

Georgia Southern University Digital Commons@Georgia Southern

Biology Faculty Publications

Biology, Department of

2010

Stream Invertebrate Responses to a Catastrophic Decline in Consumer Diversity

J. Checo Colón-Gaud

Georgia Southern University, jccolongaud@georgiasouthern.edu

Matt R. Whiles

Southern Illinois University Carbondale

Karen R. Lips

Southern Illinois University Carbondale

Catherine M. Pringle

University of Georgia

Susan Kilham

Drexel University

See next page for additional authors

Follow this and additional works at: <https://digitalcommons.georgiasouthern.edu/biology-facpubs>



Part of the [Biochemistry, Biophysics, and Structural Biology Commons](#), and the [Biology Commons](#)

Recommended Citation

Colón-Gaud, J. Checo, Matt R. Whiles, Karen R. Lips, Catherine M. Pringle, Susan Kilham, Roberto Brenes, Scot D. Peterson. 2010. "Stream Invertebrate Responses to a Catastrophic Decline in Consumer Diversity." *Journal of the North American Benthological Society*, 29 (4): 1185-1198. doi: 10.1899/09-102.1 source: <https://doi.org/10.1899/09-102.1>
<https://digitalcommons.georgiasouthern.edu/biology-facpubs/21>

This article is brought to you for free and open access by the Biology, Department of at Digital Commons@Georgia Southern. It has been accepted for inclusion in Biology Faculty Publications by an authorized administrator of Digital Commons@Georgia Southern. For more information, please contact digitalcommons@georgiasouthern.edu.

Authors

J. Checo Colón-Gaud, Matt R. Whiles, Karen R. Lips, Catherine M. Pringle, Susan Kilham, Roberto Brenes, and Scot D. Peterson

Stream invertebrate responses to a catastrophic decline in consumer diversity

Checo Colón-Gaud^{1,2,5}, Matt R. Whiles^{2,6}, Karen R. Lips^{2,7},
Catherine M. Pringle^{3,8}, Susan S. Kilham^{4,9}, Scott Connelly^{3,10},
Roberto Brenes^{2,11}, AND Scot D. Peterson^{2,12}

¹*Institute for Tropical Ecosystem Studies, University of Puerto Rico–Rio Piedras Campus, San Juan, Puerto Rico 00931 USA*

²*Department of Zoology and Center for Ecology, Southern Illinois University, Carbondale, Illinois 62901 USA*

³*Odum School of Ecology, University of Georgia, Athens, Georgia 30602 USA*

⁴*Department of Biosciences and Biotechnology, Drexel University, Philadelphia, Pennsylvania 19104 USA*

Abstract. Tadpoles are often abundant and diverse consumers in headwater streams in the Neotropics. However, their populations are declining catastrophically in many regions, in part because of a chytrid fungal pathogen. These declines are occurring along a moving disease front in Central America and offer the rare opportunity to quantify the consequences of a sudden, dramatic decline in consumer diversity in a natural system. As part of the Tropical Amphibian Declines in Streams (TADS) project, we examined stream macroinvertebrate assemblage structure and production for 2 y in 4 stream reaches at 2 sites in Panama. One site initially had healthy amphibians but declined during our study (El Copé), and 1 site already had experienced a decline in 1996 (Fortuna). During the 1st y, total macroinvertebrate abundance, biomass, and production were generally similar among sites and showed no consistent patterns between pre- and post-decline streams. However, during the 2nd y, tadpole densities declined precipitously at El Copé, and total macroinvertebrate production was significantly lower in the El Copé streams than in Fortuna streams. Functional structure differed between sites. Abundance, biomass, and production of filterers generally were higher at Fortuna, and shredders generally were higher at El Copé. However, shredder production declined significantly in both El Copé reaches in the 2nd y as tadpoles declined. Nonmetric dimensional scaling (NMDS) based on abundance and production indicated that assemblages differed between sites, and patterns were linked to variations in relative availability of basal resources. Our results indicate that responses of remaining consumers to amphibian declines might not be evident in coarse metrics (e.g., total abundance and biomass), but functional and assemblage structure responses did occur. Ongoing, long-term studies at these sites might reveal further ecological consequences of the functional and taxonomic shifts we observed.

