

Importance of Terrestrial Arthropods as Subsidies in Lowland Neotropical Rain Forest Stream Ecosystems

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ABSTRACT

The importance of terrestrial arthropods has been documented in temperate stream ecosystems, but little is known about the magnitude of these inputs in tropical streams. Terrestrial arthropods falling from the canopy of tropical forests may be an important subsidy to tropical stream food webs and could also represent an important flux of nitrogen (N) and phosphorus (P) in nutrient-poor headwater streams. We quantified input rates of terrestrial insects in eight streams draining lowland tropical wet forest in Costa Rica. In two focal headwater streams, we also measured capture efficiency by the fish assemblage and quantified terrestrially derived N- and P-excretion relative to stream nutrient uptake rates. Average input rates of terrestrial insects ranged from 5 to 41 mg dry mass/m²/d, exceeding previous measurements of aquatic invertebrate secondary production in these study streams, and were relatively consistent year-round, in contrast to values reported in temperate streams. Terrestrial insects accounted for half of the diet of the dominant fish species, *Priapichthys annectens*. Although terrestrially derived fish excretion was found to be a small flux relative to measured nutrient uptake rates in the focal streams, the efficient capture and processing of terrestrial arthropods by fish made these nutrients available to the local stream ecosystem. This aquatic-terrestrial linkage is likely being decoupled by deforestation in many tropical regions, with largely unknown but potentially important ecological consequences.

Abstract in Spanish is available in the online version of this article.

Key words: arthropod; ecosystem; food web; nutrient cycling; stream; subsidy.

STREAM ECOSYSTEMS DEPEND ON INPUTS OF ORGANIC MATTER from the riparian forest as a source of carbon and nutrients (Likens & Bormann 1974, Hynes 1975). Leaf litter inputs are an important carbon flux in small tropical streams (Colon-Gaud *et al.* 2008), but litter is typically low in nutrient content, presenting a stoichiometric imbalance for detritivores (Small & Pringle 2010, Small *et al.* 2011a). Leaf litter may even serve as a sink for dissolved nutrients (Cross *et al.* 2005), as much of this material may be exported from the stream ecosystem as fine particulate organic matter at lower carbon:nutrient ratios (Webster *et al.* 1999). Another pathway connecting riparian forests and stream ecosystems is through inputs of terrestrial arthropods. Although the influx of invertebrate biomass into streams is small relative to leaf litter, invertebrates are relatively high in nutrient content (Small & Pringle 2010) and insectivorous fishes typically excrete excess nutrients at relatively high rates (Vanni *et al.* 2002, Small *et al.* 2011b). As a result, terrestrial arthropods may represent both an important food subsidy to insectivorous fishes and an underappreciated source of dissolved nitrogen (N) and phosphorus (P) in small streams.

Despite their potential importance, no studies to date have quantified terrestrial arthropod subsidies in tropical streams.

In temperate streams, terrestrial arthropods have been shown to be important ecosystem subsidies (Baxter *et al.* 2005, Menninger *et al.* 2008, Pray *et al.* 2009), due to high influxes in the summer (up to 450 mg dry mass/m²/d; Cloe & Garman 1996). This input can serve as an important subsidy to temperate stream fishes at a time of the year when aquatic insect biomass is lowest (Nakano & Murakami 2001). Terrestrial insect inputs in temperate streams, however, decline sharply during winter (typically <1 mg dry mass/m²/d, Baxter *et al.* 2005). In contrast to temperate forests, lowland tropical wet forests are characterized by high year-round productivity, and multistratal forest canopies have high insect biomass (particularly ants, with biomass 10–100 mg/m²; Leigh 1999), suggesting that terrestrial insects should be an important subsidy. Polis *et al.* (1997) hypothesized that the degree and importance of spatial subsidies depends on the perimeter-to-area ratio, the relative productivity of the habitats, and the permeability of habitat boundaries. In small streams, the entire stream ecosystem is effectively edge habitat, due to maximal perimeter-to-area ratio. The highly-productive riparian forest far exceeds rates of primary production in shaded tropical streams (Ortiz-Zayas *et al.* 2005). The habitat boundary between riparian forest and stream ecosystems is highly permeable, as physical forces (wind, rain) and predator-avoidance behavior (Haemig 1997, Yanoviak *et al.* 2005) contribute to an influx of terrestrial

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arthropods to the stream. The actual availability of this subsidy to the local stream ecosystem should depend on both the influx of terrestrial arthropods from the canopy and also on the capture efficiency by fishes.

