drift densities among sites were tested using the Tukey–Kramer test.

## Results

### *Drift composition in piedmont and lowland sites*

Drift density and composition were dominated by insects and larval shrimp (Decapoda, see Appendix A). Most invertebrate taxa were found at all study sites over the entire study period (Table 1). Piedmont sites were dominated by Simuliidae, Elmidae, Chironomidae and Ephemeroptera (mainly Baetidae and *Leptohyphes*), while lowland sites were largely dominated by larval shrimps (Decapoda) and Ephemeroptera (mainly Baetidae and *Leptohyphes*). Simuliidae were abundant in the lowland reaches of the Salto and less so in the Sura and Pantano. The major difference in composition between piedmont and lowland sites was the lack of larval shrimps in piedmont sites (Table 1).

Percent similarity was variable among streams. Sites above and below the gradient break were more similar in the Salto than the Sura (range 26–43%, Table 2). In contrast, species composition among the three lowland sites was more similar (range 42–77%), and lowland sites of the Salto and Sura had the highest similarity (Table 2). When larval shrimps were excluded from the analysis, percent similarity between lowland and piedmont sites increased to 40–56% and similarity among lowland reaches increased to 65–75% (Table 2).

Comparisons of drift densities among sites showed high similarity (Table 3). Total drift densities ranged from 0.36 to 1.34 m<sup>-3</sup>; however, differences among sites were not significant (Table 3). The main differences between lowland and piedmont sites were the lack of larval shrimp and the higher densities of Elmidae and Diptera found in piedmont versus lowland sites (Table 3).

**Table 3** Comparison of mean invertebrate drift density at the study sites\*

	Lowland			Piedmont	
	Pantano	Salto	Sura	Salto	Sura
N	3	3	3	3	3
Total	1.34 a	0.63 a	0.88 a	1.03 a	0.36 a
Larval shrimp	0.25 a	0.38 a	0.48 a	0 a	0 a
Ephemeroptera	0.63 a	0.35 a	0.22 a	0.37 a	0.03 a
Odonata	0.02 a	0.01 a	0.02 a	0.01 a	0.04 a
Elmidae	0.05 ab	0.02 a	0.02 a	0.07 b	0.06 ab
Trichoptera	0.09 a	0.05 a	0.03 a	0.05 a	0.04 a
Diptera	0.23 ab	0.1 ab	0.08 a	0.47 b	0.16 ab

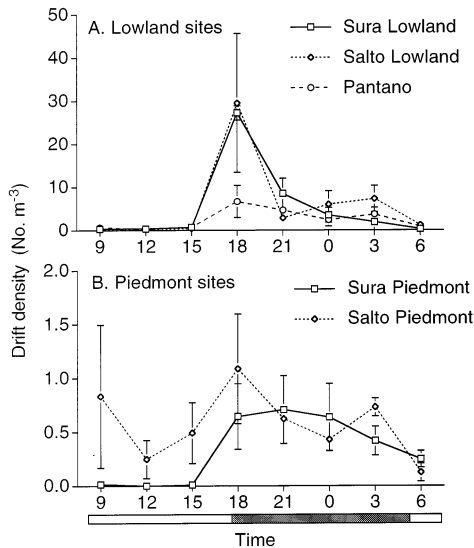
\* A Tukey–Kramer test was used to compare the sites. Different letters indicate sites that were significantly different ( $P < 0.05$ ). For this comparison only three sampling dates were used. For Salto and Sura in lowlands August–October, for Salto and Sura in piedmont September–November, and for Pantano November–January.

*Diel periodicity*

There was clear diel drift periodicity on all dates and at all sites, with increases in drift density at sunset hours (1800 hours). A typical pattern of drift periodicity for each site is presented in Fig. 2. In general, drift densities were low during the day, increased suddenly at sunset and declined over the rest of the night (Fig. 2).

In general, statistical analysis of drift densities for higher taxonomic categories (i.e. orders) showed strong nocturnal periodicity. Most taxa exhibited

peak densities at sunset and low densities throughout the rest of the diel cycle, which resulted in high variability. Total drift had strong nocturnal patterns on most dates and at all sites (Table 4). The only exception was the Pantano, where nocturnal periodicity was significant only on one date (Table 4). Larval shrimps were present in drift almost exclusively at sunset, with densities close to zero at all other times and therefore no significant differences were found between day and night (Table 4). Ephemeroptera and Diptera presented consistent nocturnal periodicity on most of the sampling dates (Table 4).



