Diel periodicity of aquatic macroinvertebrate drift in a coastal stream in northern Venezuela

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ABSTRACT
Aquatic macroinvertebrates and organic matter (OM) are transported downstream with the current, in a process that is modulated by different mechanisms in the ecosystem. Macroinvertebrate drift and OM transport are processes involving interactions between organisms and the environment at multiple spatial and temporal scales. The objective of this study was to describe benthic aquatic macroinvertebrate drift in one of the least disturbed streams of northern Venezuela during the dry season. Aquatic macroinvertebrate drift and OM transport were assessed on three different dates, sampling every three hours for each diel cycle using three drift nets. Aquatic macroinvertebrate drift exhibited a clear diel pattern, showing higher drift density values at night than those found during daylight, with significant differences among sampling times (two-way ANOVA, \(F_{14,48} = 33.51, p < 0.001\)) but not among months (\(F_{7,48} = 2.012, p > 0.05\)) with no interaction between factors (\(F_{14,48} = 1.152, p > 0.05\). All sampling dates showed the same trend for diel aquatic macroinvertebrate drift patterns with mean values ranging from 0.19 to 14.81 org.\(\times\)m\(^{-3}\). Transported OM showed no significant differences for the interaction between factors (sampling time*month) (\(F_{14,48} = 0.727, p > 0.05\)) or among sampling times (two-way ANOVA, \(F_{7,48} = 1.25, p > 0.05\)) and months (\(F_{7,48} = 0.049, p > 0.05\)) with values ranging from 79.28 to 207.49 mg.\(\times\)m\(^{-3}\). The San Miguel stream showed a definite diel trend for aquatic macroinvertebrate drift with a peak at 20:00 h dominated by larval shrimp. Our results indicate that drift samples taken at different times along a diel cycle should be considered in bioassessment studies as an important part of any biodiversity survey. This study contributes to comprehend the importance of the integrity of the freshwater–estuarine–marine corridor for the conservation of aquatic fauna and management in tropical coastal streams.

RESUMEN
Los macroinvertebrados acuáticos y la materia orgánica (MO) son transportados aguas abajo con la corriente, por un proceso que es modulado por diferentes mecanismos en el ecosistema. La deriva de macroinvertebrados acuáticos y el transporte de MO son procesos que implican interacciones entre organismos y el medio ambiente a múltiples escalas espaciales y temporales. El objetivo de este estudio fue describir la deriva de macroinvertebrados acuáticos en uno de los ríos menos perturbados del norte de Venezuela durante la estación de bajas precipitaciones. La deriva de macroinvertebrados acuáticos y el transporte de MO se muestrearon en tres fechas diferentes cada tres horas para cada ciclo diario usando tres redes de deriva. La deriva de macroinvertebrados acuáticos mostró un patrón diario definido, mostrando valores más altos durante la noche y mínimos durante el día, con diferencias significativas entre los tiempos de muestreo (ANOVA de dos vías, \(F_{14,48} = 33.51, p < 0.001\)), pero no entre los meses (\(F_{7,48} = 2.012, p > 0.05\)) sin interacción entre los factores (\(F_{14,48} = 1.152, p > 0.05\)). Todos los meses de muestreo mostraron la misma tendencia para los patrones diurnos de deriva de macroinvertebrados con valores que oscilaban entre 0.19 y 14.81 org.\(\times\)m\(^{-3}\). La MO transportada no presentó diferencias significativas para la interacción entre factores (tiempo de muestreo*meses) (ANOVA de dos vías, \(F_{14,48} = 0.727, p > 0.05\)) o entre tiempos de muestreo (\(F_{14,48} = 1.25, p > 0.05\)) y meses (\(F_{7,48} = 0.049, p > 0.05\)) con valores que van desde 79.28 a 207.49 mg.\(\times\)m\(^{-3}\). El río San Miguel mostró un patrón definido para la deriva de macroinvertebrados con un pico a las 20:00 h dominado por larvas de camarón. Nuestros resultados indican que las muestras de deriva tomadas a diferentes horas a lo largo de un ciclo diurno deben ser consideradas en estudios de biomonitorio como una parte importante de cualquier levantamiento de biodiversidad. Este estudio contribuye a comprender la importancia de la integridad del corredor agua dulce-estuario-marino para la conservación de la fauna acuática y el manejo de los ríos costeros tropicales.