We examined the importance of terrestrial arthropod inputs as a nutrient subsidy to headwater streams in a lowland tropical forest by quantifying four separate components of this pathway from the riparian to the benthic ecosystem. First, we measured biomass and associated nutrient fluxes from terrestrial insect inputs at eight different stream sites. For two focal headwater streams, we also quantified the capture efficiency by insectivorous fishes, and measured rates at which these fishes supply limiting nutrients to the stream ecosystem through excretion of terrestrially derived nutrients. We also measured nutrient uptake rates in these focal streams, allowing us to calculate the fraction of stream ecosystem nutrient demand that is ultimately supplied through inputs of terrestrial arthropods.

METHODS

SITE DESCRIPTION.—This study was conducted at La Selva Biological Station, located in the lowlands of Costa Rica's Caribbean slope (10°26' N, 84°01' W). La Selva contains 1536 ha of lowland tropical wet forest and receives nearly 4000 mm of rain annually, with a wet season (>400 mm/mo) from May to November (Sanford *et al.* 1994).

We measured terrestrial insect input along eight first- to fifth-order streams that are a subset of sites used in a long-term study of the physicochemistry of La Selva streams (Pringle & Triska 1991, Triska *et al.* 2006) (Table 1). Stream study sites are named by the watershed followed by a number indicating the approximate elevation (in m above sea level). We selected the two smallest of these streams (Carapa-60 and Saltito-100) as focal streams (because the importance of allochthonous inputs is likely to be maximized in headwater streams; Vannote *et al.* 1980), to quantify the importance of terrestrially derived nutrient excretion by the abundant insectivorous poeciliid *Priapichthys annectens*, which dominates the fish assemblage in headwater streams at La Selva (Burcham 1988).

The dense riparian vegetation along La Selva streams results in light-limited algal communities (Pringle & Triska 1991) and high inputs of allochthonous material. Canopy cover, based on spherical densitometer measurements, ranges from 81 to 88 percent across these sites (Table 1).

TERRESTRIAL ARTHROPOD INPUT RATES.—We quantified input rates of terrestrial insects using pan traps placed along the stream margin. The pan traps consisted of plastic trays (0.32 m²) filled with 5 cm of water (a mesh-covered hole prevented overflow), and a small amount of P-free surfactant to break surface tension. After 2–4 d, the contents of each pan trap were strained through 120 μm mesh. Pan traps were moved between sampling periods to integrate spatial heterogeneity in input rates. During June–July 2006, we collected pan trap samples in eight La Selva streams for a total of 195 trap-days, including 20 trap-days in the Carapa-60 and 22 trap-days in the Saltito-100. In June–July 2007, pan trap samples were collected along six streams for a total of 180 trap-days, including 30 trap-days along each of the focal streams. During these periods, a single pan trap was used at each of the eight sites, which was checked every 2 d and randomly moved to a new location within the site. To measure seasonality of terrestrial insect inputs, monthly samples from two traps (each deployed for 4 d in the same locations each month) were also collected along three La Selva streams (Arboleda-30 for 26 mo, and Piper-30 and Sura-60 for 13 mo each), from January 2007 to February 2009 (total 416 trap-days).

Terrestrial arthropods were separated from plant material and were dried at 50°C for 48 h and homogenized. We measured the elemental composition of a composite sample of terrestrial insects for each stream site collected in June–July 2006. For C and N analysis, samples were analyzed on a Carlo Erba NA 1500 CHN analyzer (Carlo Erba, Milan, Italy). For P analysis, samples were acid-digested (Aqua Regia double acid; Jones *et al.* 1991) and analyzed spectrophotometrically (ascorbic acid method). Ground pine needles (US National Institute of Standards and Technology, 1575a) were used as an external standard for P analysis. Isotope ratios for C and N are reported in delta notation

TABLE 1. Physical and chemical characteristics, and terrestrial insect input rates for study streams. Discharge (*Q*) and nutrient values (soluble reactive phosphorus, SRP) are means from monthly samples taken from 2006 to 2008. Terrestrial insect input values represent mean (±SE) from pan trap samples collected in 2006–2007.

Stream	Stream order	Q (L/s)	Width (m)	Canopy cover (%)	SRP (μg/L)	NO ₃ -N (μg/L)	NH ₄ -N (μg/L)	Ter. insect input (mg DM/m ² /d)
Carapa-60	1	2	1.1	84.8	4	157	25	22.6 (9.5)
Saltito-100	1	3	1.0	83.7	3	163	37	35.4 (17.8)
Piper-30	3	30	2.9	82.8	2	188	40	19.5 (1.6)
Saltito-60	3	110	4.6	79.9	33	98	19	11.7 (2.9)
Arboleda-30	2	170	5.4	88.1	135	126	20	29.9 (27.2)
Sura-60	4	190	6.2	82.4	3	199	21	40.5 (30.2)
Salto-60	5	450	9.8	84.1	10	180	20	4.9 (1.7)
Sura-30	4	610	7.9	87.3	83	163	18	12.0 (3.1)

(using Pee-Dee Belemnite as ^{13}C standard, and atmospheric N_2 as ^{15}N standard).

