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ASSEMBLAGE STRUCTURE, PRODUCTION AND FOOD WEB DYNAMICS OF
MACROINVERTEBRATES IN TROPICAL ISLAND HEADWATER STREAMS

by

KEYSA G. ROSAS-RODRIGUEZ

(Under the Direction of J. Checo Colón-Gaud)

ABSTRACT

Variation in long-term temperature and precipitation patterns will likely influence the decomposition and export of benthic organic matter and influence aquatic macroinvertebrate consumer communities. Tropical systems are relatively understudied; therefore basal information is urgently needed. As part of an ongoing long-term study, we monitored macroinvertebrates in two shrimp-dominated and fishless headwater streams within the Luquillo Experimental Forest in Puerto Rico from 2009-2010. We combined growth rates with yearly biomass data to calculate secondary production and examined gut contents to develop quantitative food webs. Macroinvertebrate assemblages were dominated by a few insect taxa, with similar biotic composition across streams and habitats, but different structure amongst habitats. Biomass and abundance were generally greater in pools, suggesting that pools may provide habitat stability and shelter. Alternatively, shrimp may provide secondary benefits by removing fine sediments given their high density in pools. Overall, aquatic insects had low biomass; therefore, their production was relatively low as is the case in most tropical areas. However, their turnover rates were not as high as expected. Secondary production appears to rely more on amorphous detritus and allochthonous organic matter rather than algal resources. These data are an important first step towards predicting the long-term effects that expected changes in rainfall and discharge will have in tropical stream communities.

INDEX WORDS: Food webs, Secondary production, Macroinvertebrates, Tropics, Headwater streams, Long-term dataset, Food content analysis

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by

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B.S. University of Puerto Rico at Mayaguez, 2004

A Thesis submitted to the Graduate Faculty of Georgia Southern University in Partial

Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

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CHAPTER 1. INTRODUCTION

Long-term studies have made contributions to our understanding of complex ecological processes that would be impossible to attain with short-term observations. For example, they allow for the assessment of inter-annual variation and cycles, complex abiotic and biotic interactions, and natural and anthropogenic disturbance and recovery (Jackson and Fureder, 2006). Long-term studies are particularly important with respect to slow ecological processes, rare or episodic phenomena, highly variable processes, and subtle or complex phenomena and, therefore, can play an important role in formulating and testing ecological theory (Franklin 1988, Lindenmayer and Likens, 2009). In the case of aquatic macroinvertebrates, most long-term studies have focused on economically or medically important species such as mosquitoes and blackflies or have a limited geographical scope (Jackson and Fureder, 2006). Therefore, it is imperative to establish a broader range of long-term research programs that increase our understanding of freshwater systems, especially those of understudied areas like the tropics.

An ideal place to carry out large scale long-term projects is within Long Term Ecological Research (LTER) Network sites. One of these sites, the Luquillo LTER (LUQ-LTER), located in the Luquillo Experimental Forest (LEF) in Puerto Rico (Figure 1.1) has been one of the main tropical research centers for several decades. This site has played a central role in studying how tropical forests recover after major disturbances such as hurricanes in the context of detrital pulses, carbon and nutrient storage and flow, and food web responses. Looking into the future, the forest's response to changes in climate, such as drought, will be an integral part of the research done in the site.

The research that has been carried out at the LUQ-LTER along with other long-term stations such as La Selva in Costa Rica, has also played an integral part in the current knowledge of the structure and function of neotropical aquatic systems. Substantial contributions to aquatic community ecology (Covich and McDowell, 1996, Ramirez and Hernandez-Cruz 2004, Covich *et al.* 2009), ecosystem processes (Crowl *et al.* 2001, Ortiz-Zayas *et al.* 2005), and responses to disturbances (Scatena and Larsen 1991, Pringle 1996, Covich *et al.* 2003, Covich *et al.* 2006) have been made. One of the most studied areas is the ecology of freshwater shrimp, the dominant macroconsumers in its headwater streams (Covich and McDowell, 1996). Many of these studies have focused on the interactions between shrimp and aquatic insects, as shrimps may benefit from benthic insects as a part of their diets, thus may directly influence their community structure via consumption (Crowl *et al.* 2000, March *et al.* 2001, 2002, 2003, Cross *et al.* 2008b). Other studies highlight that shrimps may also influence benthic insect assemblages indirectly by modification of habitat in the form of sediment removal that can lead to the facilitation to algal resources (Pringle 1996, Pringle *et al.* 1993, 1999, Cross *et al.* 2008b). However, some questions still remain about the specific energetic pathways that link their communities as the available studies have only focused on shrimp (Crowl *et al.* 2000, Cross *et al.* 2008a).

In general, there are very few studies that examine energy flow and invertebrate production in the tropics with only a handful focusing on entire consumer communities (see Jacobsen *et al.* 2008 for a review). In the neotropics, the only studies available are from Central America (Ramirez and Pringle 1998a, Colon-Gaud 2009, 2010a, 2010b, Frauendorf, 2013). The study of energy flow is an important topic in a changing world. For example, changes in rainfall patterns have direct effects on aquatic communities. A substantial decrease can reduce invertebrate richness due to the alteration of physiochemical conditions, loss of habitats and fragmentation of

the stream ecosystem (Boulton, 2003). Alternatively, a substantial increase can lead to a reduction insect and organic matter biomass due to scouring. Anthropogenic impacts are another important influence on aquatic ecosystems since they commonly result in decreased allochthonous organic matter inputs due to deforestation, changes in water chemistry, a flashier hydrograph, and an overall decrease in biotic diversity coupled with an increase in introduced and tolerant species (Walsh *et al.* 2005). All of these factors can drastically change basal energy sources and species interactions. Therefore, long-term and pre-disturbance community and energetic studies are imperative in order to fully understand the functioning of aquatic communities and to be able to uncouple seasonal variation from long-term changes.

The goal of this thesis is to complement the existing aquatic community knowledge by quantifying the composition, structure, production and food web of the non-shrimp macroinvertebrate communities within the LUQ-LTER. I examined the assemblage structure of benthic macroinvertebrates to assess for temporal patterns of variation throughout the sample period or if there were any spatial (by macro-habitats; riffles vs. pools) patterns. Moreover, I developed a quantitative food web to describe the energy flow in these systems. The information gathered from this study will serve as a much needed baseline dataset for long term studies within the LUQ-LTER as well as tropical stream ecosystems in general.



Figure 1.1 The Luquillo Experimental Forest (LEF) in Northeastern Puerto Rico. Source: <http://luq.lternet.edu>.

CHAPTER 2. COMPOSITION AND STRUCTURE OF MACROINVERTEBRATE ASSEMBLAGES IN TWO TROPICAL HEADWATER STREAMS, PUERTO RICO

ABSTRACT

Macroinvertebrates were monitored in two shrimp-dominated and fishless headwater streams within the Luquillo Experimental Forest in Puerto Rico from 2009-2010. Macroinvertebrate assemblages were dominated by a few insect taxa, with similar biotic composition across streams and habitats, but different structure among habitats (pools vs. riffles). Biomass and abundance were greater in depositional habitats (i.e., pools), suggesting that these macro-habitats may provide greater stability and shelter; alternatively, given the high density of shrimp in pools, my estimates suggest that macro-consumers may provide secondary benefits by removing fine sediments. These data are an important first step towards predicting the long-term effects that expected changes in rainfall and discharge will have in tropical stream communities.

INTRODUCTION

Macroinvertebrates perform important functions in stream ecosystems (Wallace and Webster, 1996). They influence nutrient cycles, decomposition rates, exchange of solutes, and constitute an important link in food webs as intermediate consumers. Their assemblage structure is shaped by landscape (land use patterns) and abiotic variables (stream physicochemistry, habitat availability) along with biotic parameters and interactions (food availability, competition, and predation) all of which can promote a patchy distribution of the community (Pringle *et al.* 1988). Also, physical disturbances such as droughts and floods can reduce invertebrate richness due to

the alteration of physiochemical conditions, loss of habitats and fragmentation of the stream ecosystem and scouring (Boulton, 2003). However, changes in discharge are essential to different ecological processes in the stream such as organic matter transport, regulation of habitat availability, modulation of nutrient cycling, and disturbance (Doyle *et al.* 2005). Therefore, macroinvertebrates that have evolved under a constant set of hydrological stressors should possess strategies that enable them to survive and readily recover from certain hydrological disturbances (Poff and Ward, 1990).

Tropical ecosystems naturally show a high variability of conditions and environments, yet they remain largely understudied with most studies focusing on descriptive research and diversity inventories (Boyero 2009). This lack of knowledge is of great significance in the light of climate change, as most predictions point at changes in hydrological regimes, which could lead to reduced resource budgets, habitat alterations and altered species interactions. Models from the neotropics predict reductions in precipitation of most of Central America (Karmalkar *et al.* 2001, Rauscher *et al.* 2008, Hidalgo *et al.* 2013). In the Caribbean Region projections suggest drier wet seasons and even drier dry seasons (Cashman *et al.* 2010). For the Luquillo Mountains and the El Yunque National Forest in Puerto Rico, there is also a predicted increase of extreme precipitation events with longer periods of drought and hurricanes being less frequent but more severe (Jennings *et al.* 2014). Furthermore, the increasing temperatures will likely result in an increase in base altitude of cloud formation, which may further decrease precipitation (Comarazamy and Gonzalez 2011).

Given the importance of discharge as a “master variable” for macroinvertebrate species (Power *et al.* 1995), changes in precipitation will alter stream discharge, directly affecting stream macroinvertebrates. These changes in discharge result in changes in habitat complexity and

availability in the form of the disappearance of riffles and the isolation of pools during extreme droughts and the re-shaping the stream bed and reduction of organic matter and small sediments during high rainfall events. Alternatively, in the absence of confounding anthropogenic factors, aquatic organisms may be resilient enough to withstand or recover from the effects of hydrologic disturbances. Therefore, long-term studies are needed to assess the response of aquatic communities to predicted climatic changes. In places where little or no data have been gathered, as is the case of the majority of tropical stream ecosystems, pilot monitoring programs need to be established. Further, in places where long-term research networks have been established, such datasets need to be continued, as they can provide extensive information on the response of aquatic organisms to natural disturbances.

In the present study, I quantify the composition and structure of macroinvertebrate assemblages in two streams located in the Luquillo Experimental Forest in northeastern Puerto Rico as the first part of a long-term research program. The goal was to examine the assemblage structure of benthic macroinvertebrates to determine if there was any temporal variation throughout the sample period or if there were any spatial (by macro-habitats; riffles vs. pools) patterns. Also, I attempted to identify factors that potentially influence these patterns. In particular, I focused on in-stream factors such as substrate and organic matter availability as these influence habitat quality along with discharge parameters, which can account for long term variability. The information gathered from this study will serve as a much needed baseline dataset for tropical stream ecosystems in general.

METHODS

Study Site

Two 100-m reaches were established within two first order streams (Quebrada Prieta, henceforth “Prieta” and Quebrada Gatos, henceforth “Gatos”) that drain the Luquillo Long Term Ecological Research (LUQ-LTER) site at approximately 350 m.a.s.l. This site is located within the Luquillo Experimental Forest (LEF) in the northeast of Puerto Rico. This region is characterized as tropical wet forest and receives an average of 3.5 m of precipitation per year distributed relatively evenly with a drier period from January to April and peaks from May to December (Reagan and Waide 1996). The streams at the LEF maintain a water temperature range from 18 to 26°C (mean 22°C). The forest of the LEF is heavily forested and dominated by *Dacryodes excelsa* (tabonuco) and *Prestoea acuminata* (previously known as *P. montana*, sierra palm) in riparian habitats between 200-600 m in elevation (Heartsill-Scalley *et al.* 2009).

Leaf fall is continuous throughout the year and often peaks during the drier part of the year, with the highest rates occurring from April to June (Reagan and Waide 1996). Stream-bottom substrates are dominated by large boulders and cobble in erosional habitats (i.e., riffles) and by fine sediments at shallow, depositional habitats (i.e., pools). The proportion of available habitats in the 100 m study reaches was assessed in November of 2009. For this, transects were established every 5 m along the entire length of each study reach. Habitat composition was estimated for each 5 m section of the stream reach and summed and divided by reach length to calculate the proportion of each major habitat type (%erosional = riffles/runs, %depositional = pools).