**Fig. 2** Invertebrate diel periodicity at all study sites, during January at the lowland sites and November at the piedmont sites. All values are mean  $\pm$  1 SE ( $n = 2$ ). Dark part of the bar indicates night time.

*Seasonal patterns*

Rainfall was significantly higher during the wet season from July to October (mean 493 mm month<sup>-1</sup>) than during the ‘dry’ season from November to May (mean 153 mm month<sup>-1</sup>; ANOVA,  $F_{1,11} = 38.3$ ,  $P < 0.0001$ ). Although drift densities were not strongly related with seasons, total drift densities were low during the wet season of 1993, increased during the dry season and remained high during the wet season of 1994 (Fig. 3). Most major insect taxa followed trends similar to those observed for total drift (Fig. 4). Total drift density varied from 0.25–12.8 m<sup>-3</sup> month<sup>-1</sup> (see Appendix A). Means per season are presented in Table 5 for all the major taxonomic groups found during the study. Statistical analyses showed significantly higher drift densities during the ‘dry’ season for total density, Ephemeroptera and Trichoptera in the Sura, and only Trichoptera in the Salto (Table 5).

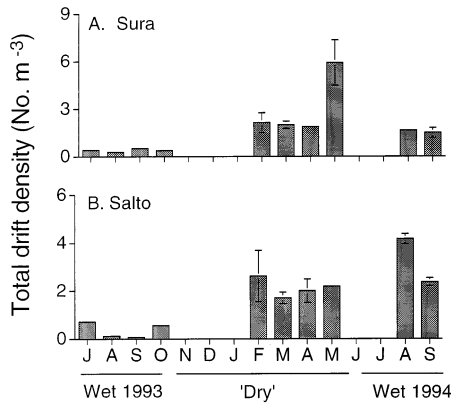
Table 4 Mean drift density (No. m<sup>-3</sup>) during day (D) and night (N) at each of the study sites (n = 4)<sup>†</sup>