CONSUMPTION EFFICIENCY OF FISHES FEEDING ON TERRESTRIAL ARTHROPODS.—We used two different approaches to quantify the feeding efficiency of the insectivorous fish assemblage on drifting terrestrial arthropods. First, we performed ant addition experiments (because ants were the major component of drift samples as well as fish gut contents), analogous to nutrient addition experiments used to measure stream nutrient uptake rates (*sensu* Stream Solute Workshop 1990). In these experiments, 100 small ants were released at the top of a 5 m reach along with 100 small (1 cm) squares of waterproof paper, which served as a conservative tracer, behaving hydrologically like inedible ants. We used an invasive ant species, *Paratrechina longicornis*, in this experiment because it was easily collected in the laboratory building at La Selva, but is not present in the forest, so individuals of this species could be separated from ants present in the ambient drift. At the bottom of the reach, drift nets were set up to capture ants and paper ‘tracers’. Consumption efficiency was calculated as $1 - (\# \text{ ants recovered} / \# \text{ paper tracers recovered})$. Five-min trials that resulted in the recovery of at least 20 percent of the paper tracers were counted as successful. A total of 14 successful trials were run in two different 5-m reaches in both the Carapa-60 and Saltito-100 streams. No more than one trial per day was performed on each reach to prevent feeding saturation. For validation of this method, an additional trial was run in one of the reaches after approximately 82 percent of fish were removed following multiple-pass depletion with dip nets. Because the large pulse of food into a small stream reach could potentially saturate the capacity of the fish to consume it, capture efficiency measured by this method is likely conservative.

We devised an additional method to estimate both capture efficiency and total area-specific consumption rates of terrestrial insects, based on the difference between expected and measured drift of terrestrial insects in a given reach. In this method, we completely blocked off six different 5-m reaches at the upstream and downstream ends using drift nets, to prevent drift from upstream from entering the study reach, and to prevent the movement of fishes into or out of the study reach during the experiment. We measured the area of this reach and estimated the total input of terrestrial insects during a 15 min trial based on the area-specific input rate from pan trap measurements. We assume that, in the absence of insectivorous fishes, all insects falling into the 5 m reach would be captured in the downstream drift nets. We also assume that temporal heterogeneity in insect input rates averages out at the reach scale, so that rates from pan traps located at that site (integrated over multiple days) reflect input rates within the 5 m reach during the 15-min trials. Therefore, the expected drift value (in mg) in the absence of fish consumption was calculated as (area-specific input rate) \times (area of reach) \times (duration of trial). The difference between the actual dry mass of terrestrial arthropods recovered in drift nets and the expected value was attributed to fish consumption. Capture efficiency was then calculated as (expected drift—

actual drift)/expected drift. The consumption rate of terrestrial arthropods by fish (in units mg dry mass/m²/h) was calculated as (expected drift—actual drift)/(area of reach \times duration of trial). A total of five to eight 15-min trials were performed on each of three different 5 m reaches along both of the focal streams.

TERRESTRIAL ARTHROPODS IN FISH DIET.—To determine the relative contribution of terrestrial and aquatic insects in the diet of *P. annectens*, we dissected guts from 42 individuals from Carapa-60 and Saltito-100. Gut contents were spread evenly over a grid of 1 mm squares, and we recorded the number of squares covered by each food category. In addition, we compared stable isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for *P. annectens* to values for terrestrial insects collected in pan traps (described above) and to values for aquatic insects collected in the Carapa-60 and Saltito-100. Aquatic insects were sampled in the two focal streams from leaf packs and natural substrate and were sorted by family and analyzed for nutrient and isotopic composition, as described above.

TERRESTRIALLY DERIVED FISH EXCRETION.—In July 2007, we estimated the population density of *P. annectens* in three, 5 m reaches on both the Carapa-60 and Saltito-100, using a triple-pass depletion method (Lockwood & Schneider 2000). In each pass, the reach was blocked with seines, and three researchers collected fish with dip nets for 5 min. A total length–wet mass relationship was established using 36 individuals ($r^2 = 0.995$). To estimate total biomass of *P. annectens* in each reach, we multiplied the abundance estimate by the size distribution from all captured individuals, which we divided into 20 size classes with 0.1 g intervals.