Macroinvertebrate Sampling

I quantified benthic macroinvertebrate biomass, benthic organic matter, water depth and substrates present in the two streams for 13 consecutive months. In each stream, monthly samples were collected from each study reach from August of 2009 to August of 2010. On each sampling date, I collected four samples from erosional habitats (small riffles) using a Surber sampler (sampling area 930 cm²; mesh size 250 μm) and four samples from depositional habitats (pools) using a stovepipe benthic corer (sampling area 314 cm²). Surber samples were collected by disturbing substrates within the sampling area (scrubbing rocks with a stiff brush and displacing sediments) allowing organisms and organic matter to drift into the sampler's net immediately downstream. The corer samples were collected by removing all materials to a depth of approximately 10cm, placing them in a bucket, elutriating the organic portion, and collecting that into a 250μm sieve. Materials retained on the Surber net or on the sieve were placed in labeled plastic bags and preserved with ~10% formalin. Additionally, along with each macroinvertebrate sample and before disturbing the sample area, I recorded the water depth and the proportions of the substrates present in each sample area (% cobble, % pebble, % gravel, % sand, % silt). In the laboratory, macroinvertebrates were sorted from other organic materials, identified to the lowest possible taxonomic level, and measured (total body length) to the nearest 1 mm. I calculated their biomass (mg/m²) using published length–mass relationships (Benke *et al.* 1999). Biomass values were estimated for depositional and erosional habitats separately and habitat-weighted values were obtained by multiplying habitat-specific values by the proportion of the respective habitat type available in each of the two 100-m study reaches then summing the products to develop an estimate for each reach (see Grubaugh *et al.* 1996). Although shrimp account for a dominant portion of the benthic consumer community, their densities could not be

assessed using the collection methods used. However, a previous study conducted in Prieta (Cross *et al.* 2008) quantified the abundance, biomass and production of the dominant shrimp species.

In the laboratory, organic materials collected along with the macroinvertebrates were passed through 1mm and 250 μm nested sieves in order to separate coarse (<1 mm) and fine (>1 mm) particulate organic matter (CPOM and FPOM, respectively). The material was dried at 60-70°C for a minimum of 48 hours, weighed, ashed at 500 °C for 1hr and re-weighed in order to obtain ash-free dry mass (AFDM). Organic matter standing stocks (g AFDM m^{-2}) were estimated for depositional and erosional habitats.

Weekly gage height and discharge data for Quebrada Prieta for the years 2000-2015 were available through the LTER network (Figure 2.1). Using these data, I calculated the average discharge for the 30 days prior to the sampling date as well as the Richards-Baker Flashiness Index (Baker *et al.* 2004). This index reflects the frequency and rapidity of short term changes in streamflow and is calculated by summing the absolute values of daily flow differences and dividing by the sum of the daily flows for each month.

Data Analysis

Using the abundance data, I calculated the following diversity indices: Total species (S), total number of individuals (N), Margalef's species richness ($d = (S - 1)/\log N$, Margalef, 1968); Pielou's evenness ($J' = H'/\log S$, Pielou, 1969), Shannon-Wiener diversity ($H' = -\sum(P_i \times \log(P_i))$, where P_i = the proportion of the total sample belonging to the i th genus, Shannon and Weaver, 1949); and Simpson's index ($1 - \lambda^2 = 1 - \sum(N_i * (N_i - 1) / (N * (N - 1)))$, Simpson, 1949). Prior to statistical analyses, abundance and biomass data values were square root transformed to down-weight the

contributions of dominant species (Clarke and Gorley, 2006). Abundance and biomass data were used to calculate a Bray-Curtis dissimilarity matrix (Bray and Curtis, 1957) to describe the assemblage structure using nonmetric multidimensional scaling (NMDS) ordination techniques and to test for differences in the assemblages using a permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001). The PERMANOVA allowed for a non-parametric multivariate approach to test the effects of stream and habitat type on macroinvertebrate assemblages. Any significant grouping of assemblages was further examined using a similarity percentages (SIMPER) analysis (Clarke, 1993), which uses Bray-Curtis dissimilarities in order to determine the contribution of each taxon to the dissimilarity between groups. All analyses were run using PRIMER-E version 7.0.8. with the PERMANOVA+ add on (PRIMER-E LTD., Plymouth, UK).

RESULTS

Gatos was composed of 31% depositional habitats (pools) and 69% erosional habitats (riffles). Prieta was composed of 9% depositional and 91% erosional habitats. Table 2.1 includes the habitat, discharge and substrate variables measured in our study. Average monthly abundance was higher in pools (1327 ind./m²; range: 236-2780 ind./m² in Gatos; 1211 ind./m²; range: 383-2859 ind./m² in Prieta) versus riffles (276 ind./m²; range: 34-809 ind./m² in Gatos; 343 ind./m²; range: 70-832 ind./m² in Prieta). Also, average monthly biomass was higher in pools (57.0 mg AFDM/m²; range: 14.4-116.7 mg AFDM/m² in Gatos; 93.6 mg/m²; range 22.0-286.6 mg AFDM/m² in Prieta) versus riffles (18.9 mg AFDM/m²; range: 2.6-64.8 mg AFDM/m² in Gatos; 25.4 mg AFDM/m²; range 5.4-81.1 mg AFDM/m² in Prieta). Monthly fluctuations in biomass

and abundance showed no seasonal pattern, with values remaining relatively stable throughout the study period and no apparent seasonality (Appendix 2.1). Even though there was a slight increase in discharge towards the end of the sample period around July and August (Table 2.2), biota showed no apparent response. After adjusting by the proportion of available habitats, both streams had similar abundance (399 ind./m²; range: 52-710 ind./m² in Gatos; 433 ind./m²; range: 98-445 ind./m² in Prieta) and biomass (15.3 mg AFDM/m²; range: 3.1-39.4 mg AFDM/m² in Gatos; 15.8 mg AFDM/m²; range 6.4-40.6 mg AFDM/m² in Prieta).

A total of 6,452 individual macroinvertebrates belonging to 45 taxa (ranging from class to species, see Appendix 2.2 for abundance and biomass values of all taxa) were identified. Within those taxa, 95% of the habitat-weighted biomass across both streams was found within 9 groups: Leptophlebiidae, Chironomidae, Elmidae, Hydropsychidae, Oligochaeta, Calamoceratidae, Tipulidae, Baetidae and Veliidae. Across sites and habitats leptophlebiid mayfly nymphs were dominant, accounting for 34% of biomass across streams, followed by chironomid midge larvae with 18%. Taxa whose abundance or biomass were >1% of the total are listed in Table 2.3. No species-specific seasonal pattern was observed. Dominant taxa were similar in both habitats.

The diversity measures showed that riffles had slightly higher richness values than pools. (Table 2.4). This difference is due in part to taxa that rely on fast-flowing waters like filter-feeders (*Smicridea*, *Simulium*, *Chimarra*), other case maker or free living caddisfly larvae (*Atopsiche*, *Macronema*, *Alisotrichia*, *Hydroptila*, *Kumansliella*), riffle beetles (*Neoelmis*, *Phanocerus*) and larval lepidopterans (*Petrophila*, *Neargyractis*). However, these groups were relatively rare, as illustrated by the lack of difference in the diversity index scores amongst habitats (Table 2.4) and their low contribution to overall dissimilarity (SIMPER, Appendix 2.3).

Assemblage structure was similar between streams, but clustered according to habitat (NMDS, Figure 2.2). This pattern was supported by the PERMANOVA (Table 2.5) which showed that the assemblage composition between habitats in both streams differed ($p = 0.001$) while assemblage composition did not vary between streams. The differences between assemblages in each habitat are likely due to differences in the relative abundances and biomass of several of the dominant species, most having greater amounts in pools (SIMPER, Table 2.6). Oligochaetes and Tanytarsini midges contributed 25% of the differences between the abundances in riffles and pools. Pentaneurini and Chironomini midges as well as the two genera of Leptophlebiidae accounted for another quarter of the dissimilarity. In terms of biomass, *Neohaghenulus* (Leptophlebiidae) attributed 10% of the dissimilarity between habitats and Oligochaeta, Pentaneurini, *Xestochironomus*, Tanytarsini, *Hexacylloepus* and *Phylloicus* also contributing to the differences in biomass between habitats.

DISCUSSION

The main objective of this chapter was to describe the composition and structure of two headwater streams at the Luquillo Experimental Forest. I found no seasonal variability during the study period. This may be attributed to the fact that it coincided with a relatively stable, dry year with no major storm events compared to the long-term (2000-2015) hydrology of the area (Figure 2.1). I hypothesize that, as analyses are expanded to include the entirety of data collected at the site (long term datasets), there will be a higher temporal influence that is mainly driven by storm events and variability of stream discharge. This could potentially result in a change in benthic macroinvertebrate assemblages, with an overall decrease in biomass and

abundance and a shift towards species adapted to higher water flow as has been found in previous studies in tropical areas (Flecker and Feifarek, 1994; Ramirez and Pringle, 1998). Alternatively, extreme droughts as the one observed in 1994 in the LEF result in isolated pools with the disappearance of riffles. This contraction in pool habitats resulted in increased densities of shrimp species, with a decrease in their reproductive activity (Covich *et al.* 2003). This loss of riffles and overcrowding of species likely affects insect assemblages in a way that is yet to be addressed. These conditions may result in assemblages dominated by lentic-adapted species, as was the case during our study period, but also in a total disappearance of filter-feeding and flow dependent species. The LEF experienced another marked drought during the duration of our long term sampling (2014-2015), therefore this hypothesis could be addressed as data at the sites continue to be acquired. A total disappearance of filter-feeders would result in the disappearance of 9% of the genera found and around 8% of the biomass described in our study period. This low value likely reflects the low flow conditions during our study year.

While no differences in the assemblages between the two study streams were found, I found differences in the composition between the habitats. Riffles are generally considered to be more complex habitats with greater water flow and substrate heterogeneity, which therefore result in greater species richness (Downes *et al.* 1998). Richness was slightly higher in riffles; however, the fast flowing water adapted species were low in abundance or rare. Moreover, even though pools comprised a much lower percentage of the available habitat within the reaches, both the total abundance and total biomass were much higher than that found in riffles. The low hydrologic conditions during the sample year likely made the lotic habitats less favorable for species that need fast flowing water. Moreover, the depth of the riffles was relatively low, decreasing the available habitat.

The fact that most macroinvertebrate biomass is centered in pools could be interpreted as these sites offering greater habitat stability as a result of less scouring, and increased food resources due to higher organic matter retention (Reice, 1980), which may also serve as shelter. This might be the case for some less mobile groups such as chironomids, as some (with the exception of Othocladiinae) thrive in low flow habitats with abundant fine sediments and fine particulate organic matter. Also, although fine sediments and organic materials are more abundant in pools than in riffles, pools in the LEF have relatively rocky stream beds. This gives them high environmental stability (versus mainly sandy bottoms), which may offer better conditions for fauna colonization (Death and Winterbourn, 1995). However, it is important to note that the study streams are populated by a large amount of shrimp biomass, in particular *Xyphocaris elongata* and *Atya lanipes*, as described in numerous previous studies (March *et al.* 2001, Cross *et al.* 2008, among others) and have no fish species present. While these shrimp may prey on smaller organisms, they also provide secondary benefits by removing the fine sediments accumulated over rocks. This removal allows for greater access to, and greater growth of, the algae and biofilm sought by scrapers and collector-gatherers. (Pringle *et al.* 1993, March *et al.* 2001). Therefore, the observed increased macroinvertebrate abundance and biomass could be an indirect result from increased shrimp interactions.

Cross *et al.* (2008) examined *Atya spp.* and *X. elongata* in Prieta and in another stream in the LEF (Quebrada Bisley) which differs in food web structure due to the presence of fish. They found that mean annual shrimp biomass and secondary production were an order of magnitude higher in the stream that lacked predatory fishes versus the stream with predatory fishes. These differences in fish and shrimp communities result in a decrease in fine sediments and organic matter removal as seen by Pringle *et al.* (1999). Therefore, if the increased macroinvertebrate

biomass in pools is mainly due to shrimp-mediated sediment removal, we would expect an increase in insect abundance upon shrimp exclusion. This pattern was observed in Prieta by Ramirez and Hernandez-Cruz (2004). However, within the same study, in the stream with lower shrimp densities and the presence of predatory fish (Quebrada Bisley) there was no difference upon shrimp exclusion. This suggests that in sites where shrimp are not dominant, insect distributions are governed by alternate factors.

In summary, while the shrimp assemblages of the LEF streams had been thoroughly assessed, no study had focused on the entire insect assemblage. With this study, I was able to describe the aquatic insect assemblages of headwater fishless streams at the LEF. I found that macroinvertebrates in these systems are greatly influenced by the in-stream habitat, and potentially, by the abundance of freshwater shrimp. I also hypothesize that their structure will likely be influenced by changes in hydrological conditions (either intra-year variation or long-term gradual change). As an important first step in the long-term description of these communities, this study allowed me to identify the dominant groups on which further studies, such as secondary production and resource consumption, should be focused.

Table 2.1. Habitat quality parameters in Prieta and Gatos in riffle and pool habitats. FPOM= fine particulate organic matter, CPOM= coarse particulate organic matter, Depth=water depth at sample location, Cobble, Pebble, Gravel, Sand, Silt = % of each substrate found at sample location. All values averages of thirteen monthly samples (each sample an average of four samples taken each month) \pm SE.