	Total		Larval Shrimp		Ephemeroptera		Odonata		Elmidae		Trichoptera		Diptera								
	D	N	D	N	D	N	D	N	D	N	D	N	D	N							
<i>Sura lowland</i>																					
July 1993	0.07	0.35	**	0.02	0.17	ns	0.03	0.13	**	0.00	0.01	**	0.00	0.00	0.01	0.54	**	0.02	0.05	**	
August	0.11	0.19	ns	0.07	0.06	ns	0.02	0.09	**	0.01	0.01	ns	0.01	0.01	0.00	0.01	*	0.01	0.03	**	
September	0.34	1.04	**	0.14	0.14	ns	0.08	0.48	**	0.02	0.08	*	0.01	0.05	**	0.03	0.07	ns	0.06	0.17	*
October	0.98	1.94	ns	0.75	1.42	ns	0.31	0.31	*	0.01	0.02	ns	0.01	0.01	ns	0.02	0.04	ns	0.06	0.09	ns
February 1994	0.40	10.30	**	0.07	6.35	ns	0.24	3.44	**	0.00	0.02	ns	0.01	0.02	ns	0.15	**	0.05	0.23	**	
March	0.50	7.40	**	0.00	3.90	ns	0.30	2.83	**	0.01	0.01	ns	0.01	0.03	ns	0.19	*	0.09	0.33	**	
April	0.55	3.45	**	0.00	0.24	ns	0.30	2.65	**	0.00	0.00	ns	0.04	0.02	ns	0.23	ns	0.09	0.22	**	
May	1.27	24.38	ns	0.09	13.74	ns	0.39	7.37	*	0.07	0.07	ns	0.23	1.26	ns	1.26	1.58	0.38	1.58	*	
August	1.78	6.42	*	1.20	3.71	ns	0.36	1.96	**	0.02	0.05	ns	0.02	0.11	ns	0.11	ns	0.13	0.46	*	
September	0.42	7.85	**	0.01	5.29	ns	0.25	1.72	**	0.01	0.08	ns	0.03	0.13	*	0.09	**	0.09	0.54	**	
<i>Salto lowland</i>																					
July 1993	0.67	1.34	ns	0.34	0.11	ns	0.13	0.80	*	0.01	0.03	ns	0.04	0.01	*	0.03	0.12	0.09	0.23	**	
August	0.06	0.42	**	0.05	0.25	ns	0.01	0.27	*	0.00	0.00	ns	0.00	0.01	ns	0.06	**	0.04	0.08	*	
September	0.40	1.31	*	0.17	1.43	ns	0.28	0.68	ns	0.00	0.02	ns	0.00	0.04	**	0.01	0.15	**	0.07	0.34	*
October	0.17	1.33	*	0.07	0.30	ns	0.07	0.80	*	0.00	0.01	*	0.00	0.04	*	0.01	0.07	ns	0.02	0.07	ns
February 1994	0.05	11.37	**	0.00	6.67	ns	0.24	3.72	**	0.00	0.01	ns	0.00	0.12	*	0.04	0.34	**	0.20	0.47	**
March	0.31	3.16	**	0.01	0.05	ns	0.17	2.21	**	0.00	0.03	ns	0.00	0.01	ns	0.42	**	0.09	0.32	*	
April	0.32	3.87	**	0.00	0.19	*	0.18	2.46	**	0.01	0.01	ns	0.00	0.00	ns	0.68	**	0.06	0.46	**	
May	0.30	13.40	*	0.01	9.34	ns	0.08	2.34	**	0.00	0.01	ns	0.01	0.08	*	0.79	ns	0.16	0.79	*	
August	6.11	8.48	ns	4.94	1.32	ns	0.93	5.14	**	0.01	0.23	**	0.00	0.09	**	0.28	**	0.22	1.25	**	
September	2.01	18.58	*	1.02	14.83	ns	0.55	2.59	**	0.01	0.07	**	0.02	0.07	ns	0.25	ns	0.29	0.72	**	
<i>Pantano</i>																					
November 1993	0.73	1.10	ns	0.04	0.08	ns	0.34	0.40	ns	0.04	0.03	ns	0.06	0.05	ns	0.17	ns	0.16	0.33	ns	
December	0.44	0.85	ns	0.01	0.01	ns	0.23	0.52	ns	0.00	0.00	ns	0.05	0.00	ns	0.00	ns	0.12	0.16	ns	
January 1994	0.60	4.30	**	0.00	1.34	**	0.22	2.04	**	0.03	0.00	ns	0.08	0.03	ns	0.24	**	0.14	0.48	**	
February	0.93	3.40	ns	0.00	0.00	ns	0.51	2.13	ns	0.01	0.02	ns	0.03	0.04	ns	0.65	*	0.49	0.62	ns	
March	0.67	4.47	ns	0.00	0.01	ns	0.29	3.34	ns	0.02	0.06	ns	0.00	0.16	*	0.08	0.16	ns	0.95	1.43	ns
April	1.13	0.61	ns	0.84	0.04	ns	0.13	0.29	ns	0.01	0.04	*	0.01	0.01	ns	0.10	ns	0.05	0.12	*	
May	0.65	0.32	ns	0.41	0.01	ns	0.15	0.16	ns	0.00	0.02	ns	0.02	0.02	ns	0.02	ns	0.05	0.05	ns	
August	0.62	0.78	ns	0.27	0.04	ns	0.16	0.39	ns	0.02	0.07	ns	0.02	0.04	ns	0.03	ns	0.09	0.14	ns	
<i>Sura piedmont</i>																					
September 1993	0.08	0.57	**			0.03	0.04	ns	ns	0.01	0.06	ns	0.01	0.14	**	0.02	0.05	0.02	0.26	**	
October	0.24	0.56	*			0.01	0.06	**	ns	0.03	0.04	ns	0	0.06	ns	0.02	0.09	*	0.16	0.28	ns
November	0.07	0.61	**			0	0.05	**	**	0	0.11	**	0	0.14	**	0.01	0.07	**	0.04	0.18	*
<i>Salto piedmont</i>																					
September 1993	0.54	1.44	*			0.25	0.65	*	*	0.01	0.04	*	0.03	0.09	*	0.05	0.11	ns	0.18	0.48	*
October	0.87	2.05	*			0.24	0.73	*	*	0	0.02	ns	0.09	0.11	ns	0.05	0.06	ns	0.43	1.12	ns
November	0.42	0.72	ns			0.07	0.26	**	**	0	0	ns	0.04	0.07	ns	0.02	0.04	ns	0.26	0.30	ns