Excretion rates for N and P were measured by incubating individual fish in a plastic bag containing 250 mL filtered stream water for 60 min. Fish were collected by dip nets and held for <15 min before excretion incubations began. Bags were suspended in the stream during incubation to maintain ambient temperature. At the conclusion of the incubation, 20 mL water samples were collected and filtered (0.45 μm pore size). Water samples were frozen within 3 h. Water samples were analyzed for ammonium ($\text{NH}_4\text{-N}$) and total dissolved phosphorus (TDP) at the University of Georgia’s Analytical Chemistry Laboratory. Ammonium-N was measured using the phenate-hypochlorite method, and TDP was measured using the molybdate blue-ascorbic acid reaction after digestion by acid-persulfate oxidation (American Public Health Association [APHA] 1988).

The increase in $\text{NH}_4\text{-N}$ and TDP in each bag, relative to control bags (incubated without fish), was attributed to fish excretion. Excretion rates were measured for 44 individual *P. annectens* (21 from Carapa-60 and 23 from Saltito-100). Per-capita N- and P-excretion were modeled as a function of fish wet weight (Hall *et al.* 2007). To estimate ecosystem-level nutrient recycling rates, we used the measured abundance and size distribution data for each of the three study reaches in the two focal streams, in combination with the size-specific N- and P-excretion rates measured for *P. annectens*. We estimated terrestrially derived N- and P-excretion based on the proportion of terrestrial insects in the average diet of

P. annectens, given our observations of nearly identical %N and %P between aquatic and terrestrial insects, and our assumption that assimilation efficiency is equal for nutrients derived from both types of food resources (see discussion for evaluation of this assumption).

STREAM NUTRIENT UPTAKE RATES.—In April 2010, we measured $\text{NH}_4\text{-N}$ and P uptake rates using short-term nutrient releases in each of the focal streams (Webster & Vallett 2006), to quantify the efficiency with which nutrients excreted by fish are retained within the stream ecosystem. The reactive solutes NH_4Cl and KH_2PO_4 were injected (on separate days) along with a conservative tracer (NaBr) for 3 h to measure plateau concentrations at downstream stations. During N injections, $\text{NH}_4\text{-N}$ concentrations were elevated to 79 $\mu\text{g/L}$ (Carapa-60) and 64 $\mu\text{g/L}$ (Saltito-100). During P injections, SRP concentrations were elevated to 65 $\mu\text{g/L}$ (Carapa-60) and 20 $\mu\text{g/L}$ (Saltito-100). Water samples were measured as described above. The rate of decline in dilution-corrected nutrient concentration over distance (k_C , or $1/\text{uptake length}$, S_W) was converted into an areal uptake rate (U) by multiplying by stream velocity, average depth, and background nutrient concentration (Stream Solute Workshop 1990).

STATISTICAL ANALYSIS.—Regression analysis was used to test for relationships between stream width and canopy cover (independent variables) and mean terrestrial insect input rates for the eight study streams. A regression model was also used to predict N- and P-excretion based on individual fish wet mass. To test for the effects of seasonality on input rates of terrestrial arthropods, we analyzed the monthly pan trap samples using a two-way ANOVA, with stream and season as categorical variables. Monthly observations were considered to be independent, given the high variability observed at shorter time scales; however, to test this assumption, we also included the previous month's input in the model as a covariate. Each 4-d pan trap sample mass was considered a replicate, and values were log-transformed to normalize the data. Wet season was defined as

May–January, and dry season was defined as February–April. We set $\alpha = 0.05$ for all analyses, and analyses were conducted using SAS (SAS Institute 2001).

RESULTS

TERRESTRIAL ARTHROPOD INPUT RATES.—Mean input rates of terrestrial arthropods across the eight study streams ranged from 4.9 to 40.5 mg dry mass/ m^2/d (Table 1) and were not related to stream width ($F_{1,6} = 1.85$, $P = 0.22$) or canopy cover ($F_{1,6} = 0.01$, $P = 0.92$). Mean input rates for the two focal headwater streams were 22.6 ± 9.5 mg dry mass/ m^2/d (mean \pm SE) in Carapa-60 and 35.4 ± 17.8 mg dry mass/ m^2/d in Saltito-100 (Table 1). Ants typically comprised most or all of the invertebrate biomass in pan trap samples. Large insects or spiders were noted in fewer than 5 percent of samples.