Stream	Habitat	FPOM (mg/m ²)	CPOM (mg/m ²)	Depth (m)	Cobble (%)	Pebble (%)	Gravel (%)	Sand (%)	Silt (%)
Prieta	Pool	21.05 \pm 6.45	69.66 \pm 17.55	0.14 \pm 0.02	9.23 \pm 2.18	17.79 \pm 2.30	26.24 \pm 2.29	25.00 \pm 3.68	21.83 \pm 3.55
	Riffle	8.28 \pm 3.69	31.74 \pm 8.23	0.09 \pm 0.01	31.44 \pm 3.79	17.17 \pm 2.36	25.87 \pm 2.59	16.58 \pm 20.39	9.9 \pm 1.70
Gatos	Pool	13.02 \pm 2.61	34.24 \pm 5.43	0.13 \pm 0.01	8.27 \pm 2.81	22.02 \pm 2.78	30.25 \pm 2.48	20.39 \pm 3.43	17.8 \pm 2.52
	Riffle	3.8 \pm 0.78	10.47 \pm 2.11	0.11 \pm 0.01	37.69 \pm 4.05	18.46 \pm 2.31	24.71 \pm 1.79	11.54 \pm 1.98	8.37 \pm 2.26

Table 2.2. Average monthly discharge and Richards-Baker Flashiness Index in Prieta. Values calculated from values obtained from the LTER. Values based on measurements taken every fifteen minutes.

Date	Discharge (m ³ /s)	Flashy
August 2009	0.013	0.001
September 2009	0.013	0.000
October 2009	0.014	0.009
November 2009	0.023	0.014
December 2009	0.024	0.002
January 2010	0.022	0.007
February 2010	0.014	0.029
March 2010	0.011	0.003
April 2010	0.012	0.003
May 2010	0.013	0.002
June 2010	0.014	0.026
July 2010	0.039	0.705
August 2010	0.071	0.602

Table 2.3 Dominant taxa in Gatos and Prieta in terms of biomass and abundance. Only taxa that comprised at least 1% of the habitat-weighted values for both streams are included.

Order	Family	Genus/Tribe	Abundance (%)		Biomass (%)	
			Gatos	Prieta	Gatos	Prieta
Ephemeroptera	Leptophlebiidae	<i>Neohaghenulus</i>	21.6	13.7	40.4	22.8
		<i>Borinquena</i>	4.3	17.3		6.8
	Baetidae	<i>Cloeodes</i>	4.1	1.9	5.8	2.3
Hemiptera	Veliidae	<i>Rhagovelia</i>			3.2	2.3
Trichoptera	Hydropsychidae	<i>Macronema</i>				13.8
		<i>Smicridea</i>			3.5	1.6
Coleoptera	Calamoceratidae	<i>Phylloicus</i>		1.8	3.5	5.0
	Elmidae	<i>Hexacylloepus</i>		2.6	1.9	14.2
Diptera	Chironomidae	Chironomini (<i>Xestochironomus</i>)	3.1	1.7	7.2	3.1
		Chironomini (other)	1.3	4.1	1.6	1.4
		Orthocladini	4.4	4.5		
		Pentaneurini	12.8	15.7	9.7	6.0
		Tanytarsini	18.1	20.6	4.9	3.8
		Ceratopogonidae	Ceratopogoninae			
	Simuliidae	<i>Simulium</i>			1.6	
	Tipulidae	<i>Hexatoma</i>				6.3
Oligochaeta			20.5	10.0	9.1	5.3
Total %			90.3	94.0	92.3	95.9

Table 2.4. Diversity measures. S= total number of species, N= total number of individuals, d= Margalef's species richness, J'= Pielou's evenness, H' = Shannon index, $1-\lambda'$ = Simpson index.

Stream	Habitat	S	N	d	J'	H'	$1-\lambda'$
Prieta	Pool	32	1327	4.31	0.64	2.21	0.84
	Riffle	36	276	6.23	0.61	2.19	0.77
Gatos	Pool	27	1211	3.66	0.68	2.24	0.86
	Riffle	35	343	5.82	0.66	2.34	0.85

Table 2.5. Results of the PERMANOVA tests performed on a Bray-Curtis similarity matrix based on the average abundance and biomass of aquatic macroinvertebrate data of the two LEF streams.

Source	df	SS	MS	Pseudo-F	P(perm)
Abundance					
Stream	1	3805.5	3805.5	0.33422	0.65
Habitat (Stream)	2	22772	11386	9.692	0.001
Residual	48	56390	1174.8		
Total	51	82967			
Biomass					
Stream	1	5558.9	5558.9	0.568	0.689
Habitat (Stream)	2	19558	9779	6.641	0.001
Residual	48	70677	1472.4		
Total	51	95793			

Table 2.6. One-way SIMPER analysis using habitat as the factor based on Bray-Curtis similarity (cut-off 50%, full table found in appendix 2.3). The average cumulative dissimilarity between habitats was 62.03% for macroinvertebrate abundance and 65.00% for macroinvertebrate biomass.

Taxa	Average Abundance in Pools	Average Abundance in Riffles	Average Dissimilarity	Dissimilarity /SD	Contributing %	Cumulative %
Abundance						
<i>Oligochaeta</i>	13.48	2.21	7.80	1.40	12.57	12.57
<i>Tanytarsini</i>	14.80	3.93	7.74	1.48	12.48	25.05
<i>Pentaneurini</i>	13.17	4.14	6.13	1.69	9.88	34.93
<i>Borinquena</i>	7.81	5.57	4.53	1.10	7.30	42.24
<i>Neohagenulus</i>	11.70	9.33	4.31	1.27	6.95	49.19
<i>Chironomini</i>	4.59	0.54	2.92	1.11	4.71	53.90
<i>Xestochironomus</i>	4.71	1.17	2.85	1.03	4.60	58.50
<i>Orthocladiinae</i>	5.27	4.06	2.71	1.21	4.37	62.88
<i>Cloeodes</i>	4.96	2.34	2.65	1.19	4.27	67.15
<i>Hexacylloepus</i>	3.08	1.08	2.04	0.99	3.28	70.43
Biomass						
<i>Neohagenulus</i>	3.95	2.80	6.52	1.38	10.04	10.04
<i>Oligochaeta</i>	2.00	0.25	5.37	1.19	8.27	18.30
<i>Pentaneurini</i>	2.30	0.84	4.72	1.47	7.25	25.56
<i>Hexacylloepus</i>	1.62	0.58	4.62	0.87	7.11	32.67
<i>Xestochironomus</i>	1.51	0.32	4.19	0.99	6.45	39.12
<i>Tanytarsini</i>	1.61	0.36	4.01	1.34	6.17	45.29
<i>Phylloicus</i>	1.11	0.37	3.37	0.79	5.18	50.47
<i>Borinquena</i>	1.14	0.88	3.30	1.19	5.08	55.56
<i>Cloeodes</i>	1.19	0.83	3.20	1.12	4.92	60.47
<i>Hexatoma</i>	0.94	0.26	2.97	0.64	5.57	65.04
<i>Rhagovelia</i>	0.26	0.93	2.94	1.00	4.52	69.56
<i>Chironomini</i>	0.83	0.11	2.43	1.07	3.73	73.29

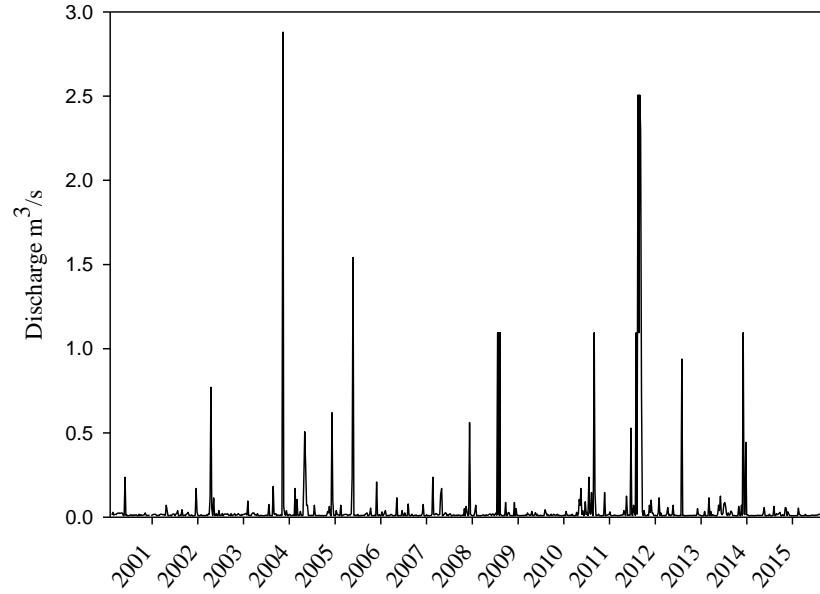


Figure 2.1. Weekly discharge in Quebrada Prieta from February 2000 to December 2015. Data from the LUQ-LTER.

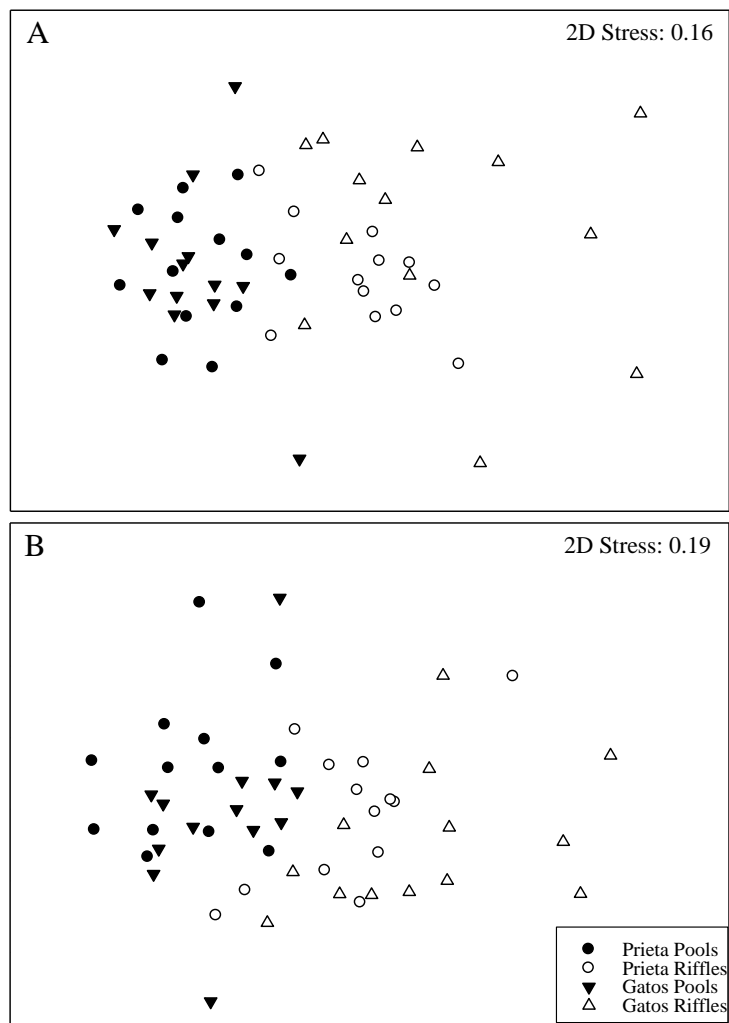
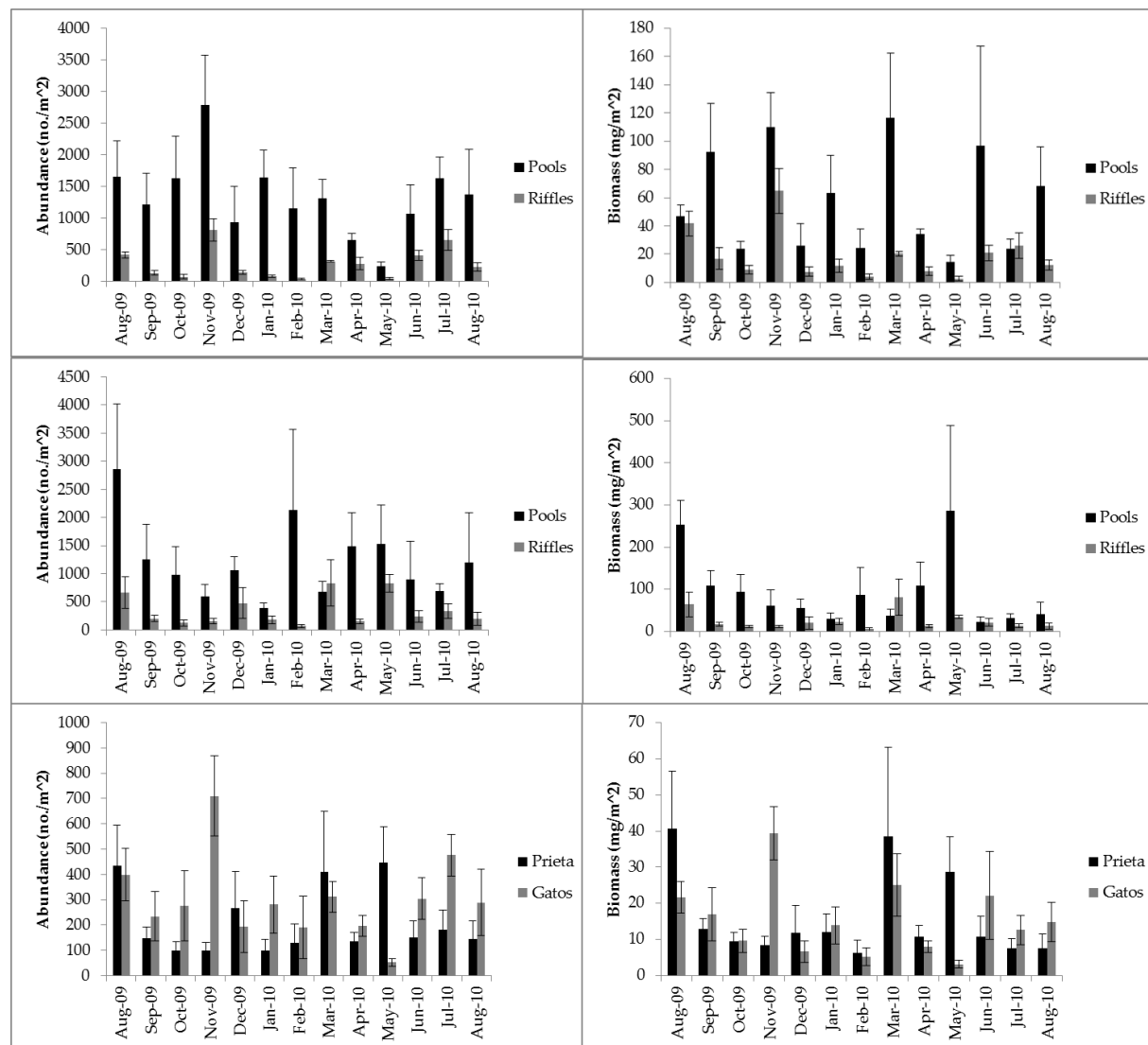


Figure 2.2. Two-dimensional NMDS plots of insect assemblages. The PERMANOVA showed significant differences in biomass and abundance between the habitats (open and closed) ($p < 0.001$), but not between the streams (circles and triangles).