Key words: macroinvertebrate production, amphibian declines, ecosystem function, community structure.

⁵ Present address: Department of Biology, Georgia Southern University, Statesboro, Georgia 30460 USA. Email address: jccolonga@georgiasouthern.edu

⁶ E-mail address: mwhiles@zoology.siu.edu

⁷ Present address: Department of Biology, University of Maryland, College Park, Maryland 20742 USA. E-mail: klips@umd.edu

⁸ E-mail addresses: cpringle@uga.edu

⁹ kilhams@drexel.edu

¹⁰ scottcon@uga.edu

¹¹ tadpole@siu.edu

¹² pete13@siu.edu

The loss of biological diversity and its potential effects on ecosystem function have been topics of increasing interest and controversy over the past 2 decades (see reviews by Srivastava and Vellend 2005, Hector et al. 2007). Despite some disagreement over details, most ecologists agree that the current rates of extinction are greatly accelerated compared to any other recent period (Chapin et al. 2000). Losses of biological diversity can create permanent changes in ecosystems as alternate species replace or overtake the roles once filled by taxa that are no longer present. These changes in assemblages can affect the function-

ing of ecosystems and their overall integrity (e.g., Tilman 1996).

Pacala and Kinzig (2002) define ecosystem function as the maintenance of energetic material standing stocks, material processing or energetic fluxes, and the turnover rates of energetic stocks over time. Maintenance of function is dependent upon the array of species that play particular roles and abiotic factors that dictate species composition over time. Events that alter ecosystems, such as natural disturbances (e.g., drought, floods) or disease, can alter assemblages as organisms rearrange in response to the new set of parameters created by the event (Tilman 1996). Shifts in assemblages might not result in ecosystem collapse or a loss in overall integrity (Naeem 1998, Müller et al. 2000) because compensatory responses of remaining species can stabilize a system and maintain some level of function. However, ecosystem function, as defined by Pacala and Kinzig (2002), might differ from that associated with the original assemblage of organisms if the new assemblages perform different roles or respond differently to biotic and abiotic factors.

Ongoing amphibian declines in the Neotropics and other regions represent dramatic stochastic events whereby an entire group of consumers is rapidly removed from the ecosystem (Lips et al. 2006), potentially influencing remaining assemblages and ecosystem function (Whiles et al. 2006). Some recent studies have addressed the effects of biodiversity losses in natural systems (see Vaughn 2010), but much of what we know about the consequences of declining biodiversity is based on assembled communities in plots or mesocosms (Loreau et al. 2001, Petchey et al. 2004). Thus, ongoing amphibian declines offer a rare opportunity to examine the consequences of a sudden decline in biodiversity in a natural ecosystem.

Amphibians reach their peak diversity in the Neotropics (Duellman 1999). Furthermore, most amphibians have complex life cycles because they inhabit terrestrial and aquatic environments through their life span and play multiple roles in both systems (Davic and Welsh 2004, Regester et al. 2006, Altig et al. 2007). Many amphibians also can contribute to reciprocal subsidies of energy and nutrients between systems because terrestrial adults deposit egg masses into aquatic habitats, and metamorphs move from aquatic to terrestrial habitats (Regester et al. 2006). Anuran larvae (tadpoles) have been considered ecosystem engineers because of their ability to modify habitat structure (Flecker et al. 1999), facilitate other consumers (Ranvestel et al. 2004, Solomon et al. 2004, Colón-Gaud et al. 2009), and alter periphyton communities,

biomass, and production (Kupferberg 1997, Ranvestel et al. 2004, Connelly et al. 2008). These influences probably are most pronounced in low-order Neotropical streams where tadpole assemblages are very diverse and reach high densities (Lips 1999, Ranvestel et al. 2004).