Monthly pan trap samples from three of the study streams were variable but were not related to seasonality ($F_{1,36} = 0.71$, $P = 0.41$; Fig. 1). Differences among the three streams were marginally significant ($F_{2,36} = 3.05$, $P = 0.06$). Samples collected over 26 mo in the Arboleda-30 ranged from 0.5 to 191.0 mg dry mass/ m^2/d , with a mean input rate of 29.9 mg dry mass/ m^2/d . Samples collected over 13 mo in the Piper-30 ranged from 2.2 to 75.2 mg dry mass/ m^2/d , with a mean of 19.5 mg dry mass/ m^2/d . In the Sura-60, monthly samples collected over 13 mo ranged from 3.1 to 89.3 mg dry mass/ m^2/d , with a mean of 40.5 mg dry mass/ m^2/d . A stream \times season interaction term was not significant ($F_{2,36} = 1.67$, $P = 0.20$). The assumption of independence among monthly observations was supported by the lack of relationship with the previous month's input ($F_{1,36} = 0.10$, $P = 0.76$).

Composite samples of terrestrial arthropods had an elemental composition of 49.6 percent C (by dry weight), 10.0 percent N, and 0.5 percent P. These values are very similar to mean N- and P-content for aquatic insects from low-solute La Selva streams (mean %N = 10.2, mean %P = 0.5; Small & Pringle 2010). By applying these values to the fish consumption

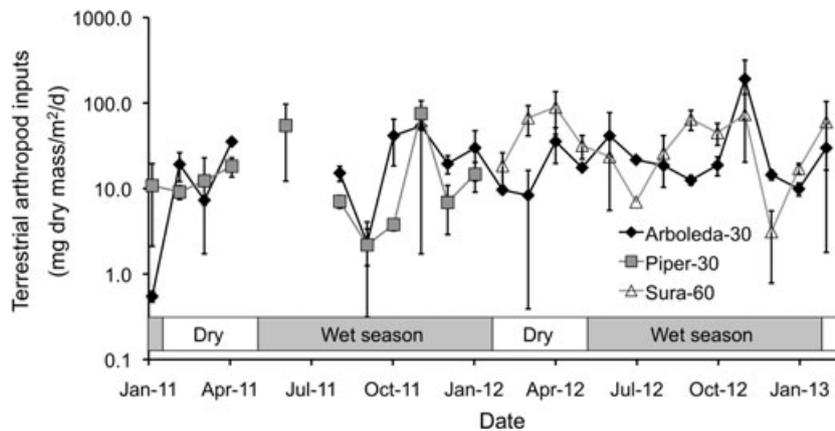


FIGURE 1. Monthly input rates of terrestrial insects in three La Selva streams from 2007 to 2008. Values are means (\pm SE) of samples collected from two 0.33 m^2 pan traps that were set out for 4 d each month in the same locations to measure seasonal variation in terrestrial insect input rates.

rates described above, we estimate that, in the two focal streams, fish ingest 11.2–17.6 mg C/m²/d, 2.3–3.5 mg N/m²/d, and 0.11–0.17 mg P/m²/d in the form of terrestrial arthropod biomass.

CONSUMPTION EFFICIENCY OF FISHES FEEDING ON TERRESTRIAL ARTHROPODS.—Experimental ant additions in four 5-m reaches in the Carapa-60 and Saltito-100 led to estimates of mean consumption efficiency (# consumed vs. # available) ranging from 44 to 74 percent across the four study reaches (Table 2). For the reach in which we removed nearly all fish, we measured a consumption efficiency of 3 percent.

Using ambient drift measurements to measure fish consumption of terrestrial arthropods, we estimated values for consumption efficiency ranging from 35 to 93 percent in six 5-m reaches in the Carapa-60 and Saltito-100 (Table 3). We estimated fish ingestion rates of terrestrial insects ranging from 0.33 to 1.28 mg dry mass/m²/h. Based on the mean nutrient content of terrestrial invertebrates in pan trap samples, fish ingested 33.2–138.0 μg N/m²/h, and 1.59–6.62 μg P/m²/h via this source.

TERRESTRIAL ARTHROPODS IN FISH DIET.—Mean gut contents (by volume) for *P. annectens*, across 42 individuals, were evenly divided (50.0%) between aquatic and terrestrial insects, although

the gut contents of individual fish ranged from 100 percent aquatic insects to 100 percent terrestrial insects. There was no relationship between fish size and diet. Ants were the most commonly observed terrestrial insect in fish guts, including the common genera *Atta* and *Pheidole*.