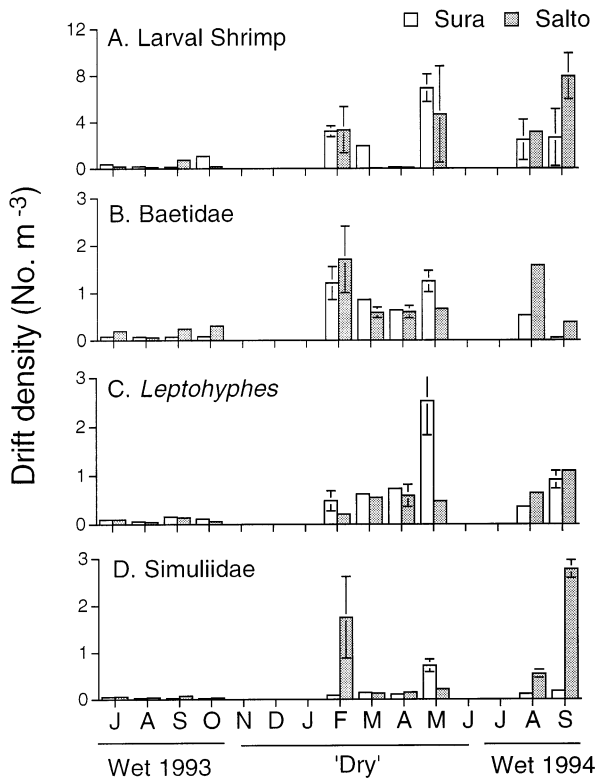
<sup>†</sup> Differences between day and night were tested using the Wilcoxon test. Probability values are \* P < 0.10, \*\* P < 0.05.

**Discussion**

Our understanding of drift dynamics in tropical streams has increased in recent years; however, studies remain limited to a few geographic areas and to short periods of time (e.g. Turcotte & Harper, 1982; Flecker, 1992; Füreder, 1994; March *et al.*, 1998; Pringle & Ramírez, 1998; Ramírez & Pringle, 1998b).



**Fig. 3** Monthly variations in total drift density in lowland sites in the Sura and Salto streams.



**Fig. 4** Monthly variations in drift density of larval shrimps, Baetidae, *Leptohyphes* and Simuliidae in lowland sites of the Sura and Salto streams.

**Table 5** Mean drift density (No. m<sup>-3</sup>) during dry and wet season at each of the lowland study sites<sup>†</sup>

	Sura		Salto			
	Dry	Wet	Dry	Wet		
<i>n</i>	4	6	4	6		
Total	6.03	1.95	*	4.16	3.41	ns
Larval Shrimp	3.05	1.17	ns	2.03	2.07	ns
Ephemeroptera	2.19	0.5	**	1.43	1.02	ns
Odonata	0.02	0.03	ns	0.01	0.03	ns
Elmidae	0.04	0.02	ns	0.03	0.03	ns
Trichoptera	0.28	0.05	**	0.29	0.09	**
Diptera	0.37	0.15	ns	0.33	0.29	ns

<sup>†</sup> Differences were tested using the Wilcoxon test; \*  $P < 0.10$ , \*\*  $P < 0.05$ , ns =  $P > 0.10$ .

The present study contributes to our understanding of drift dynamics by assessing temporal and spatial drift patterns in streams draining a tropical landscape.

*Drift composition and density*

Invertebrate drift composition in our study streams at La Selva was similar to those previously reported for other sites in Costa Rica (Füreder, 1994; Pringle & Ramírez, 1998; Ramírez & Pringle, 1998b). For example, insect-dominated drift has been reported for low-order (i.e. <3rd order) mountain streams (>700 m; Füreder, 1994; Pringle & Ramírez, 1998), while dominance by larval shrimps (over insects) in drift was reported for lowland forest streams (<40 m; Füreder, 1994; Pringle & Ramírez, 1998; Ramírez & Pringle, 1998b) and in highly disturbed streams draining banana plantations (Pringle & Ramírez, 1998).