As part of the Tropical Amphibian Declines in Streams (TADS) project, our goal was to assess the ecological consequences of the loss of tadpoles from headwater streams in the Neotropics through system-scale field studies. Specifically, we quantified macroinvertebrate abundance, biomass, production, and assemblage structure in 2 stream reaches that experienced massive amphibian declines in 1996 and 2 reaches that were initially unaffected, but experienced a massive decline in amphibian populations during the 2nd y (2004) of our study. We hypothesized that catastrophic losses of tadpoles would result in changes in macroinvertebrate production and assemblage structure as macroinvertebrates responded to losses of other consumers (i.e., competitive releases) or altered resource availability (e.g., increases in algal biomass). In particular, we predicted that grazing macroinvertebrates would show positive responses because many dominant tadpole taxa in these systems are grazers.

Methods

Study sites

We conducted our study in 4 upland headwater stream reaches, each 100 m in length. Two of the study reaches are 2nd-order tributaries of the Río Guabal in Parque Nacional Omar Torrijos Herrera, El Copé, Coclé Province, in central Panamá (lat 8°40'N, long 80°35'W). This region receives on average 350 cm of rain each year and has mean annual water temperatures of 21°C. The reaches drain mostly secondary growth, premontane to moist montane rainforest catchments, and elevations range between 700 and 900 m asl. At the onset of the study, El Copé streams harbored ~40 species of riparian anurans, ~½ of which had a stream-dwelling larval stage (Whiles et al. 2006).

The 2 other study streams are 1st- to 2nd-order tributaries draining into the Río Chiriquí in the Reserva Forestal Fortuna, Chiriquí Province, in western Panamá (lat 8°42'N, long 82°14'W). This region receives on average of 450 cm of rain each year. Mean annual water temperatures of the Fortuna streams are ~18°C. Fortuna streams are surrounded mainly by premontane rainforest with elevation ranging between 1000 and 2200 m asl. Before

amphibian declines in the region, Fortuna harbored an abundant and diverse community of amphibians including many stream-dwelling species (Lips 1999). However, a massive die-off associated with chytridiomycosis in 1996 severely reduced amphibian populations in the area.

Both El Copé and Fortuna streams are perennial, heavily forested (~71% canopy cover), high-gradient streams characterized by riffle and run sequences with a few isolated pools and mostly cobble and pebble substrates. Mean annual discharge ranges from 31 to 113 L/s and average wetted widths and depths are 3 m and 0.13 m, respectively (Colón-Gaud et al. 2008). Two distinct seasons characterize this region, a dry season that usually extends from January to mid-May and a pronounced wet season that lasts from late May to December. More detailed descriptions of the 4 study reaches can be found in Colón-Gaud et al. (2008).

During the 2nd y of our study (September 2004), amphibian declines associated with a disease wave of chytridiomycosis began at El Copé (Brem and Lips 2008, Lips et al. 2008). This disease caused a rapid, massive die-off of adult amphibians, whereas larval populations declined slowly but steadily through the year. Hence, we considered the El Copé sites to be in a transitional phase during year 2, in that tadpoles were present, but steadily declining in abundance during this period. This situation allowed us to examine ecological responses to the early stages of an amphibian decline.

Benthic sampling

We collected benthic samples monthly from all 4 study reaches from June 2003 to May 2004 (year 1; Colón-Gaud et al. 2009), every other month in the El Copé study streams from July 2004 to May 2005, and twice seasonally from Fortuna study streams in September and November 2004 and February and April 2005 (year 2). On each sampling date, we collected 7 replicate samples from dominant habitats (i.e., erosional and depositional), 4 Surber samples (930 cm², 250- μ m mesh) in riffles and runs, and 3 stove-pipe benthic cores (314 cm² sampling area) in pools. We elutriated samples through a 250- μ m sieve in the field and preserved materials remaining on the sieve in ~10% formalin. For very fine particulate organic matter (VFPOM) samples, we collected materials that passed through the sieve in a bucket, recorded the total volume, and collected a subsample. In erosional habitats, we collected an additional core sample adjacent to the Surber sample (mesh = 250 μ m) to collect VFPOM.