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Introduction

Drift is a term that defines the downstream transport of organisms such as fishes or aquatic macroinvertebrates in lotic systems [1]. Macroinvertebrate drift has been studied since the 1960’s in temperate regions [2] but studies in tropical regions have been rare. Benthic aquatic macroinvertebrates can be transported downstream in response to predation, competition, water physicochemical changes (temperature and discharge, or changes induced by anthropogenic disturbances), or passively by life histories and circadian rhythms [3–7]. Generally, drift activity is higher at night than during daylight and most taxa often show a peak right after dusk [8]. Nocturnal macroinvertebrate drift varies among size and taxa as a mechanism to reduce predation by visually feeding vertebrates, so that less vulnerable taxa are nearly aperiodic and more vulnerable taxa are strongly nocturnal [9].

In Neotropical streams, drift activity patterns of aquatic macroinvertebrates have been studied in Caribbean coastal streams [3–5,10] and Andean streams [1,7]. Macroinvertebrate drift in lowland coastal streams is dominated by larval shrimps [3,4]. Shrimp species in coastal streams are adapted to fresh water, with some of them having amphidromous life histories and requiring marine or estuarine conditions to complete their development; others are completely adapted to fresh water (Freshwaterization) [11,12]. Amphidromous shrimps breed and spawn in fresh water, but larvae and early juveniles develop and metamorphose to post-larvae in estuaries or fully marine waters and then migrate upstream into rivers [12–17]. Freshwater shrimp larvae in streams are passively transported by drifting and show a diel periodicity pattern that generally occurs at night [10].

In addition to aquatic macroinvertebrate drift, allochthonous organic matter (OM) is passively transported downstream with the current in a unidirectional fashion [18]. Coarse particulate organic matter (CPOM) input to streams is dominated by leaves, logs, tree roots, fruits, seeds, and flowers, while fine particulate organic matter (FPOM) is generated by the processing of CPOM through physical and biological factors. Apart from the CPOM transport downstream, detrital dynamics in streams also include retention and processing of the OM that enters into the channel [8,19]. CPOM supports low-order stream food webs (through ecological subsidies across terrestrial–aquatic ecosystem boundaries) integrating ecosystem processes throughout entire stream networks [18].

Aquatic macroinvertebrate drift and OM transport are fluvial processes involving interactions between organisms and the environment at multiple spatial and temporal scales. The objective of this study was to describe benthic aquatic macroinvertebrate drift in one of the least disturbed streams of Northern Venezuela during the dry season. With this study we aim to provide a reference for diel patterns of aquatic macroinvertebrate drift in coastal streams of central Venezuela (Southern Caribbean).

Materials and methods

Study site

The San Miguel stream drains the Northern slope of the Venezuelan coastal mountain range Cordillera de la Costa, with a watershed area of approximately 3300 ha emptying into the Bay of Turiamo in the Southern Caribbean. The lower reaches of the San Miguel spread across a narrow coastal plain located within a Venezuelan Naval Base, with no human settlements in the area and
minimal development, except for a few military facilities, making it one of the least disturbed streams of Northern Venezuela (Montoya et al., unpublished). Upstream, the entire watershed of the San Miguel is within the boundaries of Henri Pittier National Park. Therefore, this watershed can be considered one of the least disturbed among Northern Venezuela’s coastal streams. The average annual precipitation and temperature is 826 mm and 27 °C, respectively (data from the Ocumare de la Costa’s meteorological station, located nearby at 10° 28’ N and 67° 46’ W at 15 masl). This region is under a dry–wet rainfall regime: it is dry from November to April and wet from May to October.

The sampling site is located 2 km upstream from the mouth of the stream at 23 masl without the influence of tides (10° 25’46.3” N and 67° 50’55.9” W). At this site the San Miguel is a fifth-order lowland stream with a meandering course. Bottom substrate is characterized by gravel and sand, presence of submerged leaf litter pockets and a number of large dead tree trunks. The riparian forest is dominated by large stands of bamboo (Bambusa vulgaris Schrad. ex J.C.Wendl). Hydrologically, this stretch of the stream is wadeable and it is dominated by runs with some spare riffles and pools.