Drift densities were similar to previous reports from other streams draining the Caribbean slope of Costa Rica (Füreder, 1994; Pringle & Ramírez, 1998), but lower than a previous study in a larger stream (Sábalo stream, 4th order) at La Selva Biological Station (Ramírez & Pringle, 1998b). Moreover, drift densities were within the upper range of densities reported for other tropical streams (e.g. Hynes, 1975; Turcotte & Harper, 1982; Füreder, 1994). Temperate studies have reported drift densities between 0.5 and 5 m<sup>-3</sup> (e.g. Armitage, 1977; O'Hop & Wallace, 1983; Cellot, 1989), which are generally similar to monthly values found in this study, with the exception of peak densities in the Sura and Salto during the 'dry' season

(see Appendix A). High densities of larval shrimps migrating downstream have been reported for several tropical streams (e.g. March *et al.*, 1998; Ramírez & Pringle, 1998b; Benstead *et al.*, 1999). Although larval shrimp densities were variable, they were low relative to those found in a larger stream at La Selva (Ramírez & Pringle, 1998b) and in other streams in the Caribbean (March *et al.*, 1998; Benstead *et al.*, 1999).

#### *Effects of landscape geomorphology*

Landscape features can result in changes in benthic invertebrate assemblages along the stream continua, as proposed by the river zonation concept (Illies, 1964; Hynes, 1971; Harrison & Rankin, 1975). Within a single stream, geomorphic features (e.g. waterfalls, canyons and rapids) can potentially restrict the distribution of macroconsumers, promoting changes in species assemblages above and below them. The presence of large waterfalls in some Puerto Rican streams results in fish-dominated communities in lowlands and shrimp-dominated communities in upper reaches, because most fish taxa are unable to surmount large waterfalls (Covich & McDowell, 1996; Pringle, 1997; March *et al.*, 1998). The gradient break at La Selva is only a subtle change in elevation that probably does not affect terrestrial communities. Most vegetation-based classification systems that have been applied to La Selva include the station within a single unit. For example, Hartshorn & Peralta (1988) describe the entire station and adjacent areas as part of the tropical wet forest life zone based on the Holdridge life zone classification system (Holdridge *et al.*, 1971). Within La Selva, dominant vegetation types and plant composition patterns are mainly the result of the interaction between soil types and the slope of the terrain (Hartshorn & Hammel, 1994). For streams, however, the gradient break represents the point at which streams change from piedmont to lowland. Such a change was reflected in drift composition. The major difference was a shift from dominance by insects in piedmont sites to larval shrimps in the lowlands.

Previous studies in the area indicate that populations of *Macrobrachium* shrimps, the most common taxa, are found from sea level to high elevation (e.g. 1800 m). Pringle & Ramírez (1998) conducted an assessment of benthic invertebrate communities in

streams along an altitudinal gradient on Costa Rica's Caribbean slope and found adult shrimps as high as 1800 m a.s.l., while larval shrimps were restricted to lowland sites (< 50 m a.s.l.). Although we sampled for only a few months above the gradient break, previous studies have found larval shrimp migrations during the entire year with no evidence of seasonality (e.g. Lewis & Fish, 1969; Ramírez & Pringle, 1998b). The restriction of larval shrimp migration to lowland reaches is evidence for a change in species composition of the shrimp community and/or a change in population behaviour (e.g. larval development strategy) with respect to the gradient break. For example, Magalhaes & Walker (1988) found shrimp populations with migratory larvae only in areas near large rivers and estuaries of the Amazon River basin, while populations farther inland completed their entire life cycle in freshwaters.