Isotopic signatures of *P. annectens* measured $-26.00 \pm 0.42\%$ for $\delta^{13}\text{C}$ (mean \pm SD) and $9.44 \pm 0.25\%$ for $\delta^{15}\text{N}$. Terrestrial arthropods from composite pan trap samples had a $\delta^{13}\text{C}$ value of $-28.49 \pm 0.61\%$ and a $\delta^{15}\text{N}$ value of $3.43 \pm 1.47\%$. Aquatic insects sampled from the Carapa-60 and Saltito-100 ranged in $\delta^{13}\text{C}$ from -26.80 to -32.43 (mean -28.95 ± 1.25) and in $\delta^{15}\text{N}$ from 3.91 to 8.64 (mean 6.58 ± 1.40). The $\delta^{13}\text{C}$ signatures between these two food resources overlap extensively and preclude the use of this isotope in partitioning the diet of *P. annectens*. Using mean $\delta^{15}\text{N}$ values for the two food resources and a mean $\delta^{15}\text{N}$ fractionation value of $1.4 \pm 0.21\%$ (for consumers feeding on invertebrate diets; McCutchan *et al.* 2003), no solutions exist in a simple mixing model; however, $\delta^{15}\text{N}$ values for *P. annectens* more closely match aquatic insects.

TERRESTRIALLY DERIVED FISH EXCRETION.—*Priapichthys annectens* accounted for an estimated 98 percent of the fish assemblage in the Carapa-60 and Saltito-100 (232 of 236 captured individuals). Population densities for *P. annectens* in the six focal reaches ranged from

TABLE 2. Consumption efficiency of fish assemblage from ant tracer experiment. Mean values (\pm SE) for all successful trials, where at least 20 percent of paper squares were recovered, are reported here for each study reach. One release was performed after nearly all fish were removed from the study reach.

Site	Successful trials	Paper squares recovered	Ants recovered	Consumption efficiency (%)
Carapa-60 A	3	33.0 (9.5)	10.0 (3.2)	60.4 (16.9)
Carapa-60 B	2	33.0 (2.0)	8.5 (1.5)	74.4 (3.0)
Saltito-100 A	5	49.6 (12.7)	18.8 (5.2)	50.5 (16.6)
Saltito-100 B	4	67.0 (7.5)	35.3 (7.5)	44.1 (15.2)
Saltito-100 B (no fish)	1	64.0	62.0	3.1

TABLE 3. Consumption efficiency and absolute consumption rates for *Priapichthys annectens* feeding on terrestrial arthropods. Values for mass of arthropod recovered represent means of five to eight drift samples.

Site	Surface area (m ²)	Estimated input during trial (mg/15 min)	Arthropod mass recovered (mg/15 min)	Estimated Fish consumption (mg/15 min)	Consumption efficiency (%)	Areal consumption (mg/m ² /h)
Carapa-60 A	7.50	1.77	0.39	1.38	78	0.73
Carapa-60 B	5.25	1.24	0.80	0.44	35	0.33
Carapa-60 C	4.25	1.00	0.90	0.10	10	0.65
Saltito-100 A	4.18	1.54	0.10	1.44	94	1.38
Saltito-100 B	4.88	1.80	0.76	1.04	58	0.85
Saltito-100 C	8.15	3.01	0.05	2.96	98	1.33

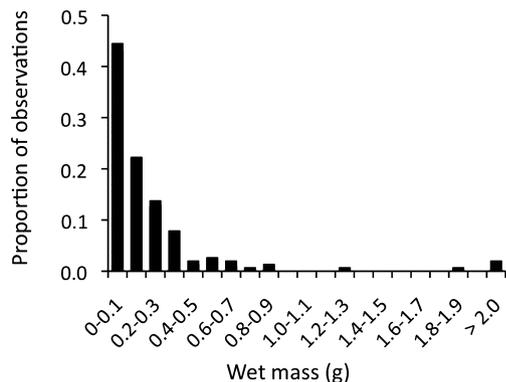


FIGURE 2. Size distribution of *P. annectens* in the two focal streams (data pooled from all study reaches).

3.9 to 14.0 individuals/m². Mean wet weight for *P. annectens* was 0.472 g (± 0.107), but the size distribution was strongly skewed toward small individuals (Fig. 2).