Physico-chemical variables, such as conductivity, pH, temperature, dissolved oxygen, total suspended solids, and discharge were recorded every three hours on the three different sampling dates. Temperature, dissolved oxygen, pH, and conductivity were measured in situ using YSI multiparametric sondes. Total suspended solids were determined gravimetrically, and liquid discharge was estimated through the velocity-area method [8]. Differences in the diel periodicity for those variables (taken at eight different times on three dates) were not statistically significant, with the exception of temperature. Average values (for the three sampling dates) of conductivity and pH were 61.00 μS.cm⁻¹ (± 2.08 SE, n = 3), and 7.11 (± 0.15 SE, n = 3), respectively. Dissolved oxygen concentration and percentage of saturation averaged 6.67 mg.l⁻¹ (± 0.26 SE, n = 3), and 79.81% (± 2.71 SE, n = 3), respectively. Suspended solids showed greater variation, averaging 2.24 mg.l⁻¹ (± 0.44 SE, n = 3). Discharge with an average of 0.13 m³.s⁻¹ (± 0.03 SE, n = 3), was higher in November (0.22 m³.s⁻¹), intermediate in January (0.11 m³.s⁻¹), and lowest in March (0.06 m³.s⁻¹). Finally, the average water temperature of the sampling site was 24.85 °C (± 0.61 SE, n = 3) showing significantly lower values at the end of the night and higher values on afternoons.

**Sampling design**

Macroinvertebrate drift and organic matter transport was sampled on three different dates (on 23–24 November 2009, 13–14 January 2010, and 23–24 March 2010) every three hours for a diel cycle (24 h) starting at 17:00 h each sampling date. All sampling dates coincided with periods of low moon illumination. At each sampling time, we deployed three drift nets (300 μm mesh size) parallel to the stream current for 15–45 min according to the discharge and visual assessment of the obstruction of the nets. We estimated the stream discharge (m³.s⁻¹), and the water volume that passed through each drift net using the area–velocity method [8]. Macroinvertebrate drift density and OM transport were estimated for each net by dividing the number of retained benthic aquatic macroinvertebrates or the dry mass of the organic matter in the net by the volume of water that passed through it [20]. We sampled OM along with aquatic macroinvertebrates to quantify exclusively the passive downstream transport of material.

Aqueous macroinvertebrates and organic matter were separated by passing the samples through standard sieves (1000, 500 and 63 μm). Macroinvertebrates retained on the 500 and 1000 μm were separated and identified to lowest taxonomic level possible using taxonomic keys [21,22]. CPOM (≥1000 μm) consisting of leaves, stems, flowers, and fruits was placed in an oven at 60 °C for 48 h to constant dry weight. We separated this material between “bamboo” and “others”. Material retained on 500 and 63 μm (a fraction of FPOM) was placed together and dried as described for CPOM.

Qualitative benthos samples were taken on each sampling date using a D-frame net of 300 μm mesh size, kicking the substrate for 30 s. For this purpose, transects were randomly established along a 160 m stream segment upstream from the sampling site and four replicates were taken. Aquatic macroinvertebrates were sorted out and processed in the same way as drift samples.

**Data analyses**

To assess whether or not there were differences among the total densities of macroinvertebrate drift at different sampling times and months, we carried out a two-way analysis of variance (two-way ANOVA). For this analysis, the first factor was sampling time with eight levels (17:00, 20:00, 23:00, 02:00, 05:00, 08:00, 11:00, and 14:00 h) and the second factor was month, with three levels: November, January, and March (sampling dates). Each factorial combination had three replicates (density drift on each net). Normality and homoscedasticity of variance, assessed through Kolmogorov–Smirnov’s and Levene’s tests, respectively, conformed to ANOVA assumptions after log(X + 1) transformation of data. Both tests were run using the statistical package PAST [23]. We used a post hoc Tukey test to check which homogeneous groups were significantly different from each other. Differences among sampling times and months for OM transport were also assessed using a two-way analysis of variance (two-way ANOVA). For OM data no transformation was needed to accomplish ANOVA assumptions,
which were assessed in the same way as for the transformed macroinvertebrate drift density data. We applied a nonparametric Mann–Whitney U test using the statistical package PAST [23] to determine if there were differences between the components of the organic matter drift (CPOM and FPOM).