#### *Temporal patterns in lowland sites*

Densities of drifting invertebrates were higher during night than daylight hours. This pattern has been reported for other streams at La Selva (Füreder, 1994; Pringle & Ramírez, 1998; Ramírez & Pringle, 1998b), and for tropical and temperate regions as well (see reviews by Waters, 1972; Brittain & Eikeland, 1988; Allan, 1995). The 'risk of predation' hypothesis was developed as one explanation for this pattern (Allan, 1995). According to this hypothesis, benthic invertebrates are more active during the night in the presence of diurnal drift-feeding predators, such as fishes (Flecker, 1992; Allan, 1995). In addition, the presence of nocturnal benthic predators/omnivores, such as adult *Macrobrachium* shrimps in our study streams, may result in increased nocturnal drift as insects release themselves into the water column to escape predation (Sih & Wooster, 1994; Wooster, 1994). Previous studies at La Selva have demonstrated that both diurnally-feeding fishes and nocturnally-feeding shrimps significantly reduce benthic insect densities in different benthic habitats (Pringle & Hamazaki, 1997, 1998; Rosemond, Pringle & Ramírez, 1998). Other factors that may also play a role in determining invertebrate drift periodicity include diel changes in temperature and the circadian rhythms of invertebrates (Brewin & Ormerod, 1994). Of these factors, temperature changes were very small in our study streams (< 2 °C) and probably did not play a major



role in defining periodicity. Circadian rhythms of aquatic invertebrates (i.e. in the absence of predators) have not been studied at La Selva.

Seasonal patterns in abundance of stream invertebrates are difficult to assess in tropical regions and studies dealing with seasonality of aquatic insect populations in the tropics suggest the need for long-term data sets (> 4 years) to draw conclusions on seasonal patterns (e.g. Wolda & Flowers, 1985). Previous studies in other streams at La Selva Biological Station have obtained mixed results regarding the responses of benthic communities to rainfall patterns. While there is evidence that floods during the wet season reduce the abundance of benthic insect assemblages (Pringle & Hamazaki, 1997; Ramírez & Pringle, 1998a), variations in densities of mayflies over 3 years did not coincide with rainfall fluctuations (Flowers & Pringle, 1995). Although we found high drift densities in all reaches during the 'dry' season, there was no consistency between wet seasons (Fig. 3). The lack of seasonality supports the hypothesis that benthic communities in tropical streams that are characterized by warm water temperatures have continuous reproduction throughout the year (e.g. Jackson & Sweeney, 1995). Further research is needed to understand how changes in precipitation and discharge affect tropical benthic stream communities.

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**Appendix A** Monthly drift densities (No. m<sup>-3</sup>) at the all sampling sites, at La Selva Biological Station, Costa Rica

	1993				1994					
	July	August	September	October	February	March	April	May	August	September
<b>Sura, lowland site</b>										
Total	0.806	0.477	0.658	1.465	5.336	3.952	2.004	12.810	4.104	4.138
<i>Larval shrimp</i>	0.398	0.191	0.138	1.092	3.211	1.954	0.126	6.919	2.459	2.653
<i>Ephemeroptera</i>										
Baetidae	0.079	0.075	0.074	0.083	1.228	0.881	0.662	1.291	0.525	0.054
<i>Stenonema</i>		0.002			0.012			0.002	0.003	0.005
<i>Hexagenia</i>	0.001		0.003	0.002				0.002	0.002	
<i>Traverella</i>	0.001	0.001			0.001		0.001	0.049	0.003	
<i>Thraulodes</i>	0.005	0.005	0.002	0.005	0.013	0.007	0.019		0.015	0.010
<i>Leptohyphes</i>	0.101	0.061	0.158	0.120	0.481	0.633	0.743	2.545	0.364	0.916
<i>Tricorythodes</i>	0.022	0.024	0.032	0.010	0.112	0.041	0.056		0.252	
<i>Odonata</i>										
Libellulidae	0.004	0.002	0.013	0.003	0.001			0.022	0.007	0.005
Calopterygidae	0.004	0.002	0.006	0.002	0.001			0.014	0.007	0.020
Megapodagrionidae	0.006	0.002	0.008	0.001	0.001			0.024	0.003	0.013
Gomphidae	0.002	0.003	0.008	0.003	0.006			0.002	0.008	0.003
Protoneuridae	0.001	0.001	0.011	0.003					0.003	0.003
Coenagrionidae	0.002				0.001	0.005	0.001		0.010	
<i>Coleoptera</i>										
Elmidae larvae	0.010	0.011	0.024	0.007	0.014	0.015	0.028	0.074	0.033	0.003
Elmidae adults	0.002	0.006	0.002	0.002	0.002		0.001	0.016		0.003
<i>Lepidoptera</i>										
Pyralidae	0.003	0.002	0.006	0.013		0.020	0.029	0.053	0.012	0.016
<i>Trichoptera</i>										
Glossosomatidae	0.002	0.001	0.007							
Hydropsychidae	0.050	0.017	0.023	0.016	0.063	0.110	0.149	0.451	0.037	0.056
Hydroptilidae	0.019	0.001	0.012	0.011	0.016	0.008	0.013	0.262	0.023	0.024
Leptoceridae	0.001			0.001						
Philopotamidae	0.001				0.004			0.036	0.003	
<i>Diptera</i>										
Tipulidae			0.001	0.001				0.010	0.005	0.018