Per-individual N-excretion rates ($\mu\text{g NH}_4\text{-N/fish/h}$) were calculated as $\log \text{NH}_4\text{-N-excretion} = 0.52 \times \log [\text{wet mass}] + 1.30$ ($F_{1,19} = 5.81$, $P = 0.03$, $r^2 = 0.23$). Per-individual P-excretion rates ($\mu\text{g TDP/fish/h}$) were calculated as $\log \text{TDP excretion} = 0.29 * \log [\text{wet mass}] + 0.18$ ($F_{1,38} = 2.05$, $P = 0.16$, $r^2 = 0.05$). Although P-excretion rates were only weakly related to fish wet mass, we chose to keep this term in the model as removing it (*i.e.*, using a mean per-individual P-excretion rate for all size classes) would overestimate the reach-scale P-flux due to the high abundance of small individuals. Total N-excretion for *P. annectens* populations in the six study reaches averaged $64.8 \pm 13.7 \mu\text{g NH}_4\text{-N/m}^2/\text{h}$ (mean \pm SE) and total P-excretion averaged $7.0 \pm 1.5 \mu\text{g TDP/m}^2/\text{h}$. Differences in estimated nutrient recycling rates are due to differences in fish density among reaches.

Because mean N- and P-content was similar between aquatic and terrestrial insects, then, the amount of N and P ingested, and (assuming equal assimilation rates) excreted, by *P. annectens* from aquatic and terrestrial insects should depend on the proportion of these food resources in the diet (50% for each category, based on gut content analysis). We estimate that terrestrially derived N-excretion rates averaged $32.4 \pm 6.8 \mu\text{g NH}_4\text{-N/m}^2/\text{h}$ (mean \pm SE) across the six study reaches in the focal streams. Rates of terrestrially derived P-excretion averaged $3.5 \pm 0.7 \mu\text{g TDP/m}^2/\text{h}$ in the focal streams.

STREAM NUTRIENT UPTAKE RATES.—We measured $\text{NH}_4\text{-N}$ uptake length of 143 m in the Carapa-60 and 157 m in the Saltito-100, corresponding to areal uptakes rate of 500 and 1386 $\mu\text{g/m}^2/\text{h}$, respectively. Based on this measurement, total NH_4^+ excreted by *P. annectens* (mean $64.7 \mu\text{g NH}_4\text{-N/m}^2/\text{h}$) was 5–16 percent of the magnitude of stream $\text{NH}_4\text{-N}$ demand, with terrestrially derived N-excretion composing half of this amount. We measured P uptake lengths of 43 m in the Carapa-60 and 56 m in Saltito-100, corresponding to areal uptake rates of 788 and 691 $\mu\text{g P/m}^2/\text{h}$, respectively. Total P-excretion by *P. annectens* (mean $9.1 \mu\text{g P/m}^2/\text{h}$) was approximately 1 percent of the magnitude of

measured stream P uptake, with terrestrially derived P-excretion accounting for half of this total.

DISCUSSION

The relatively constant year-round input rates of terrestrial arthropods, combined with the high contribution of terrestrial arthropods to the diet of the dominant fish species, indicate that terrestrial insects are an important food-web subsidy in these tropical streams. Input rates of terrestrial insects in these rain forest streams were distributed fairly evenly throughout the year (Fig. 1), in contrast to the strong seasonality of terrestrial subsidies reported in some temperate streams, where summer input rates of terrestrial insects can be up to 100-fold higher than winter rates (*e.g.*, Cloe & Garman 1996, Nakano & Murakami 2001), and where large periodic inputs of terrestrial insects have been documented (Carlton & Goldman 1983, Menninger *et al.* 2008, Pray *et al.* 2009). Mean influx rates in our study streams were lower than some of the reported summer values for temperate deciduous forest headwater streams, which range from 111 to 450 $\text{mg/m}^2/\text{d}$ (Baxter *et al.* 2005). Annual inputs of terrestrial insect biomass from the three streams in which monthly samples were collected (7.1–14.8 $\text{g/m}^2/\text{y}$), however, were similar to annual inputs reported for forested streams in Japan (8.7 $\text{g/m}^2/\text{y}$; Kawaguchi & Nakano 2001) and Scotland (11 $\text{g/m}^2/\text{y}$; Bridcut 2000). The relative importance of terrestrial arthropods as a trophic subsidy is apparent given that input rates in our study (ranging from 4.9 to 40.5 $\text{mg/m}^2/\text{d}$) were generally two to six times greater than rates of secondary production of midge larvae (Diptera: chironomidae), the dominant group aquatic invertebrates, measured in these same study streams by Ramírez and Pringle (2006).