We ordinated drifting sampling times based on a Bray–Curtis resemblance matrix generated from the non-transformed densities of macroinvertebrate orders (Collembola, Odonata, Ephemeroptera, Plecoptera, Hemiptera, Coleoptera, Diptera, Lepidoptera, Trichoptera, Decapoda, Acari) using a non-metric multidimensional scaling procedure (NMDS). The bi-dimensional ordination of the sampling times generated by NMDS was grouped using cluster overlay on the NMDS plot. The cluster analysis routine with a group average linkage choice was performed on a resemblance Bray-Curtis matrix of the data. Boundaries of groups generated by the cluster were set to a similarity value of 50% and graphed accordingly. Multivariate analyses were conducted using PRIMER v6 [24].

Results
Macroinvertebrate drift in the San Miguel stream showed a clear diel pattern, with higher drift density values at night (peaked at 20:00 h) and lows during daylight sampling times (Figure 1). The three sampling dates showed the same trend for diel macroinvertebrate drift patterns with mean values ranging from 0.19 to 14.81 org.m\(^{-3}\). Differences among sampling times were statistically significant (two-way ANOVA, \(F_{7,48} = 33.51, p < 0.001\)), but there were no differences among months (\(F_{2,48} = 2.012, p > 0.05\) with no interaction between sampling time and month (\(F_{14,48} = 1.152, p > 0.05\)). A Tukey post hoc test showed 3 homogeneous groups: a first group (a), corresponding to daylight sampling times, and the other two groups (b and c) representing night-time samplings, although sampling times 08:00 and 17:00 h, corresponding to the dawn and dusk sampling hours, overlapped homogeneous groups a (day) and b (night). Group c corresponded to the sampling time that showed a peak in density drift values (20:00 h) (Figure 1).

Macroinvertebrate drift was composed of several taxa including crustaceans, insects, and arachnids (Table 1). Larval shrimps of the genus *Macrobrachium* (Decapoda, Palaemonidae) accounted for most of the total number of aquatic macroinvertebrates collected (76%). Ephemeroptera, Trichoptera, and Diptera were also abundant and represented more than 70% of insect drifters. Most aquatic macroinvertebrates showed higher drift densities at night with a peak at 20:00 h dominated by larval shrimps drifting downstream. The orders Collembola, Hemiptera, and Hydracarina showed no definite diel trends (Figure 2).

Qualitative benthic samples, taken haphazardly from different mesohabitats, such as bare sand and gravel, leaf litter pockets, and snags showed a less diverse array of taxa than that found in the drift samples. Benthic aquatic macroinvertebrates were represented by Diptera (mostly Chironomidae), Decapoda: *Macrobrachium olfersii* (Wiegmann, 1836), *M. faustinum* (de Saussure, 1857) and *Potimirim sp.*, Trichoptera: *Leptonema* and *Smicridea*, Ephemeroptera: *Baetidae* and *Leptohyphidae*, and Hemiptera (Veliidae) (Table 1).

Non-metric multidimensional scaling (NMDS) based on drift density of macroinvertebrate taxa showed a stress value of 0.08, which is considered a good and reliable ordination [24]. A cluster overlay, set at 50% boundary similarity, on the NMDS plot defined our three different groups which were labeled: (a) “day”, (b) “night”, and (c) “peak night” (Figure 3(a)). At 20:00 h, the drift was mostly composed of Decapoda shrimp larvae (Figure 3(b)), which accounted for the peak drift activity.

Figure 1. Diel aquatic macroinvertebrate drift (organisms per cubic meter, org.m\(^{-3}\)) at the San Miguel stream. November 2009, January and March 2010 samplings are represented by clear, gray, and filled bars, respectively (mean ± SE, \(n = 3\)).