## Appendix A (Continued)

	1993				1994					
	July	August	September	October	February	March	April	May	August	September
Simuliidae	0.054	0.032	0.030	0.023	0.089	0.141	0.108	0.721	0.118	0.180
Chironomidae	0.023	0.017	0.072	0.041	0.054	0.063	0.049	0.233	0.156	0.116
Ceratopogonidae	0.006	0.003	0.001	0.008	0.002			0.010	0.013	0.006
<b>Salto, lowland site</b>										
Total	0.928	0.249	0.831	0.751	5.949	1.732	2.099	6.857	7.298	10.3
<i>Larval shrimp</i>	0.213	0.131	0.761	0.185	3.332	0.03	0.099	4.676	3.128	7.926
<i>Ephemeroptera</i>										
Baetidae	0.254	0.065	0.256	0.334	1.735	0.621	0.64	0.703	1.937	0.423
<i>Stenonema</i>	0.002		0.005	0.002	0.003	0.003	0.005	0.003		0.017
<i>Hexagenia</i>										
<i>Traverella</i>										
<i>Thraulodes</i>	0.01	0.012	0.012	0.015	0.003	0.003	0.023	0.031	0.017	0.022
<i>Leptohyphes</i>	0.096	0.046	0.154	0.067	0.209	0.566	0.619	0.478	0.644	1.099
<i>Tricorythodes</i>	0.051	0.011	0.037	0.02	0.031		0.039		0.429	
<i>Odonata</i>										
Libellulidae	0.01		0.007	0.001		0.003				0.006
Calopterygidae	0.006	0.001	0.013	0.001	0.003	0.005		0.003	0.028	0.017
Megapodagrionidae	0.004	0.001	0.002					0.003		0.015
Gomphidae			0.005		0.003				0.017	
Protoneuridae				0.003						
Coenagrionidae		0.001				0.006			0.067	
<i>Coleoptera</i>										
Elmidae larvae	0.024	0.007	0.022	0.006	0.465	0.001	0.012	0.01	0.045	0.223
Elmidae adults	0.001	0.003	0.005	0.015		0.003	0.003	0.035		0.134
<i>Lepidoptera</i>										
Pyralidae	0.007	0.001	0.007	0.005	0.063	0.008	0.01		0.028	0.134
<i>Trichoptera</i>										
Glossosomatidae				0.001						
Hydropsychidae	0.048	0.018	0.055	0.032	1.016	0.186	0.251	0.256	0.106	1.205
Hydroptilidae	0.012	0.001	0.014	0.007	0.436	0.025	0.102	0.141	0.022	0.161