Appendix 2.1. Monthly average total assemblage abundance and biomass values \pm SE.

Abundance (left panel) and biomass (right panel) found in Gatos (top), Prieta (center) and habitat weighted (bottom).



Appendix 2.2 – Average yearly abundance and biomass of all taxa found in the two study streams. All values averages of thirteen monthly samples (each sample an average of four samples taken each month) \pm SE. Values reported without SE mean taxa only found within one sampling date.

Class	Order	Family	Subfamily/ Tribe/Genus	Abundance				Biomass				
				Gatos		Prieta		Gatos		Prieta		
				Pools	Riffles	Pools	Riffles	Pools	Riffles	Pools	Riffles	
Insecta	Ephemeroptera	Baetidae	<i>Cloeodes</i>	52.14 \pm 17.60	13.41 \pm 4.46	23.42 \pm 7.91	5.40 \pm 1.90	2.82 \pm 0.86	1.56 \pm 0.50	1.96 \pm 0.87	0.79 \pm 0.25	
		Caenidae	<i>Caenis</i>	2.27 \pm 1.63	0.40	0	0	0.04	0.06	0	0	
		Leptophlebiidae	<i>Borinquena</i> <i>Neohagenulus</i>	39.29 \pm 20.93 222.91 \pm 57.85	30.22 \pm 12.30 123.47 \pm 40.70	189.66 \pm 58.89 120.15 \pm 24.27	79.44 \pm 37.56 92.25 \pm 19.49	0.30 \pm 0.14 21.41 \pm 5.81	0.31 \pm 0.14 9.23 \pm 2.49	5.13 \pm 1.61 18.24 \pm 3.83	2.99 \pm 1.27 8.87 \pm 1.58	
	Odonata	Coenagrionidae	<i>Enallagma</i>	1.51	0	5.29 \pm 2.64	0.40	0.03	0	0.23 \pm 0.18	0.04	
	Hemiptera	Hebridae		0.76	0.60	0	0	0.01	0.41	0	0	
		Veliidae	<i>Rhagovelia</i>	1.51	5.80 \pm 3.32	2.27 \pm 1.63	4.80 \pm 2.22	0.59	1.85 \pm 1.06	0.63 \pm 0.43	2.08 \pm 1.10	
	Trichoptera	Calamoceratidae	<i>Philloicus</i>	11.33 \pm 4.70	2.00 \pm 1.15	24.94 \pm 10.82	2.80 \pm 1.60	2.54 \pm 1.39	0.14 \pm 0.08	4.74 \pm 2.53	1.23 \pm 0.81	
		Glossosomatidae	<i>Cariboptila</i>	0	0	0.76	0	0	0	0.05	0	
		Hydrobiosidae	<i>Atopsyche</i>	0	1.00 \pm 0.55	0	0.60 \pm 0.32	0	0.13 \pm 0.07	0	0.14 \pm 0.09	
		Hydropsychidae	<i>Macronema</i>	0	0	0.76	1.20 \pm 0.86	0	0	16.07	0.35 \pm 0.34	
			<i>Smicridea</i>	3.78 \pm 3.05	7.00 \pm 2.86	0.76	9.21 \pm 6.08	1.25 \pm 1.24	1.43 \pm 0.86	0	1.95 \pm 1.05	
		Hydroptilidae	<i>Alisotrichia</i>	2.27 \pm 1.63	4.40 \pm 1.94	0	0.60 \pm 0.32	0.01	0.09 \pm 0.04	0	0.01	
			<i>Hidroptila</i>	0.76	0.60 \pm 0.43	0	0	0.09	0.01	0	0	
			<i>Kumansliella</i>	0	0	0	0.40	0	0	0	0	
				<i>Neotrichia</i>	0.76	1.00 \pm 0.63	0	1.00 \pm 0.55	0	0.02 \pm 0.01	0	0.02 \pm 0.01
			Philopotamidae	<i>Chimarra</i>	0	0.60	0	0	0	0.47	0	0
			Polycentropodidae	<i>Cernotina</i>	0	0	1.51	0	0	0	0.63	0
		Lepidoptera	Crambidae	<i>Neargyractis</i>	0	0	0.76	1.00 \pm 0.63	0	0	0.02	0.25 \pm 0.19
	<i>Petrophila</i>			0	0.20	0	0.20	0	0.29	0	0.19	
	Coleoptera	Elmidae	<i>Hexacylloepus</i>	9.82 \pm 4.97	1.00 \pm 0.63	35.51 \pm 11.80	4.80 \pm 1.69	1.33 \pm 0.71	0.09 \pm 0.05	14.93 \pm 6.82	1.92 \pm 0.89	
			<i>Neelmis</i>	0	0	0.76	1.00 \pm 0.69	0	0	0.97	0.17 \pm 0.16	
			<i>Phanocerus</i>	2.27 \pm 1.63	1.00 \pm 0.47	0.76	3.20 \pm 1.59	0.44 \pm 0.33	0.06 \pm 0.04	0.13	0.41 \pm 0.23	
		Psephenidae		0	0.20	0	0	0	0.01	0	0	
		Ptilodactylidae		9.82 \pm 6.95	0	0	0.20	0.63 \pm 0.39	0	0	0.04	
	Diptera	Ceratopogonidae	<i>Atrichopogon</i>	3.02	3.00 \pm 1.44	0	0.40 \pm 0.27	0.02	0.04 \pm 0.02	0	0	
			Ceratopogoninae	6.80 \pm 2.05	0.80 \pm 0.45	11.33 \pm 3.66	3.40 \pm 1.78	0.47 \pm 0.20	0.05 \pm 0.03	1.03 \pm 0.29	0.25 \pm 0.16	
		Chironomidae	Chironomini	20.40 \pm 4.65	0.40	61.21 \pm 26.25	3.00 \pm 2.16	1.18 \pm 0.37	0.03	1.55 \pm 0.71	0.17 \pm 0.14	
Orthoclaadiinae			43.83 \pm 11.91	26.01 \pm 7.56	49.12 \pm 25.36	20.61 \pm 7.75	0.24 \pm 0.08	0.25 \pm 0.07	0.15 \pm 0.06	0.27 \pm 0.17		
Pentaneurini			191.17 \pm 38.02	14.21 \pm 3.58	214.60 \pm 48.85	30.22 \pm 9.08	6.69 \pm 1.81	0.67 \pm 0.19	6.02 \pm 1.32	1.15 \pm 0.29		
Tanytarsini			280.34 \pm 76.58	9.41 \pm 3.22	278.07 \pm 70.15	42.82 \pm 16.05	3.62 \pm 1.12	0.07 \pm 0.03	4.12 \pm 1.61	0.39 \pm 0.14		
		<i>Xestochironomus</i>	47.60 \pm 21.25	2.40 \pm 1.40	22.67 \pm 5.14	4.20 \pm 1.30	5.25 \pm 2.81	0.21 \pm 0.12	3.33 \pm 1.30	0.32 \pm 0.11		
Corethrellidae			12.85 \pm 4.22	1.80 \pm 0.62	2.27 \pm 1.19	0	0.15 \pm 0.05	0.03 \pm 0.01	0.03 \pm 0.01	0		
Dixidae			0	0.20	0	2.60 \pm 1.84	0	0	0	0.13 \pm 0.09		
Dolichopodidae			2.27 \pm 1.63	0.60 \pm 0.43	1.51	0.60	0.02	0.01	0.03	0.01		
Empididae		<i>Hemerodromia</i>	3.02 \pm 1.31	1.80 \pm 1.23	0	0.40 \pm 0.27	0.10 \pm 0.04	0.16 \pm 0.13	0	0.02		
Psychodidae		<i>Maruina</i>	3.02 \pm 1.72	4.60 \pm 1.77	0	1.20 \pm 0.56	0.02 \pm 0.01	0.04 \pm 0.02	0	0.02 \pm 0.01		
Simuliidae	<i>Simulium</i>	9.07 \pm 8.28	6.40 \pm 2.63	0	8.00 \pm 6.00	0.78 \pm 0.55	0.43 \pm 0.17	0	0.49 \pm 0.36			
Stratiomyidae		3.02 \pm 1.72	0.20	0	0.20	0.01 \pm 0.00	0	0	0			
Tipulidae	<i>Hexatoma</i>	0	0.60 \pm 0.32	9.07 \pm 2.07	1.60 \pm 0.69	0	0.26 \pm 0.21	7.27 \pm 3.04	0.28 \pm 0.11			
	<i>Limonia</i>	0	1.00 \pm 0.47	0.76	0	0	0.29 \pm 0.21	0.04	0			
Arachnida	Acari		0.76	1.40 \pm 0.81	2.27	2.60 \pm 1.14	0.01 \pm 0.01	0.02 \pm 0.01	0.03	0.03 \pm 0.01		
Oligochaeta			321.90 \pm 84.08	7.40 \pm 2.18	148.10 \pm 48.28	8.00 \pm 2.92	6.74 \pm 2.62	0.12 \pm 0.06	6.18 \pm 2.77	0.18 \pm 0.12		
Ostracoda			6.05 \pm 4.09	0	0	0	0.05 \pm 0.04	0	0	0		
Turbellaria	Tricladida	Planariidae	10.58 \pm 5.15	0.60	3.02 \pm 1.31	4.80 \pm 1.79	0.16 \pm 0.06	0.01	0.10 \pm 0.05	0.27 \pm 0.18		

Appendix 2.3. One-way SIMPER analysis using habitat as the factor based on Bray-Curtis similarity. The average cumulative dissimilarity between habitats was 62.03% for macroinvertebrate abundance and 65.00% for macroinvertebrate biomass.