Notes: Continuous line indicates the average of the three sampling dates. Letters indicate homogeneous groups after a Tukey post hoc test. Groups: ‘a’ day, ‘b’ night / dawn and dusk, and ‘c’ peak night. Bar at the bottom of the graph depicts daylight (clear) and night (filled) sampling times.
Transported OM presented no interaction between factors (sampling time*month) \((F_{14,48} = 0.727, p > 0.05)\) and non-significant differences among sampling times \((F_{7,48} = 1.25, p > 0.05)\) or months \((F_{2,48} = 0.049, p > 0.05)\) were found. Average OM transport ranged from 79.28 to 207.49 mg.m\(^{-3}\) and non-diel pattern was found (Figure 4). There was a significant difference between the components of organic matter, CPOM, and FPOM (Mann–Whitney U test, \(p < 0.001\)), with a dominance of CPOM fraction over FPOM. Average transported OM ranged between 58.48 and 189.97 mg.m\(^{-3}\) for CPOM, and

Table 1. Absolute number of aquatic macroinvertebrates for each of the three sampling dates in drift samples and presence/absence of taxa for qualitative benthic samples in the San Miguel stream.

| Taxa                | Aquatic macroinvertebrate Drifter | Qualitative benthic aquatic macroinvertebrates |
|---------------------|-----------------------------------|-----------------------------------------------|
|                     | November | January | March |                               |
| Collembola          | 5        | –       | 12    |                               |
| Odonata             | –        | 4       | –     |                               |
| Calopterygidae      | 1        | 2       | –     |                               |
| Coenagrionidae      | 1        | –       | –     |                               |
| Gomphidae           | 1        | –       | –     |                               |
| Ephemeroptera       |          |         |       |                               |
| Baetidae            | 612      | 56      | 60    | X                             |
| Caenidae            | 23       | 12      | 1     |                               |
| Leptophlebiidae     | 173      | 37      | –     |                               |
| Leptophlebiidae     | 48       | 25      | 35    |                               |
| Farrodes            | 123      | 12      | 9     |                               |
| Plecoptera          |          |         |       |                               |
| Perlidae            | 4        | –       | –     |                               |
| Hemiptera           | 11       | 5       | 3     | X                             |
| Gerridae            | 12       | 6       | 8     |                               |
| Coleoptera          |          |         |       |                               |
| Elmidae             | 1        | –       | –     |                               |
| Psephenidae         | 5        | 39      | –     |                               |
| Scirtidae           | 8        | –       | –     |                               |
| Diptera             |          |         |       |                               |
| Chironominae undet. | 158      | 65      | 115   | X                             |
| Chironominae         | 211      | 48      | 92    | X                             |
| Orthocladiinae      | 76       | 63      | 5     | X                             |
| Tanytarsinae        | 103      | 90      | 77    |                               |
| Simulidae           |          |         |       | X                             |
| Simulium            | 1        | –       | –     |                               |
| Ceratopogonidae     | 30       | 11      | –     |                               |
| Ceratopogonidae pupae | 33     | 12      | 9     |                               |
| Psychodidae         | 2        | –       | –     |                               |
| Tipulidae           | 2        | 2       | 9     |                               |
| Muscidae            |          | 4       | –     |                               |
| Lepidoptera         |          |         |       |                               |
| Pyralidae           | 1        | 4       | –     | X                             |
| Trichoptera         |          |         |       |                               |
| Hydropsychidae      |          |         |       |                               |
| Leptonema           | 88       | 108     | 135   | X                             |
| Simisciida          | 49       | 64      | 83    | X                             |
| Hydroptilidae       | 45       | 12      | 5     |                               |
| Leptoceridae        |          |         |       |                               |
| Nectopsyche         | 27       | 20      | 4     |                               |
| Odontoceridae       | 5        | –       | –     |                               |
| Glossosomatidae     | 16       | 26      | –     |                               |
| Decapoda            |          |         |       |                               |
| Palemonidae         |          |         |       |                               |
| Macrobrachium spp. larveae | 4232 | 611      | 1100 |                               |
| Macrobrachium spp. | 1        | 1       | –     |                               |
| Macrobrachium olfersi | 1      | –       | 1     |                               |
| Macrobrachium fuscissimum | 1 | –       | –     |                               |
| Macrobrachium spp juvenile | 2 | 4         | 2     |                               |
| Macrobrachium sp    | 2        | –       | –     |                               |
| Atyidae             |          | 4       | –     |                               |
| Potamobius sp       |          |         |       |                               |
| Acari               | 6        | 31      | 17    |                               |

Note: X = presence.

at that time. Ephemeroptera, Trichoptera, and Diptera drifted largely at night (Figure 3(c) for Ephemeroptera).