In contrast to its importance as a subsidy for the stream food web, our results suggest that the significance of terrestrial insects as a biogeochemical flux in the focal headwater streams was limited. Estimated excretion of terrestrially derived nutrients by the dominant fish species in the two focal streams was a small component of stream nutrient dynamics, <3 percent of the magnitude of measured N and P uptake fluxes. We selected the two first-order streams as focal streams in this study because shallow streams with high fish densities should have the greatest biogeochemical impact per gram of terrestrial insect that enters the stream. Despite relatively high population densities (4–14 fish/m²), most individuals were juveniles (80% of individuals were <3 g wet weight). As a result, the total fish biomass was relatively low (0.9–3.4 g wet weight/m²). By contrast, in a related study in the nearby fourth-order Sura-60 stream, which has lower fish abundance but higher total fish biomass, N and P recycling by the fish assemblage slightly exceeded stream nutrient demand (Small *et al.* 2011b). In that study, excretion by the omnivorous characid *Astyanax aeneus* accounted for an estimated 71 percent of the stream P-demand, and the diet of this species consists of 65 percent terrestrial insects, suggesting that the biogeochemical importance of terrestrial arthropod subsidies may be higher in this larger stream.

In addition to low total fish biomass in the focal headwater streams, high measured nutrient uptake rates in these small streams (compared with the uptake rates measured on the 4th-order Sura-60; Small *et al.* 2011b) resulted in the apparently limited importance of terrestrially derived fish excretion. These nutrient uptake values should be interpreted with caution, as nutrient addition experiments can overestimate uptake length by saturating stream uptake capacity (Mulholland *et al.* 2002), and our single nutrient releases do not account for the possibility of temporal variability. Thus, it is possible that terrestrially derived P-excretion has a greater biological importance than our results indicate. Furthermore, low-solute headwater streams at La Selva are P-limited (Pringle & Triska 1991), and even small increases in dissolved-P can result in large increases in microbial respiration (Ramírez *et al.* 2003) and leaf decomposition (Rosemond *et al.* 2002), suggesting that, while small in magnitude, this pathway of P entering the stream ecosystem could still be ecologically important.

Our results show that insectivorous fish play an important role in efficiently retaining terrestrial arthropod inputs within the stream ecosystem. Most insects were consumed by fish within 5 m, and nutrients excreted by these fish were taken up within 150 m (N) or 50 m (P). The importance of insectivorous fishes in the capturing and processing of terrestrially derived nutrients has been the subject of some debate, as Wurtsbaugh (2007) argued that once insects enter a body of water, they become part of the nutrient budget of that respective aquatic ecosystem, and, even in the absence of fishes, these nutrients would eventually be mineralized by microbes. In contrast to lakes (*e.g.*, Mehner *et al.* 2005), terrestrial insects falling into high-gradient headwater streams drift rapidly downstream in the absence of fish, as illustrated by the very low consumption efficiency in our ant-release trial where most fish had been removed (Table 2), or may escape from the stream upon reaching the stream margin or a debris dam. Although fish may be redundant in their capacity to mineralize nutrients from terrestrial insect biomass, they are playing a unique role in their capacity to capture and retain these nutrients within short distances, ultimately making them available to the local stream ecosystem.

We estimated that half of the N and P excreted by *P. annectens* was terrestrially derived, based on observations that gut contents contained 50 percent terrestrial insects and 50 percent aquatic insects on average, and that N- and P-content was similar between terrestrial and aquatic insects. This calculation also is based on the assumption that assimilation efficiency was similar for both food sources. Terrestrial insects can have large amounts of N invested in cuticular chitin (Sterner & Elser 2002), however, which could be assimilated at a lower efficiency. Stable isotope signatures for *P. annectens* suggest that the fish biomass is composed of more aquatically derived nutrients, which, given our observations of equal proportions of aquatic and terrestrial insects in the fish guts, implies a greater assimilation efficiency for aquatic insects. If so, our calculations have overestimated the fraction of fish excretion that originated as terrestrial insects. For example, if assimilation efficiency for terrestrial invertebrates were on average one-half as high as for aquatic invertebrates, then one-third rather than one-half of total N-excretion should be attributed to terrestrial inputs. Greater

assimilation efficiency for aquatic insects would also imply that fecal material of *P. annectens* was dominated by terrestrial insects, and that consumption by these fish is still important in retaining and processing this subsidy.

Understanding cross-boundary food-web subsidies has been a focus of extensive ecological research in recent years. Our results show that terrestrial insects may be important in some nutrient-poor tropical headwater streams due to year-round high input rates, and that insectivorous fishes play an important role by efficiently retaining and recycling terrestrially derived nutrients, making them available to the local ecosystem. Extensive deforestation throughout the tropics is likely to alter terrestrial insect subsidies and shift trophic pathways in stream food webs. To better understand the consequences of severing connections between different ecosystems, we must be able to accurately measure the baseline importance of these cross-boundary flows.

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