Taxa	Average Abundance in Pools	Average Abundance in Riffles	Average Dissimilarity	Dissimilarity /SD	Contributing %	Cumulative %
Abundance						
Oligochaeta	13.48	2.21	7.8	1.4	12.57	12.57
Tanytarsini	14.8	3.93	7.74	1.48	12.48	25.05
Pentaneurini	13.17	4.14	6.13	1.69	9.88	34.93
<i>Borinquena</i>	7.81	5.57	4.53	1.1	7.3	42.24
<i>Neohagenulus</i>	11.7	9.33	4.31	1.27	6.95	49.19
Chironomini	4.59	0.54	2.92	1.11	4.71	53.9
<i>Xestochironomus</i>	4.71	1.17	2.85	1.03	4.6	58.5
Orthoclaadiinae	5.27	4.06	2.71	1.21	4.37	62.88
<i>Cloeodes</i>	4.96	2.34	2.65	1.19	4.27	67.15
<i>Hexacylloepus</i>	3.08	1.08	2.04	0.99	3.28	70.43
<i>Phylloicus</i>	2.77	0.81	1.81	0.91	2.92	73.35
Ceratopogoninae	2.28	0.79	1.45	1.16	2.34	75.69
Planariidae	1.57	0.86	1.16	0.97	1.88	77.57
<i>Smicridea</i>	0.48	1.69	1.16	0.85	1.87	79.43
Corethreliidae	1.7	0.45	1.16	0.87	1.87	81.3
<i>Rhagovelia</i>	0.46	1.57	1.13	1.01	1.82	83.12
<i>Simulium</i>	0.52	1.5	1.09	0.71	1.76	84.88
<i>Hexatoma</i>	1.23	0.57	0.99	0.91	1.59	86.47
<i>Maruina</i>	0.41	1.04	0.77	0.83	1.24	87.71
<i>Alisotrichia</i>	0.29	0.89	0.7	0.71	1.13	88.84
<i>Phanocerus</i>	0.41	0.76	0.64	0.68	1.03	89.87
<i>Enallagma</i>	0.79	0.09	0.62	0.48	1	90.88
Acari	0.33	0.79	0.59	0.72	0.95	91.83
<i>Atrichopogon</i>	0.24	0.67	0.52	0.61	0.84	92.67
<i>Hemerodromia</i>	0.48	0.43	0.51	0.62	0.83	93.5
Ptilodactilidae	0.69	0.06	0.46	0.34	0.75	94.24

Dolicopodidae	0.46	0.26	0.41	0.49	0.66	94.91
<i>Neotrichia</i>	0.12	0.47	0.34	0.53	0.55	95.46
Stratyiomidae	0.41	0.12	0.3	0.43	0.49	95.95
Ostracoda	0.48	0	0.28	0.29	0.45	96.4
<i>Atopsyche</i>	0	0.42	0.26	0.52	0.42	96.82
Dixidae	0	0.42	0.26	0.36	0.41	97.23
<i>Limonia</i>	0.12	0.27	0.24	0.46	0.38	97.62
<i>Caenis</i>	0.29	0.09	0.22	0.34	0.36	97.98
<i>Neoelmis</i>	0.12	0.2	0.2	0.34	0.32	98.3
<i>Neargyractis</i>	0.12	0.23	0.18	0.39	0.3	98.6
<i>Macronema</i>	0.12	0.21	0.17	0.34	0.27	98.87
Hebridae	0.12	0.11	0.15	0.27	0.23	99.1
<i>Hydroptila</i>	0.12	0.15	0.14	0.35	0.23	99.33
<i>Petrophila</i>	0	0.12	0.11	0.28	0.17	99.5
<i>Cernotina</i>	0.17	0	0.09	0.2	0.15	99.65
<i>Chimarra</i>	0	0.11	0.06	0.2	0.09	99.75
Psephenidae	0	0.06	0.06	0.19	0.09	99.84
Glossosomatidae	0.12	0	0.05	0.2	0.09	99.92
<i>Kumanskiella</i>	0	0.09	0.05	0.2	0.08	100
Biomass						
<i>Neohagenulus</i>	3.95	2.8	6.52	1.38	10.04	10.04
Oligochaeta	2	0.25	5.37	1.19	8.27	18.3
Pentaneurini	2.3	0.84	4.72	1.47	7.25	25.56
<i>Hexacylloepus</i>	1.62	0.58	4.62	0.87	7.11	32.67
<i>Xestochironomus</i>	1.51	0.32	4.19	0.99	6.45	39.12
Tanytarsini	1.61	0.36	4.01	1.34	6.17	45.29
<i>Phylloicus</i>	1.11	0.37	3.37	0.79	5.18	50.47
<i>Borinquena</i>	1.14	0.88	3.3	1.19	5.08	55.56
<i>Cloeodes</i>	1.19	0.83	3.2	1.12	4.92	60.47
<i>Hexatoma</i>	0.94	0.26	2.97	0.64	4.57	65.04
<i>Rhagovelia</i>	0.26	0.93	2.94	1	4.52	69.56
Chironomini	0.83	0.11	2.43	1.07	3.73	73.29
<i>Smicridea</i>	0.17	0.74	2.18	0.76	3.35	76.64

<i>Ceratopogoninae</i>	0.63	0.19	1.74	1.11	2.68	79.32
<i>Simulium</i>	0.17	0.36	1.29	0.72	1.98	81.3
<i>Macronema</i>	0.56	0.09	1.17	0.23	1.8	83.1
<i>Orthoclaadiinae</i>	0.34	0.4	1	1.19	1.55	84.65
<i>Phanocerus</i>	0.18	0.23	1	0.62	1.54	86.18
<i>Planariidae</i>	0.22	0.17	0.91	0.8	1.39	87.58
<i>Neoelmis</i>	0.14	0.07	0.62	0.28	0.95	88.53
<i>Corethrelliidae</i>	0.18	0.06	0.61	0.86	0.94	89.47
<i>Ptilodactilidae</i>	0.18	0.03	0.58	0.37	0.9	90.37
<i>Hemerodromia</i>	0.09	0.11	0.56	0.57	0.86	91.22
<i>Petrophila</i>	0	0.13	0.52	0.27	0.8	92.03
<i>Atopsyche</i>	0	0.17	0.48	0.47	0.74	92.76
<i>Enallagma</i>	0.13	0.03	0.47	0.44	0.73	93.49
<i>Limonia</i>	0.03	0.12	0.45	0.34	0.69	94.18
<i>Alisotrichia</i>	0.02	0.12	0.4	0.65	0.61	94.79
<i>Maruina</i>	0.03	0.1	0.35	0.76	0.55	95.33
<i>Hebridae</i>	0.02	0.09	0.35	0.21	0.54	95.88
<i>Acari</i>	0.04	0.09	0.32	0.7	0.49	96.36
<i>Neargyractis</i>	0.02	0.11	0.29	0.31	0.45	96.81
<i>Atrichopogon</i>	0.02	0.07	0.25	0.54	0.39	97.19
<i>Dixidae</i>	0	0.09	0.24	0.35	0.37	97.57
<i>Dolicopodidae</i>	0.05	0.03	0.23	0.45	0.35	97.91
<i>Caenis</i>	0.04	0.03	0.22	0.31	0.35	98.26
<i>Chimarra</i>	0	0.1	0.21	0.2	0.32	98.58
<i>Cerlotina</i>	0.11	0	0.2	0.2	0.31	98.89
<i>Neotrichia</i>	0.01	0.06	0.19	0.49	0.3	99.19
<i>Hydroptila</i>	0.04	0.02	0.17	0.31	0.25	99.45
<i>Ostracoda</i>	0.04	0	0.12	0.28	0.18	99.63
<i>Stratyiomidae</i>	0.02	0.02	0.12	0.43	0.18	99.81
<i>Psephenidae</i>	0	0.01	0.06	0.19	0.09	99.90
<i>Glossosomatidae</i>	0.03	0	0.05	0.2	0.08	99.98
<i>Kumanskiella</i>	0	0.01	0.02	0.2	0.02	100.0

CHAPTER 3. TROPHIC BASIS OF INSECT SECONDARY PRODUCTION IN TWO TROPICAL HEADWATER STREAMS, PUERTO RICO

ABSTRACT

Quantitative food webs describe trophic linkages between consumers and resources, and also combine diet analyses with taxon-specific production estimates to determine energy flow among taxa. The resulting web denotes the overall contribution of each food source to the production of each species and their trophic position. In this study I estimated annual secondary production and develop a quantitative food web of the benthic insect communities present in two small streams at the Luquillo Experimental Forest (LEF), Puerto Rico. I examined the gut content of the dominant aquatic insect groups: leptophlebiid and baetid mayflies, calamoceratid and hydropsychid caddisflies and chironomid midges, and found that these groups rely heavily on amorphous detritus and plant tissue. Overall, aquatic insects in the LEF have low biomass; therefore, their production is relatively low compared with available estimates. Habitat weighted production values were similar in both streams ($528.5 \text{ mg m}^{-2} \text{ yr}^{-1}$ - $591.5 \text{ mg m}^{-2} \text{ yr}^{-1}$) but production values were over twice as high in pool habitats versus riffles. Most of the production was attributed to *Neohagenulus* ($259.1 \text{ mg m}^{-2} \text{ yr}^{-1}$ - $352.2 \text{ mg m}^{-2} \text{ yr}^{-1}$). Secondary production appears to rely more on allochthonous organic matter, rather than primary production; however, energetic composition of amorphous detritus was not assessed. This study is one of the first to quantify the production and food web of the benthic insect community in tropical island streams.

INTRODUCTION

Secondary production is a comprehensive measure of fitness because it combines variables such as density, biomass, individual growth rate, fecundity, survivorship, body size, and life span (Benke, 2010). Classically, work on secondary production focused on community-level energy flow involving the formation of trophic level biomass and its transfer to succeeding trophic levels (Benke, 2010). However, in past decades, research (mainly on aquatic ecosystems) has expanded to examine questions related to predator-prey relationships, food resource use, effects of nonnative species and pollutants, effects of catchment land use change and the development of quantitative food webs (Benke and Huryn, 2010). Therefore, secondary production estimates may represent a useful proxy with regard to the functional responses of populations or communities subjected to various environmental stressors. In the light of global change, secondary production may provide insight into ecosystem dynamics, as it combines both static and dynamic components of a population's ecological performance in terms of bioenergetics and ecosystem functioning (Dolbeth *et al.* 2012).

One application of secondary production is in constructing quantitative of food webs. These types of webs not only describe the connectivity between consumers and resources, but they combine diet analysis with taxon-specific secondary production in order to determine the amount of energy flow between species (Benke and Wallace 1980, 1997). Quantitative differences in ingestion flows can serve as a measure of bottom-up interaction strength between species and their food resource (Benke and Wallace, 1997). Also, the ratio of these ingestion flows to production of the resource from which they came may be used as a measure of top-down interaction strength (Benke *et al.* 2001). The resulting web tells us how much each food source is responsible for the production of each species and the trophic position of those species. With this

information, negative or positive cascade effects caused by anthropogenic and/or climate impacts in the ecosystem may be predicted as a result of removal/reductions of resources (i.e., deforestation, drought) or increases in production of opportunistic or tolerant species after disturbance events (Johnson *et al.* 2011; Dolbeth *et al.* 2012).

The majority of secondary production studies have been from temperate systems with very few in tropical streams (Jacobsen *et al.* 2008). Tropical streams have several characteristics that would lead us to believe that the patterns that we observe in the more studied temperate counterparts may not hold true. For example, the high precipitation and subsequent high discharge are major factors determining the structure of benthic communities (Ramirez and Pringle, 1998). -Ramirez and Pringle (1998) in Costa Rica found that secondary production in their study stream was low in comparison to results obtained in subtropical and temperate regions. However, they also found that annual production to biomass (P/B) ratios were high, indicating rapid population turnover. They suggested that the low observed secondary production and low amount of insect shredders may be attributed to the abundance of macroconsumers (e.g., fish and benthic shrimp) because they potentially reduce food and prey upon insects. Shrimp often dominate the biomass of tropical island streams and are known to have strong effects on stream ecosystem structure and function (Cross *et al.* 2008). Therefore, in the tropics, energy is potentially flowing through pathways other than insects from primary producers and detritus to upper trophic levels. Colón-Gaud *et al.* (2009) studied the effects of amphibian declines on the secondary production of macroinvertebrate communities in Panama. While no changes in total production were observed, there was a shift in taxonomic composition and functional structure of macroinvertebrate consumers likely due to the changes in the availability of energy sources in sites pre and post amphibian decline.

For streams in the Luquillo Experimental Forest, our study system, only one estimate of stream consumer production exists (Cross *et al.* 2008); however, this study only addressed shrimp assemblages. Therefore, in this study my goal was to carry out one of the first studies to quantify the production and food web of the non-shrimp benthic consumer communities in tropical island streams and develop a quantitative food web to describe the energy flow in these systems. The information gathered in this study complements the existing work and allow me to further link consumers to ecosystem processes. In general, there are limited community-wide studies and limited knowledge of the effects of biotic interactions that limit the current understanding of the mechanisms that control stream productivity (Huryn and Wallace, 2000). Understanding the factors that help shape aquatic communities in this region provides critical information for the conservation of these ecosystems (Pringle 1997). Extirpation and extinction rates in tropical freshwater habitats are high (Dudgeon *et al.* 2006). Therefore, baseline information on tropical freshwater communities of these relatively understudied regions is critical for the conservation and management of the existing systems, and for quantifying the consequences of future losses of biodiversity and global change.

METHODS

Study Site

I sampled two first order streams (Quebrada Prieta and Quebrada Gatos; henceforth Prieta and Gatos) that drain the Luquillo Experimental Forest (LEF) as described in Chapter 2. Streams in the LEF are believed to be detritus based and consumer food webs have few trophic linkages (Covich and McDowell, 1996) with either fish or shrimp as the dominant top consumer group. Some studies however, highlight the importance of algal energy sources even in forested

headwater streams (March and Pringle, 2003). In the two study streams, predatory fish are absent due to the presence of natural barriers in the form of large waterfalls downstream which prevent upstream dispersal. The absence of predatory fishes results in high densities of shrimp (~25 individuals per m²). Shrimp assemblages in these streams commonly include 4 species of Atyidae, one species of Xiphocaridae, and five species of Palaemonidae. However, over 90% of the assemblage is dominated by two taxa, *Xiphocaris elongata* and *Atya lanipes*, with low numbers of all other taxa (Cross *et al.* 2008).