Besides drifting aquatic macroinvertebrates, terrestrial arthropods were also found drifting throughout the diel cycle with no recognizable pattern. Average values for terrestrial drifters ranged between 0.01 and 2.60 orgs.m\(^{-3}\). Nymphs and adults of bamboo lace bugs (Hemiptera: Tingidae) represented more than 50% of the total number of drifting terrestrial arthropods. Other terrestrial taxa were represented by ants and wasps, adult mosquitoes, bugs, and beetles.
between 13.54 and 38.16 mg.m$^{-3}$ for FPOM. Leaf litter, stems, and detritus from $B. vulgaris$ accounted for most of CPOM at all sampling times and dates (ranging from 67 to 83% of total CPOM).

**Discussion**

Diel periodicity of macroinvertebrate drift showed a distinctive pattern with high drift density values at night-time (with a peak at the beginning of the night) and reduced drift during daylight hours. This diel pattern conforms to previous studies in tropical lowland streams [1,3–5]. This characteristic diel drift pattern had been explained by different ecological hypotheses such as visual predation presence, macroinvertebrate’s life histories, and physicochemical responses. It is assumed that an adaptation to avoid predation by visual macro-predators such as fishes, crabs, and shrimps is the most accepted explanation [1,9,25]. Macroinvertebrate drift composition in tropical streams is typically dominated by insects in high gradient streams, and by larval decapods in lowland coastal rivers [4].

The observed pattern of diel periodicity of macroinvertebrate drift in the San Miguel stream was driven mostly by larval shrimp, which appeared in large numbers at drift peak hours. Previous studies in tropical coastal streams have also recorded the importance of larval *Macrobrachium* (Decapoda: Palaemonidae) drift during night time in Central America [3,4,10] and in Southeast Asia [17,26]. Coastal streams host unique fauna including fish and invertebrates that move between freshwaters and estuarine/marine waters.

**Figure 2.** Aquatic macroinvertebrate orders drift (organisms per 100 cubic meters, org.100 m$^{-3}$) in the San Miguel stream during the dry season (mean ± SE, $n = 3$). Notes: Light grey and black lines correspond to taxa showing no daily trends, or definite daily trends, respectively. Bar at the bottom of the graph depicts daylight (clear) and night (filled) sampling times.
Ephemeroptera, Trichoptera, Diptera, and Coleoptera also had a high drift density during night time. Flecker [1], Ramírez and Pringle [3,4] and Pringle and Ramírez [5] found similar patterns in lowland streams and they have proposed the risk of predation or competition as a plausible explanation for this outcome. Our results are similar to studies that have fish predator presence [1,3,5,9], with the San Miguel stream ichthyofauna consisting primarily of invertivorous fishes.

Amphidromous shrimp from coastal streams have a life history strategy that require access to brackish or marine waters as newly hatched larvae in order to complete their initial developmental stages [15,27]. In the case of the San Miguel stream, Macrobrachium larvae are passively transported by drifting and show a diel periodicity pattern that generally occurs at night time, behavior that has been corroborated in both laboratory studies and field observations [10].

Figure 3. A two-dimensional plot of the non-metric multidimensional scaling (NMDS) ordination based on the aquatic macroinvertebrate drift orders with overlay cluster groups delineated in dashed lines at a boundary similarity value of 50% (A). Bottom panels show bubble plots representing drift density of Decapoda (B) and Ephemeroptera (C).

Figure 4. Average diel pattern of transporting organic matter (milligrams per cubic meter, mg.m⁻³, mean ± SE, n = 3) in the San Miguel stream for the three sampling dates. Notes: Coarse particulate organic matter (CPOM) and fine particulate organic matter (FPOM) are represented as stacked clear and gray bars, respectively. Bars at the bottom of the graphs depict daylight (clear) and night (filled) sampling times.
such as *Gobiomorus dormitor* Lacépède, 1800, *Awaous banana* (Valenciennes, 1837), *Eleotris* spp., *Agonostomus monticola* (Bancroft, 1834), and *Astyanax bimaculatus* (Linnaeus, 1758) (authors’ personal observation). The nocturnal drift periodicity and high insect drift densities might reflect interspecific relations between aquatic macroinvertebrates and macroconsumers. The predation hypothesis indicates that in the presence of diurnal predators, benthic invertebrates would be more active during the night [1,8], and the macroconsumers visual senses provide awareness and allow better capture during light hours [28].