## Appendix A (Continued)

	1993				1994					
	July	August	September	October	February	March	April	May	August	September
Leptoceridae										
Philopotamidae	0.005	0.012			0.074	0.003	0.011	0.015	0.006	
<i>Diptera</i>										
Tipulidae	0.004	0.001								
Simuliidae	0.062	0.041	0.08	0.033	1.753	0.131	0.152	0.216	0.546	2.777
Chironomidae	0.089	0.021	0.085	0.01	0.949	0.094	0.809	0.245	0.185	1.206
Ceratopogonidae	0.002	0.001	0.011	0.003				0.005	0.006	0.116
	1993		1994							
	November	December	January	February	March	April	May	August		
<b>Pantano, lowland site</b>										
Total	1.047	0.74	2.463	2.166	2.918	1.202	3.563	0.904		
<i>Larval shrimp</i>	0.065	0.015	0.669				0.332			
<i>Ephemeroptera</i>										
Baetidae	0.244	0.278	0.799	0.633	1.238	0.546	1.196	0.091		
<i>Stenonema</i>	0.006		0.001	0.014	0.016	0.008	0.042	0.003		
<i>Hexagenia</i>										
<i>Traverella</i>										
<i>Thraulodes</i>	0.013	0.008	0.006	0.005			0.033			
<i>Leptohyphes</i>	0.133	0.063	0.099	0.417	0.737	0.224	0.616	0.141		
<i>Tricorythodes</i>	0.02	0.055	0.21	0.25	0.065	0.03				
<i>Odonata</i>										
Libellulidae	0.014	0.004					0.018	0.038		
Calopterygidae	0.017	0.003	0.001		0.016			0.019		
Megapodagrionidae	0.004		0.004	0.003				0.028		
Gomphidae			0.017	0.005				0.046		
Protoneuridae										
Coenagrionidae	0.003			0.007	0.032		0.032	0.006		

**Appendix A** (Continued)

	1993		1994					
	November	December	January	February	March	April	May	August
<i>Coleoptera</i>								
Elmidae larvae	0.065	0.009	0.05	0.031	0.061	0.096	0.111	0.131
Elmidae adults		0.021	0.006	0.006	0.029			0.003
<i>Lepidoptera</i>								
Pyralidae			0.003	0.003	0.009			
<i>Trichoptera</i>								
Glossosomatidae								
Hydropsychidae	0.124	0.093	0.11	0.332	0.078	0.138	0.341	0.049
Hydroptilidae	0.003	0.007	0.021	0.012	0.047		0.086	0.013
Leptoceridae								
Philopotamidae	0.014		0.006		0.013	0.023	0.031	0.004
<i>Diptera</i>								
Tipulidae								
Simuliidae	0.042	0.048	0.049	0.087	0.032	0.015	0.05	0.084
Chironomidae	0.143	0.101	0.262	0.312	1.263	0.122	0.608	0.167
Ceratopogonidae	0.003		0.004				0.012	0.018
<hr/>								
	Sura piedmont			Salto piedmont				
	September	October	November	September	October	November		
<hr/>								
<b>Piedmont sites</b>								
Total	0.349	0.403	0.335	1.22	1.461	0.571		
<i>Larval shrimp</i>								
<i>Ephemeroptera</i>								
Baetidae	0.025	0.03	0.018	0.14	0.278	0.026		
<i>Stenonema</i>								
<i>Hexagenia</i>								
<i>Traverella</i>								
<i>Thraulodes</i>			0.002	0.129	0.034	0.063		

## Appendix A (Continued)

	Sura piedmont			Salto piedmont		
	September	October	November	September	October	November
<i>Leptohyphes</i>	0.007	0.002	0.002	0.161	0.124	0.07
<i>Tricorythodes</i>	0.01	0.004	0.005	0.098	0.046	0.006
<i>Odonata</i>						
Libellulidae	0.002	0.01	0.011	0.01	0.01	
Calopterygidae	0.003	0.01	0.016	0.01	0.005	
Megapodagrionidae	0.013	0.003	0.007	0.005		
Gomphidae		0.011	0.007	0.003		
Protoneuridae			0.004	0.005		
Coenagrionidae	0.005		0.002			
<i>Coleoptera</i>						
Elmidae larvae		0.002	0.002	0.041	0.075	0.027
Elmidae adults	0.074	0.03	0.067	0.032	0.026	0.03
<i>Lepidoptera</i>						
Pyralidae	0.005			0.011	0.008	0.002
<i>Trichoptera</i>						
Glossosomatidae		0.004		0	0.011	
Hydropsychidae	0.019	0.05	0.039	0.064	0.03	0.015
Hydroptilidae	0.017	0.002		0.023		0.006
Leptoceridae			0.002	0.002		0.002
Philopotamidae		0.004				
<i>Diptera</i>						
Tipulidae						
Simuliidae	0.101	0.15	0.078	0.239	0.669	0.256
Chironomidae	0.047	0.07	0.034	0.15	0.09	0.02
Ceratopogonidae	0.002			0.006	0.015	



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