Organic matter

To estimate available food resources, we quantified benthic organic matter standing stocks from benthic samples in all 4 study streams throughout the duration of the study. We separated organic portions of samples into coarse fractions (CPOM; >1 mm), fine fractions (FPOM; <1 mm, >250 μ m), and very fine fractions (VFPOM; <250 μ m, >1.6 μ m) with nested sieves. We sorted CPOM into recognizable materials (e.g., leaves, wood, seeds) and miscellaneous CPOM. We estimated ash-free dry mass (AFDM) by drying fractions at 55°C to constant mass, weighing them, combusting them in a muffle furnace at 500°C for 1 h, and reweighing. We estimated standing stocks (g AFDM/m²) for erosional (e.g., riffles) and depositional (e.g., pools) habitats and then weighted the estimates by habitat by correcting for the proportion of each habitat in each stream reach (e.g., Grubaugh et al. 1996).

We measured algal standing crop (estimated as g AFDM/m² of biofilm) monthly in both sites as part of a concurrent study (Connelly et al. 2008). We used a modified benthic sampler (Loeb 1981) to scrub biofilm samples from known areas of coarse substrata in the stream bottom. We collected 5 benthic biofilm subsamples from rock surfaces during baseflow conditions in each of 5 pools and 5 riffles along a 200-m reach of stream at each site. We pooled subsamples to yield 5 riffle and 5 pool samples monthly for each site (10 samples per site per month). We homogenized biofilm samples, diluted them when necessary, and filtered 100 mL through Whatman glass-fiber filters (0.7 μ m). We processed filters for AFDM as described above. We corrected habitat-specific AFDM for the proportion of each habitat in each stream reach.

Tadpoles

We quantified tadpole densities in the El Copé study reaches monthly for the duration of the study with methods based on Heyer et al. (1994). We combined our estimates with data from a concurrent study (RB, unpublished data) from 2 additional reaches of Río Guabal, which also is in the Parque Nacional Omar Torrijos Herrera, to obtain more robust estimates of tadpole densities in these streams. We sampled the Fortuna stream reaches seasonally with the same methods to confirm the absence of tadpoles at Fortuna. On each sampling date, we randomly chose 3 sampling sites in each of 3 major habitat types (e.g., riffles, pools, and isolated pools) along each reach for a total of 9 samples per reach per date. We used 250- μ m D-nets (22 \times 46 cm) to sample

riffle habitats by disturbing substrates with our feet while holding nets immediately downstream of the disturbed area. We sampled pools with a stove-pipe benthic corer (22 cm diameter; same as for benthic samples) and isolated pools with exhaustive removal sampling with a dip net until 3 consecutive scoops produced no tadpoles. For large, deep pools, we used direct observational counts using an underwater viewer (Aqua Scope IITM, Water Monitoring Equipment and Supply, Seal Harbor, Maine). For all sampling methods, we identified each collected tadpole to species and measured body length with dial calipers (± 0.01 mm). We developed length–mass relationships to obtain size-specific biomass for the dominant taxa following procedures of Benke et al. (1999). We corrected numbers of tadpoles in each sample for area sampled to obtain density and biomass estimates and habitat-weighted estimates based on the proportion of habitat types in each study reach.

Macroinvertebrates

Before organic matter analyses, we removed all macroinvertebrates from coarse fractions of benthic samples. We occasionally subsampled fine fractions (from $\frac{1}{2}$ – $\frac{1}{32}$ depending on size) using a Folsom plankton splitter. We identified (usually to genus, except for Chironomidae and noninsect groups) and measured (total body length) all macroinvertebrates. We used published length–mass relationships (Benke et al. 1999) or relationships developed with our own specimens to estimate taxon- and size-specific AFDM. We then summed total AFDM for each taxon for the sampling date to obtain biomass estimates. Abundance and biomass estimates were habitat-weighted based on proportions of each major habitat type in each study reach.