Taxa Selection

Taxa selection was based on their relative biomass in the study site during the initial year-long sampling (see Chapter 2) and their viability to withstand laboratory incubation conditions. The taxa included were two mayflies: *Neohagenulus* sp. (Leptophlebiidae), *Cloeodes* sp. (Baetidae); two caddisflies: *Smicridea* sp. (Hydropsychidae), *Phylloicus pulchrus* (Calamoceratdidae); and three midges Chironominae, Tanypodinae, Orthocladiinae (Chironomidae). These seven groups accounted for approximately 70% of the biomass found in the yearly study among the two streams, as described in Chapter 2.

Macroinvertebrate Growth Rates

Size-class specific instantaneous growth rates for each target taxon were obtained by hand collecting insects from the study streams during the summer of 2014, measuring them, and incubating them for 3-7 days in growth chambers in a laboratory setting. For most taxa, the chambers consisted of twelve 235 ml containers that have three 3cm x 6cm holes covered with a vinyl mesh (in order to allow water movement) within a larger container (58.4 x 41.3 x 15.2 cm) with approximately 20 L of stream water and aquarium air pumps for aeration. In order to

maintain a strong current and promote their natural filter feeding behavior, the chambers for *Smicridea* sp. consisted of 15 ml centrifuge tubes modified to have a mesh covering each end of the tube. The tubes were kept horizontally by securing them about halfway of water column to a piece of foam the width of the chamber. On one end of the large container, we placed two aquarium pumps to create water flow. Water was able to flow through the chambers and back to the front of the large container. All chambers contained substrates (rocks, small sediment, leaves) as a food and shelter source. Water temperature was maintained at approximately 22 °C. The insects were photographed over a 1mm grid before being placed in each chamber and photographed again at the end of the incubation period. The change in size was calculated using Image Tool v. 3.00. For most taxa, insects were divided into 3 different size classes: less than 2mm long, 2 to 4 mm long and greater than 4mm long. Given how *Phylloicus* spp. are larger bodied than the rest, the size classes used for the members of this taxon were: less than 4mm, 4-8 mm and greater than 8 mm. For groups where I was unable to collect all size classes, the growth rates were supplemented with published growth rates from small tropical streams (Ramirez and Pringle 1996). The instantaneous growth rates (IGR) were estimated using the equation: $IGR = \ln(W_f - W_i) / t_i$, where W_i is the average individual mass at the beginning and W_f the average individual mass at the end of the incubation period (t_i).

Macroinvertebrate Biomass and Production

Benthic macroinvertebrate biomass for depositional and erosional habitats were calculated separately and combined for an overall habitat-weighted value for each reach in the two streams for 13 consecutive months as described in Chapter 2. Secondary production and Production to Biomass (P/B) ratios were also calculated for erosional and depositional habitats in the two study streams. The instantaneous growth method (IGR) (Benke and Huryn 2006) was

used due to the fact that our study organisms have asynchronous cohorts and short development times. This method calculates daily production by multiplying the size specific instantaneous growth rates to the mean biomass of the population of each size class for two consecutive dates and summing those products.

Gut Content Analysis

Organisms from selected taxa were hand collected within the study streams during the summer of 2014 and preserved in Kalhe's solution (Wiggins 1996). Although the samples were collected four years after the initial biomass sampling, the hydrological patterns of those years (Figure 2.1) do not suggest major differences in the study years as both years were relatively dry. Also, no major change in habitat quality or forest cover occurred in the interim. Therefore, I do not expect the sampling gap to create a bias. I analyzed the gut content of a total of 97 individuals (Range: 5-25 per target taxa, average: 12) of all available size classes (not analyzed separately). The contents of the foregut of each insect were dissected and the contents were suspended in water. The suspensions were filtered into a 45 μm nitrocellulose membrane filter; each filter was dried at 60 °C for 15 minutes, placed on a microscope slide, cleared with immersion oil and covered with a cover slip. Each slide was observed under a compound microscope at 100-400X and the particles found in 10 randomly chosen quadrants (40 fields of view at 100X magnification) were identified and classified. Particles were classified as fungi, amorphous detritus, plant detritus, animal, diatoms, and algae.

Quantitative Food Web

The quantitative food web was constructed by incorporating the annual secondary production estimates for dominant taxa, mean annual percent of each food category consumed

and gross production efficiency (GPE) estimates for each taxon. GPE is the product of net production efficiency (NPE) and assimilation efficiency (AE) for each food type. NPE (production/assimilation) for all taxa was assumed to be 50% and AE (assimilation/ingestion) values were assumed to be: 10% for fungi, 10% for amorphous detritus, 10% for plant detritus, 70% for animal, 30% for diatoms, and 30% for algae (Benke and Wallace 1980). The relative contribution of each food type to production was estimated by multiplying the mean annual percentage of each food type consumed by its respective AE and NPE. To estimate the percentage of production attributed to each food type, each relative contribution of food type to production was divided by the sum of all contributions to production. To calculate the production attributed to each food type, the production estimate of each taxon was multiplied by the percentage of production attributed to each food type. This value was divided by the GPE to estimate the amount of each food type consumed. Estimates were weighed by the annual production of each taxon and those values were used to construct quantitative food webs for the dominant insect groups.

Statistical Analysis

For the production and biomass estimates, I constructed 95% confidence intervals using bootstrap techniques (Efron and Tibshirani, 1993). Bootstrapped data sets were generated by randomly resampling individual data sets with replacement 1000 times. Differences in mean secondary production between communities of the two study streams were estimated by comparing the degree of overlap of confidence intervals at an alpha of 0.05 (Benke and Huryn, 2006).

RESULTS

Size specific growth rates are presented in Table 3.1. Given how the selected taxa encompassed 70% of the overall insect biomass in the study streams (as described in Chapter 2), I consider my estimates a good proxy for the aquatic insect assemblages present. Habitat weighted production estimates were similar in both streams, with 591.5 mg m⁻² yr⁻¹ for Gatos (359.8 in riffles; 1107.3 in pools) and 528.5 mg m⁻² yr⁻¹ for Prieta (464.7 in riffles; 1174.4 in pools). While pools encompassed a lesser proportion of the available habitat, average production values were over twice as high in comparison to riffles. Species specific production estimates using the IGR method are shown in Table 3.2. The taxon with the highest production (accounting for about half of the entire assemblage production) was *Neohagenulus* with 352.2 mg m⁻² yr⁻¹ for Gatos (260.6 in riffles; 556.1 in pools) and 259.1 mg m⁻² yr⁻¹ for Prieta (242.7 in riffles; 425.7 in pools). Most groups (except *Smicridea*, a collector-filterer) had average production values higher in pools than in riffles. While comparing the 95% confidence intervals, there were statistically significant differences between pools and riffles for the following taxa: *Neohagenulus*, Tanypodinae, and Chironominae in Gatos and *Smicridea*, Tanypodinae, and Chironominae in Prieta. The annual P/B ratios were similar among streams, but slightly higher in erosional habitats than in depositional with 27.42 in Gatos (27.99 in riffles; 26.17 in pools) and 26.99 in Prieta (27.40 in riffles; 22.78 in pools). Chironominae had the highest overall P/B ratios with 48.03 in Gatos (46.05 in riffles; 52.45 in pools) and 55.78 in Prieta (54.81 in riffles; 65.68 in pools). *Phylloicus* showed high P/B ratios with 49.08 in Gatos (50.4 in riffles; 46.15 in pools) and 40.1 in Prieta (39.70 in riffles; 44.11 in pools).

Diet varied among taxa; however, most of the food particles consumed were in the form of amorphous detritus (Figure 3.1). *Phylloicus*, the dominant shredder of the study streams,

consumed mainly plant matter. Only 2 taxa, *Smicridea* and Tanypodinae, showed any notable omnivory across food types; although these taxa mainly fed on fungi and amorphous detritus. As was expected, none of the study taxa can be considered predatory with animal particles making up only 0.51% of the total particles identified. The second most important source of energy was plant detritus with a third of food particles analyzed (33.44%), highlighting the importance of allochthonous food sources in these headwater streams. Fungi comprised 6.6% of the overall particles ingested. Primary producers (algae and diatoms) were rare across taxa and only contributed 0.33% of all particles identified. Since we did not examine the specific composition of the amorphous detritus we are unable to determine the origin of this energy source.

Across sites and habitats, the majority of production was attributed to amorphous detritus, with the exception of *Phylloicus*, which derived most of its energy from plant materials (Table 3.3). Plant tissue and fungi attributed the next highest amount of energy. Animal tissue, diatoms and algae provided the least amount of energy for production. The quantitative food webs illustrated that the energetic pathways are similar among streams and habitats, with most of the energy flow originating from amorphous detritus followed by plant tissue and fungi (Figure 3.2). A greater amount of energy is transferred in pools, across all taxa (Figure 3.2 A, C). The dominant energy transfers across sites and habitats are by the consumption of amorphous detritus and plant detritus by *Neohagenulus* and *Phylloicus*. The highest diversity of energy resources consumed was seen in *Smicridea* and Tanypodinae.

DISCUSSION

The overall goal of my study was to quantify the secondary production and develop a quantitative food web of the non-shrimp benthic consumer communities in fishless headwater streams of the LEF. The production values recorded in my study were similar to those reported for other tropical sites, but low in comparison to temperate sites (Table 3.4). One exception was for Leptophlebiidae, which showed elevated values compared to other tropical counterparts. A pattern between tropical and temperate P/B is not as clear, with a lot of variation among sites and some, like in the case of Baetidae, having values lower than those previously reported. This result was surprising as one might expect population turnover to be much faster in warmer climates, a pattern which has been observed in previous studies (Hauer and Benke, 1991; Ramirez and Pringle, 2006; Hall *et al.* 2011). Furthermore, *Phylloicus* was among the taxa with the highest P/B in our study, with values similar to those recorded for some chironomids. This value was surprising, but it might be influenced by the fact that most of the individuals found in our samples belonged to smaller size classes. As growth rates progressively slow down during the larval life span, our sample might reflect the rapid turnover of the early life stages. *Phylloicus* is very common throughout the tropics and many ecological studies of members of this genus exist (Graça, *et al.* 2001, Rincón and Martínez, 2006; Moreti *et al.* 2009, among many others); however, I am unaware of any other study that assesses its production in order to see our results in context.

Amorphous detritus was consumed in far greater amounts than any other resource and served as the trophic basis of production for these streams as has been found in other studies (Frauendorf *et al.* 2013; Benke and Wallace, 2014). Other than *Phylloicus*, a shredder with most of its proportion attributed to plant tissue, the other dominant insect consumers groups are consuming

similar types of resources which implies a high degree of redundancy with low resource competition and high resource availability (Salas and Dudgeon, 2003). A very low proportion of the production was attributed to animal tissue. Other studies of filter-feeding, net-spinning caddisflies (Hydropsychidae) have reported that as much as 80% of their production can be attributed to animal tissue (Benke and Wallace 1980, 1997). This proportion was shown to vary among sites with differing resource quality, with higher production from detrital sources in sites with higher food quality in the form of higher microbial composition. Our low amount of animal tissue production may suggest high detrital quality. The only predator in our study, Tanypodinae, also showed a low amount of production coming from animal tissue. A study by Baker and McLachlan (1979) showed similar results in terms of gut content and concluded that this group will utilize a range of available stand-by foods when in adverse conditions, but in ideal foraging conditions they are primarily predators. It is important to note that there are other insect predators present in these streams, specifically nymphal dragonflies and damselflies. These taxa were rare in my sampling protocol due to their clinging behavior. While abundant on submerged vegetation, they were rarely sampled using our streambed quantitative sampling methods.

Comparing the resulting quantitative food webs among streams and habitats, more energy is transferred in depositional habitats, in particular from detrital and fungal origin, than in erosional habitats. While the production data used to construct food webs were acquired separately for riffles and pools, the food content data did not take this into consideration. In this study we found that resource availability and species abundance vary by habitat (depositional vs. erosional) (Chapter 2). Given the potential biases that preferential consumption may introduce to the analysis, in a separate experiment (K. Rosas, unpublished), I studied the food preference of the

dominant group, Leptophlebiidae mayfly nymphs, in both riffles and pools relative to the availability of algal versus detrital resources. Further, along with the assessment of separate habitats, a gradient of stream size was studied and preliminary results suggest that there are differences in resource availability between habitats and stream sizes (as expected), but there are no differences in the gut particles identified. While my results suggest that no changes in consumption due to resource availability are visible using gut content analysis, further analyses are needed to characterize the energy sources of the particles and how much of that energy is assimilated by the organism.

The low occurrence of autochthonous algal food items suggests that detrital allochthonous sources of carbon may play a central role in energy flow in these headwater streams as would be predicted by the River Continuum Concept (Vannote *et al.* 1980). However, previous studies using stable isotope analyses in small forested headwater streams in Puerto Rico (March and Pringle, 2003) and Hong Kong (Salas and Dudgeon, 2003, Li and Dudgeon, 2008, Lau *et al.* 2009a, Lau *et al.* 2009b) have suggested that consumer biomass is based mainly on algal sources versus terrestrial inputs. Our results do not contradict or confirm those findings as the energetic source of the amorphous detritus was not assessed. This category is generally used to encompass items that are difficult to classify because of maceration by the insect along with items of dissolved organic matter origin which have been incorporated into the fine particulate organic matter (Hershey *et al.* 2007). Some amorphous detritus can be rich in bacterial biomass or other autochthonous sources such as macrophytes or diatoms (Benke and Wallace, 2014). Given the low light availability on both of these heavily forested streams (versus the sites used by March and Pringle, 2003 also within the LEF), and the fact that algal biomass is low (C. Pringle, A. Ramirez, unpublished data) I would expect the amorphous detritus composition to be mainly of

non-algal origin. Nevertheless, detailed analyses of amorphous detritus composition must be done in order to obtain a more thorough assessment for these streams.