In this study, drift samples were taken exclusively during the dry season, and despite absolute drift density values varying between sampling dates, their day–night relative proportions were maintained and a drift pattern for the San Miguel during dry season is clearly evident in our study. However, drift density pattern clearly changes between seasons in tropical streams [4–7], showing patterns with a distinctly higher drift activity during basal flows (dry season) and the absence of defined trends in drift activity during the rainy season or periods of high flow. A recent observation of the diurnal pattern of macroinvertebrates drift during an unpredictable torrential flow in the dry season at San Miguel showed a similar drift pattern such as the one described in this study. Therefore, we recommend long-term studies in tropical streams, acknowledging their high seasonal hydrological variability. This recommendation is particularly pertinent since there is a paucity of studies dealing with macroinvertebrate drift in the continental coastal streams of South America.

In our study, we also found terrestrial arthropods drifting. Previous studies have shown that terrestrial arthropods input to streams are an important energy source for stream predators, but these trophic linkages are poorly studied in the tropics [29–31]. This energy subsidy of terrestrial arthropods into streams is affected by riparian vegetation [32]. In our case, bamboo lace bugs (Heteroptera: Tingidae) were the dominant taxa, reflecting the importance of bamboo as riparian species to this lotic system.

Qualitative benthic samples showed a less diverse array of taxa than those found in the drift samples. Drift and benthic sampling techniques provided important and often complementary information on stream macroinvertebrate diversity. The drift sampler was effective in sampling shrimp larvae and collecting rare taxa, while the benthic sampler was more effective collecting insects and large decapods. The use of both sampling techniques is important to characterize benthic fauna in lowland streams [5,6].

Litter allochthonous input of OM is a fundamental energy and nutrient source for aquatic communities [8]. This input can be either processed *in situ*, exported or sequestered [8,19]. As expected, there was no discernable diel periodicity pattern for organic matter transport, with our results being similar to values recorded by Rodríguez et al. [33] for a tropical headwater stream. More than 75% of drifting CPOM was *B. vulgaris* litter, directly related with its abundance on the stream margins. OM transport is strongly influenced by the phenology of the riparian vegetation, rainy period, and hydrological events [34–36]. Although OM transport has been found correlated with stream discharge, there is no consensus explaining this relationship, but for tropical streams Crowl et al. [35] found that macrobiota influences OM transport and this process interacts with hydrology producing erratic patterns.

This study provides evidence of a definite aquatic macroinvertebrate diel drift pattern in one of the least disturbed streams of Northern Venezuela. Our results support that drift samples should be considered in bioassessment studies as an important part of any biodiversity survey, including sampling at different times along a diel cycle. As shown by Johnson & Covich [37] and Montoya et al. [38] sampling at night produces a more precise richness estimation of the fauna and gives a better understanding of animal behavior. Our results also showed that the aquatic macroinvertebrates diel drift pattern is driven by shrimp larvae. For amphidromous decapods in coastal streams, drift is a fundamental part of their life histories and the integrity of the freshwater–estuarine–marine corridor in coastal streams is central for the persistence of populations of these types of organisms [16,39,40]. Alterations to this stream corridor through damming, land use, and water pollution by human activities [41,42] could adversely impact the conservation of amphidromous species, their ecosystems [43,44], and even human health [45].

**Geolocation information**
San Miguel stream, Aragua State, Venezuela. 10° 25′ 46.3″ N and 67° 50′ 55.9″ W.

**Acknowledgments**

The Venezuelan Army granted access to the Naval Base in Turiamo allowing us to conduct our research. We thank Evelyn Medina, Eber Pérez, Victoria D’Orlemont, Massiel Pinto, Gabriela Sánchez, and Giovana Acha for fieldwork support. Beatriz López provided valuable help identifying shrimps and Katusca González in identifying fish. We also thank Bruno Mattern for logistic support. We are grateful to Edwin Juarez for correcting the English. We also thank the two anonymous reviewers whose suggestions helped to improve this manuscript.

**Associate Editor:** Blanca Rios-Touma.

**Disclosure statement**

No potential conflict of interest was reported by the authors.
Funding
This research was funded by IVIC under [project number 938], “Stream metabolism of coastal streams of Cordillera de la Costa”.

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