We used the size–frequency method (Benke and Huryn 2006), corrected for cohort production intervals, to estimate annual secondary production for most taxa. For taxa with rapid turnover rates (i.e., chironomid midges and small mayflies), annual production was estimated using instantaneous growth rate estimates from individuals reared in growth chambers in the study streams following methods of Huryn and Wallace (1986). We estimated interval production as the product of mean biomass (g AFDM/m²) and growth rates between sampling dates, and total production (g AFDM m⁻² y⁻¹) as the sum of the interval estimates (Benke and Huryn 2006). We estimated instantaneous growth rates for black fly larvae (Simuliidae) by applying a relationship developed by Hauer and Benke (1987) to our sampling-date

biomass estimates. More detailed information on methods used for biomass and production estimates is presented in Colón-Gaud et al. (2009).

We assigned individual macroinvertebrate taxa to functional feeding groups (FFG) based on Merritt et al. (2008) or natural abundance stable isotope data from a concurrent study (Verburg et al. 2007) in nearby streams when functional information for a given taxon was not available.

Statistical analyses

We assessed differences in organic matter resources (mean annual standing stocks) and macroinvertebrate mean annual abundance and biomass among sites and years with 2-way analysis of variance (ANOVA) (PROC GLM, $\alpha = 0.05$, Type III sums of squares) in SAS software (version 9.1; SAS Institute, Cary, North Carolina). We treated the 2 sampling reaches as blocks for each site and used an average estimate for each site to facilitate analyses. We did not use ANOVA for analyses of production because this procedure results in just 1 value (annual production) for each stream each year. We used a bootstrap technique (Efron and Tibshirani 1993) to construct 95% confidence intervals for annual abundance, biomass, and production values. This technique generates random data sets by resampling individual sample replicates 1000 times without replacement. For production estimates, we considered values with nonoverlapping confidence intervals to be significantly different at $\alpha = 0.05$ (Chadwick and Huryn 2005, 2007, Colón-Gaud et al. 2009).

We used nonmetric dimensional scaling (NMDS) ordination techniques to examine patterns of macroinvertebrate assemblage structure. We compared macroinvertebrate assemblages based on mean monthly abundance and biomass during year 1 ($n = 48$, total taxa = 75) and year 2 ($n = 20$, total taxa = 70) and based on annual production during year 1 and year 2 combined ($n = 8$, total taxa = 49). We standardized the output to unit maxima. NMDS seeks an ordination in which the distances between all pairs of sample variables are in rank order agreement with their dissimilarities in species composition (McCune and Grace 2002). We calculated community dissimilarities based on the Bray–Curtis Index (Bray and Curtis 1957) and did the analysis in 1 to 4 dimensions based on a satisfactory stress-stopping value of < 0.01 as recommended by Minchin (1987). We determined dimensionality by examining scree plots (stress vs number of dimensions) and interpretability of the results. We tested for differences in macroinvertebrate assemblages between sites with analysis of similar-

TABLE 1. Mean (SE) habitat-weighted standing stocks (g ash-free dry mass/m²) of coarse particulate (CPOM), fine particulate (FPOM), very fine particulate (VFPOM), total benthic (TOTBOM) organic matter, and benthic biofilms (algal biofilm) in the El Copé and Fortuna study reaches during years 1 and 2. Data were analyzed by 2-way analysis of variance (Type III Sums of Squares, $\alpha = 0.05$).