This study was one of the first to quantify the production and food web of the non-shrimp macroinvertebrate consumer community in tropical island streams. Understanding the trophic roles of consumers is essential to improve our knowledge of stream energy flow pathways and nutrient cycling (Mihuc, 1997). Changes in species composition and resource bases are likely to affect the energetic pathways of stream ecosystems; therefore, long-term and pre-disturbance studies are imperative. My findings provide a critical baseline dataset that will allow for future assessments in a time of rapid biodiversity losses and global change.

Table 3.1 Growth Rates for each size class of study taxa. Missing values were supplemented in the analysis from published values (Ramirez and Pringle, 1996).

Taxa	Size	GR	SE
<i>Cloeodes</i>	<2	0.1199	0.0177
	2-4	0.0758	0.0085
	>4	0.0302	
<i>Neohagenulus</i>	<2	0.2128	0.0369
	2-4	0.1101	0.0141
	>4	0.0507	0.0114
<i>Phylloicus</i>	<4	0.1318	0.0263
	4-8	0.1370	0.0160
	>8	0.0812	0.0187
<i>Smicridea</i>	<2	0.0317	
	2-4	0.1307	0.0317
	>4	0.0680	0.0057
Chironominae	<2		
	2-4	0.3510	
	>4	0.1199	0.0224
Orthoclaadiinae	<2		
	2-4	0.0937	0.0152
	>4	0.0279	
Tanypodinae	<2		
	2-4	0.0407	
	>4	0.0782	0.0183

Table 3.2. Estimates of mean annual abundance (inds./m²), biomass (mg/m²), production (mg m⁻² yr⁻¹), and production to biomass ratios of the study species in the two sites. Ranges presented below means are 95% confidence intervals.

Species	Site	Erosional Habitats				Depositional Habitats				Habitat Weighted			
		Abundance	Biomass	Production	P:B	Abundance	Biomass	Production	P:B	Abundance	Biomass	Production	P:B
<i>Cloeodes</i>	Gatos	11.06 (6.46 - 15.59)	1.46 (0.71 - 2.21)	24.51 (13.76 - 35.24)	16.75	45.84 (27.82 - 63.23)	2.82 (1.37 - 4.25)	58.25 (32.65 - 83.16)	20.65	21.84 (13.08 - 30.36)	1.88 (0.92 - 2.84)	34.97 (19.62 - 50.10)	17.96
	Prieta	5.53 (2.61 - 8.54)	0.81 (0.33 - 1.30)	14.07 (5.44 - 22.94)	17.34	23.74 (11.64 - 36.62)	2.05 (0.40 - 3.77)	41.34 (10.98 - 72.82)	20.15	7.17 (3.43 - 11.07)	0.92 (0.34 - 1.53)	16.53 (5.94 - 27.43)	17.60
<i>Neohagenulus</i>	Gatos	121.08 (92.48 - 149.72)	9.31 (6.77 - 11.88)	260.62 (196.77 - 324.67)	27.99	223.89 (168.77 - 279.36)	21.25 (12.78 - 29.95)	556.10 (372.83 - 743.13)	26.17	152.95 (116.13 - 189.91)	13.01 (8.63 - 17.48)	352.22 (251.35 - 454.40)	27.42
	Prieta	89.64 (55.98 - 122.09)	8.86 (5.86 - 11.74)	242.66 (160.07 - 322.61)	27.40	119.92 (77.33 - 161.19)	18.69 (10.17 - 27.01)	425.71 (245.77 - 600.22)	22.78	92.37 (57.90 - 125.61)	9.74 (6.25 - 13.12)	259.14 (167.78 - 347.60)	26.99
<i>Phylloicus</i>	Gatos	1.84 (0.68 - 2.99)	0.30 (0. - 0.60)	15.16 (0.84 - 29.58)	50.40	11.46 (6.10 - 16.96)	5.41 (0.20 - 10.41)	249.72 (16.35 - 474.22)	46.15	4.82 (2.36 - 7.32)	1.88 (0.06 - 3.64)	87.87 (5.65 - 167.42)	49.08
	Prieta	2.82 (0 - 5.78)	2.57 (0 - 5.46)	101.91 (0 - 204.83)	39.70	27.01 (10.19 - 44.22)	10.66 (1.52 - 19.86)	470.06 (76.31 - 865.75)	44.11	5.00 (0.68 - 9.24)	3.29 (0 - 6.76)	135.04 (4.45 - 264.31)	40.10
<i>Smicridea</i>	Gatos	6.07 (3.16 - 9.08)	1.29 (0.16 - 2.43)	35.16 (7.39 - 63.54)	27.31	3.68 (0 - 7.67)	1.35 (0 - 3.47)	31.02 (0 - 75.91)	22.99	5.33 (2.05 - 8.64)	1.31 (0 - 2.75)	33.88 (0.57 - 67.38)	25.97
	Prieta	9.97 (2.46 - 17.58)	2.12 (0.32 - 3.94)	62.56 (9.91 - 116.01)	29.58	0.82 (0 - 2.21)	0.00 (0 - 0.01)	0.05 (0 - 0.13)	12.54	9.15 (2.18 - 16.19)	1.93 (0.29 - 3.58)	56.94 (9.02 - 105.58)	28.04
Chironominae	Gatos	0.43 (0 - 1.15)	0.04 (0 - 0.09)	1.62 (0 - 4.29)	46.05	21.28 (10.30 - 32.25)	1.09 (0.43 - 1.76)	57.24 (23.14 - 91.58)	52.45	6.90 (2.97 - 10.79)	0.36 (0.12 - 0.61)	18.86 (6.35 - 31.35)	48.03
	Prieta	3.25 (0.84 - 5.74)	0.18 (0.02 - 0.34)	9.85 (1.36 - 18.56)	54.81	66.31 (17.77 - 114.85)	1.67 (0.48 - 2.86)	110.01 (28.67 - 191.32)	65.68	8.93 (2.37 - 15.56)	0.31 (0.07 - 0.57)	18.86 (3.81 - 34.10)	55.78
Orthoclaadiinae	Gatos	24.61 (14.94 - 33.93)	0.24 (0.13 - 0.34)	8.17 (4.42 - 11.84)	34.28	45.43 (21.70 - 69.18)	0.26 (0.12 - 0.40)	7.72 (3.45 - 11.96)	29.58	31.06 (17.04 - 44.85)	0.25 (0.13 - 0.36)	8.03 (4.12 - 11.88)	32.82
	Prieta	21.35 (6.74 - 34.80)	0.28 (0 - 0.58)	6.89 (0 - 13.31)	24.22	52.80 (7.72 - 97.88)	0.16 (0.06 - 0.26)	4.81 (2.02 - 7.61)	30.46	24.18 (6.83 - 40.48)	0.27 (0 - 0.55)	6.70 (0.12 - 12.79)	24.79
Tanypodinae	Gatos	13.98 (10.37 - 17.62)	0.67 (0.40 - 0.96)	14.54 (7.28 - 22.07)	21.61	190.32 (133.55 - 247.03)	6.83 (4.95 - 8.65)	147.24 (104.09 - 189.04)	21.57	68.65 (48.56 - 88.73)	2.58 (1.81 - 3.34)	55.67 (37.29 - 73.83)	21.60
	Prieta	31.54 (14.18 - 50.04)	1.21 (0.60 - 1.87)	26.71 (7.21 - 41.10)	22.02	227.57 (124.88 - 334.18)	6.30 (3.58 - 9.11)	122.47 (73.02 - 172.87)	19.43	49.19 (24.15 - 75.62)	1.67 (0.87 - 2.52)	35.33 (18.59 - 52.96)	21.79

Table 3.3 Annual secondary production attributed to food type ($\text{mg m}^{-2} \text{yr}^{-1}$) in Gatos and Prieta.

Erosional Habitats												
Taxa	Gatos						Prieta					
	Amorphous detritus	Fungi	Diatoms	Algae	Animal	Plant	Amorphous detritus	Fungi	Diatoms	Algae	Animal	Plant
<i>Cloeodes</i>	22.08	2.13	0.30	0.00	0.00	0.00	12.68	1.22	0.17	0.00	0.00	0.00
<i>Neohagenulus</i>	196.40	2.25	1.59	0.00	0.00	60.39	182.87	2.09	1.48	0.00	0.00	56.23
<i>Phylloicus</i>	2.68	0.25	0.13	0.00	0.00	12.10	18.00	1.69	0.85	0.00	0.00	81.38
<i>Smicridea</i>	15.09	12.03	0.39	1.16	0.90	5.60	26.86	21.40	0.69	2.06	1.60	9.96
Chironominae	1.37	0.10	0.00	0.00	0.00	0.15	8.35	0.59	0.00	0.00	0.00	0.91
Orthoclaadiinae	7.55	0.24	0.07	0.00	0.00	0.32	6.36	0.20	0.06	0.00	0.00	0.27
Tanypodinae	6.32	4.27	0.95	0.76	1.34	0.89	11.62	7.84	1.75	1.40	2.46	1.64
Total	251.49	21.26	3.43	1.92	2.24	79.45	266.73	35.04	5.00	3.46	4.06	150.38

Depositional Habitats												
Taxa	Gatos						Prieta					
	Amorphous detritus	Fungi	Diatoms	Algae	Animal	Plant	Amorphous detritus	Fungi	Diatoms	Algae	Animal	Plant
<i>Cloeodes</i>	52.46	5.06	0.72	0.00	0.00	0.00	37.23	3.59	0.51	0.00	0.00	0.00
<i>Neohagenulus</i>	419.07	4.79	3.38	0.00	0.00	128.85	320.81	3.67	2.59	0.00	0.00	98.64
<i>Phylloicus</i>	44.10	4.14	2.07	0.00	0.00	199.41	83.01	7.80	3.90	0.00	0.00	375.35
<i>Smicridea</i>	13.32	10.61	0.34	1.02	0.79	4.94	0.00	0.00	0.00	0.00	0.00	0.00
Chironominae	48.53	3.42	0.00	0.00	0.00	5.29	93.27	6.58	0.00	0.00	0.00	10.16
Orthoclaadiinae	7.13	0.23	0.06	0.00	0.00	0.30	4.45	0.14	0.04	0.00	0.00	0.19
Tanypodinae	64.05	43.20	9.67	7.74	13.54	9.03	53.28	35.94	8.05	6.44	11.26	7.51
Total	648.65	71.46	16.26	8.76	14.34	347.81	592.05	57.72	15.09	6.44	11.26	491.85

Habitat Weighted												
Taxa	Gatos						Prieta					
	Amorphous detritus	Fungi	Diatoms	Algae	Animal	Plant	Amorphous detritus	Fungi	Diatoms	Algae	Animal	Plant
<i>Cloeodes</i>	31.49	3.04	0.43	0.00	0.00	0.00	14.89	1.44	0.21	0.00	0.00	0.00
<i>Neohagenulus</i>	265.43	3.04	2.14	0.00	0.00	81.61	195.28	2.23	1.58	0.00	0.00	60.04
<i>Phylloicus</i>	15.52	1.46	0.73	0.00	0.00	70.17	23.85	2.24	1.12	0.00	0.00	107.84
<i>Smicridea</i>	14.54	11.59	0.37	1.12	0.87	5.39	24.44	19.48	0.62	1.87	1.46	9.06
Chironominae	15.99	1.13	0.00	0.00	0.00	1.74	15.99	1.13	0.00	0.00	0.00	1.74
Orthoclaadiinae	7.42	0.24	0.07	0.00	0.00	0.31	6.19	0.20	0.06	0.00	0.00	0.26
Tanypodinae	24.22	16.34	3.66	2.93	5.12	3.41	15.37	10.37	2.32	1.86	3.25	2.17
Total	374.61	36.82	7.40	4.04	5.99	162.64	296.01	37.08	5.90	3.73	4.71	181.11

Table 3.4 Summary of selected production studies from the published literature. Values represent a wide range of genera, but all within the same families as those used in the present study. Ranges include data reported for multiple sites or multiple years within the same study. For studies that tested an effect, only reference site values were cited. Another total invertebrate production summary can be found in Benke, 1993.

Taxa	Production (mg m ⁻² yr ⁻²)	P/B	Location	Reference
Baetidae	16.5-35.0	17.6-18.0	Puerto Rico	<i>This study</i>
	0.7	-	Venezuela	Hall <i>et al.</i> 2011
	35.6-39.5	38.5	Costa Rica	Ramirez and Pringle, 1998
	23.2-175.8	77.3-109.8	China	Salas and Dudgeon, 2003
	3787.6	69.6	USA (GA)	Benke and Jacobi, 1994
	20100	106.2	USA (AZ)	Jackson and Fisher, 1986
	630-1112	30-38	USA (NC)	Wallace and Gurtz, 1986
	398-707	-	USA (CO)	Carlisle and Clements, 2003
Leptophlebiidae	259.1-352.2	27.0-27.4	Puerto Rico	<i>This study</i>
	2.2	-	Venezuela	Hall <i>et al.</i> 2011
	87.07	24.3	Costa Rica	Ramirez and Pringle, 1998
	88.3-225.7	44.1-62.8	China	Salas and Dudgeon, 2003
	140	9	USA (KS)	Stagliano and Whiles, 2002
	307	5.8	New Zealand	Winterbourn <i>et al.</i> 2008
Hydropsychidae	33.9-56.9	26.0-28.0	Puerto Rico	<i>This study</i>
	665.4-987.6	-	China	Dudgeon, 1999
	913.8	5.27	USA (GA)	Benke and Wallace, 1980
	10269	8.1-15.7	USA (GA)	Benke and Wallace, 1997
	1075.76	3.4	Argentina	Brand and Miserendino, 2011
	1457	10	USA (KS)	Stagliano and Whiles 2002
Chironominae	18.9	48.0-55.8	Puerto Rico	<i>This study</i>
	469-767	-	USA (CO)	Carlisle and Clements, 2003
	15804	198-255	USA (GA)	Benke, 1998
	1274	21-43	USA (KS)	Stagliano and Whiles, 2002
Orthocladiinae	6.7-8.0	24.8-32.8	Puerto Rico	<i>This study</i>
	36683	158	USA (GA)	Benke, 1998
	39-61	-	USA (CO)	Carlisle and Clements, 2003
	32400-59500	118-124	USA (TN)	Runk, 2007
	2585	46	USA (KS)	Stagliano and Whiles, 2002
Tanypodinae	35.3-56.7	21.6-21.8	Puerto Rico	<i>This study</i>
	10.07	69	Costa Rica	Ramirez and Pringle, 1998
	657	233	USA (GA)	Benke, 1998
	541	27	USA (KS)	Stagliano and Whiles, 2002
Chironomidae (Total)	60.90-82.6	25.9-27	Puerto Rico	<i>This study</i>
	7.4	-	Venezuela	Hall <i>et al.</i> 2011
	74.47	-	Costa Rica	Ramirez and Pringle, 1998
	29700	4.7-21.9	USA (IN)	Berg and Hellenthal, 1991
	58300	121.3	USA (AZ)	Jackson and Fisher, 1986
	3859	42	USA (KS)	Stagliano and Whiles, 2002
	22656-26804	228-231	USA (GA)	Benke, 1998
	528.5-591.5	27.8-29.1	Puerto Rico	<i>This study</i>
Total Community	3096-4370	12.1-13.4	Panama	Colon-Gaud <i>et al.</i> 2009
	363.65	-	Costa Rica	Ramirez and Pringle, 1998
	6101	-	USA (KY)	Johnson <i>et al.</i> 2013
	15131-26208	8.5-10.2	USA (IL)	Walther and Whiles, 2011
	1084-3540	8.4-9.3	USA (KS)	Whiting <i>et al.</i> 2011

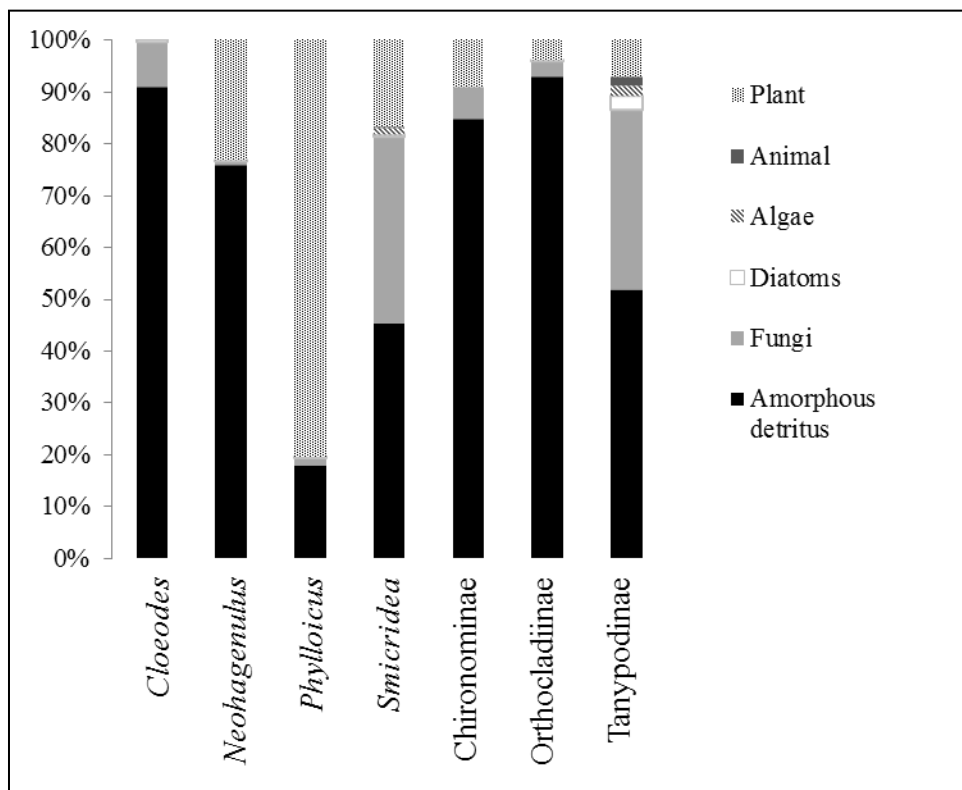


Fig 3.1 Percent foregut food content of each taxon. Particles were classified as plant, animal, algae, diatom, fungi, or amorphous detritus. The amorphous detritus category was used for particles whose origin was unable to be identified.

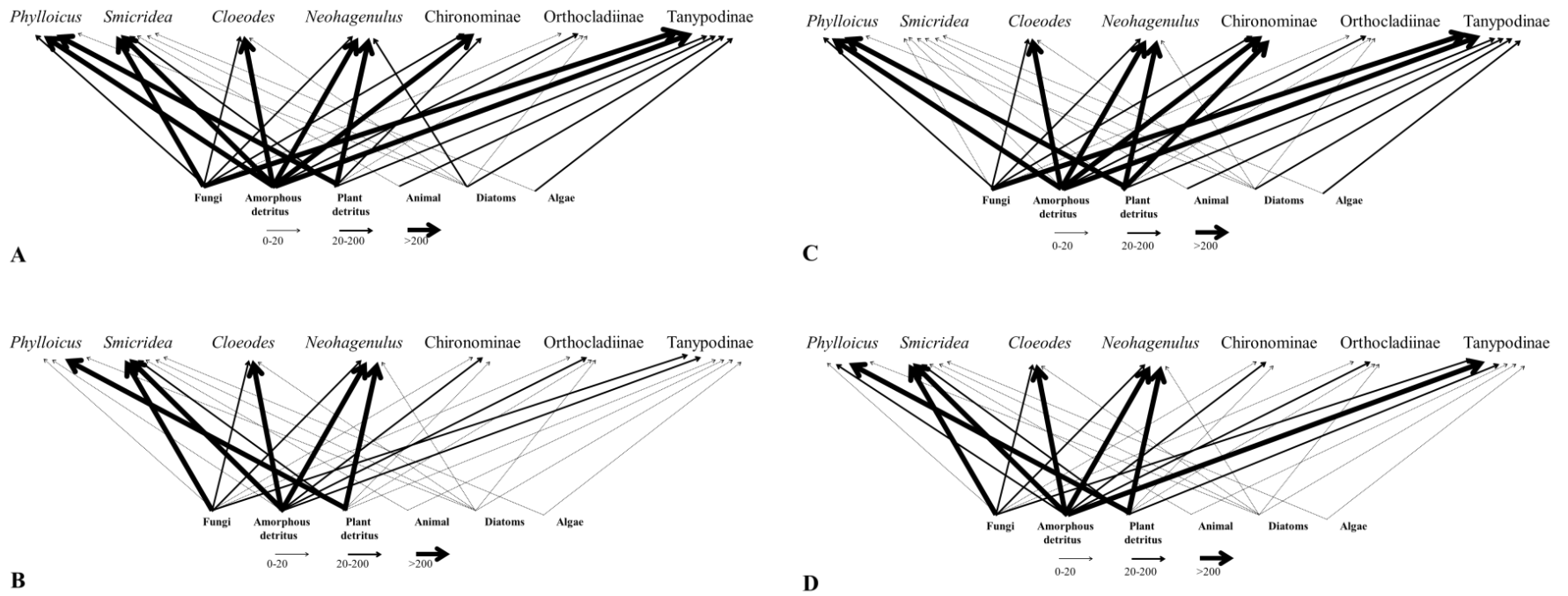


Fig 3.2 Food resource consumption by macroinvertebrates in Gatos and Prieta in pool and riffle habitats. (A- Gatos, pools; B-Gatos, riffles; C-Prieta, pools; D- Prieta, riffles). Thicknesses of arrows indicate order of magnitude ingestion flows and numbers along each arrow give specific values ($\text{mg m}^{-2} \text{yr}^{-1}$).

CONCLUSIONS AND FURTHER DIRECTIONS

With this study I was able to expand on the knowledge of the structure of the aquatic communities in headwater, tropical island streams and their role in energy flow. I found that macroinvertebrates in these systems are greatly influenced by the in-stream habitat, and potentially the abundance of freshwater shrimp. I also quantified the secondary production of the dominant non-shrimp macroinvertebrates found at the LEF and developed a quantitative food web for seven taxa and their associated resources. Secondary production appears to rely more on amorphous detritus and allochthonous organic matter, rather than algal resources, as has been reported in other studies from the tropics (Ramirez and Pringle, 1998, Salas and Dudgeon, 2003, Colon-Gaud *et al.* 2009, Hall *et al.* 2011).

My study was a snapshot of what occurs with aquatic macroinvertebrates in streams of a specific size, under relatively pristine conditions, with a specific biotic composition (dominated by shrimp and lacking fish), and during a specific hydrological regime (low discharge variability). However, this snapshot can serve as a much needed starting point for much wider studies, in particular, those focusing on long term changes due to climate change and anthropogenic alterations. Previous comparative production studies have been useful in assessing the effects that species composition changes (Colon-Gaud *et al.* 2009, Hall *et al.* 2011), variation in hydrology (Dudgeon, 1999), increases in temperature (Winterbourn *et al.* 2008), variation in nutrients (Ramirez and Pringle 2006), and effects of contaminants (Carlisle and Clements, 2003; Runk, 2007; Johnson *et al.* 2013) have on macroinvertebrate communities. Due to the long-term nature of our research program we can continue to monitor the insect populations and species interactions and how they change under different environmental conditions. During the time that

our sampling has occurred we have gone from a relatively dry, hydrologically stable year (this study), to years with large and unpredictable storms, to a year with a severe drought. This hydrological variation and potential disturbance is likely to have an effect on the available resources and the species composition found in these streams.

These changes in resources and consumers will likely affect the energetic pathways in these ecosystems. Previous empirical food web studies have been able to track how changes in temperature (Petchey *et al.* 1999), changes in hydrology (Cross *et al.* 2011, Ledger *et al.* 2013), changes in species composition (Power, 1990; Crowl *et al.* 2000, Barnum *et al.* 2015), and changes in resource bases (Hall *et al.* 2000, March and Pringle, 2003; Benstead and Pringle, 2004) can affect food web structure. As the study expands, we can create a traditional food web or ecological network using the organisms found in the streams and their feeding behaviors as inferred from published literature. That initial network can then be expanded by incorporating our observed abundance and biomass data, thus linking community and ecosystem network approaches (Reuman and Cohen, 2005). In traditional community studies the nodes of the ecological networks are comprised of individuals and their links indicate population effects; however, by incorporating additional information the links can emphasize pools and fluxes of energy, biomass, or nutrients rather than taxonomic units (Ings *et al.* 2009). Furthermore, those ecological networks can incorporate quantitative variation in species interaction in order to make predictions of food web structure and community stability (Proulx *et al.* 2005). For example, under anthropogenic stress macroinvertebrate assemblages undergo a shift in species composition from sensitive to tolerant taxa as water and habitat quality decrease. By incorporating these shifts, we could predict changes in community stability.

In summary, my study is a first step in understanding species composition and energy flow of relatively undisturbed systems. The data I have acquired can be used to empirically track, as well as model, the responses of macroinvertebrate communities to a wide variety of long-term changes. This information not only complements larger datasets generated as part of the Long Term Ecological Research Network for the site (LUQ-LTER), but will also guide the direction of ongoing and future projects. In particular, my work will provide the foundation for future studies of the role of aquatic macroinvertebrates in streams at the site and potentially for other streams in the island of Puerto Rico. These studies are generally lacking, not only for Puerto Rico, but for tropical island streams in general.

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