Category	El Copé		Fortuna	
	Year 1	Year 2	Year 1	Year 2
CPOM	73.37 (13.39) ^b	36.10 (5.53) ^b	80.91 (9.19) ^b	19.92 (4.74) ^b
FPOM	13.59 (1.31)	13.11 (1.68)	13.65 (0.99)	12.11 (3.87)
VFPOM	59.77 (10.08) ^a	58.16 (2.60) ^a	43.16 (7.79) ^a	30.15 (4.92) ^a
TOTBOM	146.74 (18.44) ^b	107.38 (6.88) ^b	137.71 (12.63) ^b	62.17 (7.66) ^b
Algal biofilm	13.02 (0.52) ^b	20.18 (2.27) ^b	14.56 (1.04)	16.60 (0.92)

^a Statistically significant site effect

^b Statistically significant year effect

ties (ANOSIM; Clarke 1993). We used the Gower metric (10,000 permutations) to generate an *R*-value ranging from -1 to 1. Positive values indicate similarities within groups, and negative values indicate similarities among groups. Significance was tested at an a priori $\alpha = 0.05$.

We conducted vector-fitting analyses (Minchin 1989) with sample traits (organic matter resources) to aid interpretation of macroinvertebrate assemblage data. We included the following variables: CPOM, FPOM, VFPOM, total benthic organic matter (TOTBOM), and a variable to denote the presence or absence of amphibians (Amphibian). We included the Amphibian variable with organic matter resource variables because it was directly correlated with net primary production availability (Colón-Gaud et al. 2009). We also included a year variable (1 vs 2) in the ordination based on macroinvertebrate annual production to denote differences between sampling years. We did NMDS, ANOSIM, and vector-fitting analyses with the DECODA[®] software package (version 3.00 b38; Southern Illinois University, Edwardsville, Illinois).

Results

Organic matter

TOTBOM standing stocks were similar between sites (Table 1), but were significantly lower in year 2 than in year 1 at both sites ($F = 9.98$, $p < 0.01$). A similar pattern was noted for CPOM resources. Standing stocks decreased significantly by nearly 50% at El Copé and >70% at Fortuna during year 2 ($F = 13.79$, $p < 0.001$). Standing stocks of FPOM were similar between sites and years (Fig. 1A), whereas standing stocks of VFPOM were significantly higher at El Copé than at Fortuna sites ($F = 4.67$, $p = 0.03$;

Fig. 1B). Overall, VFPOM and CPOM (range 81–90%) contributed most to total organic matter resources throughout the study (Fig. 1B, C).

Biofilm AFDM significantly increased in El Copé ($F = 11.51$, $p < 0.01$) during year 2 of the study ($\sim 1.5 \times$ higher; Table 1), with most changes occurring during the dry season (January–May 2005) when amphibian densities were lowest (Fig. 2). Although no significant differences in biofilm AFDM were found between El Copé and Fortuna streams, periphyton standing stocks differed marginally between sites across study years ($F = 3.55$, $p = 0.07$). After amphibian declines, El Copé algal biofilm standing stocks reached the highest estimates obtained for either site throughout the entire study (Fig. 2).

Tadpoles

A total of 1481 tadpoles representing 12 species were collected during year 1 at El Copé, including 4 dominant taxa (Colostethinae, *Hyloscirtus* spp., Centrolenidae, and *Lithobates warszewitschii*). Tadpole mean monthly density in El Copé reaches was 9 ± 5 individuals (ind.)/m², and mean monthly biomass was 117 ± 85 mg AFDM/m² (mean $\pm 95\%$ confidence interval) during year 1. Tadpole densities and biomass peaked during the dry season (15 ± 13 ind./m²; 138 ± 31 mg AFDM/m²) and were lower during the wet season (5 ± 4 ind./m²; 99 ± 20 mg AFDM/m²). *Hyloscirtus* spp. accounted for most of tadpole biomass during year 1 (38%), followed by Colostethinae (28%), *L. warszewitschii* (26%), and Centrolenidae (8%).

During the 2nd y, 322 tadpoles belonging to 8 species were sampled at El Copé. Three of the 4 dominant taxa were still present in year 2, but Centrolenidae were not encountered during year 2. Tadpole mean monthly density at El Copé decreased to 3 ± 1 ind./m² and mean monthly biomass to $51 \pm$

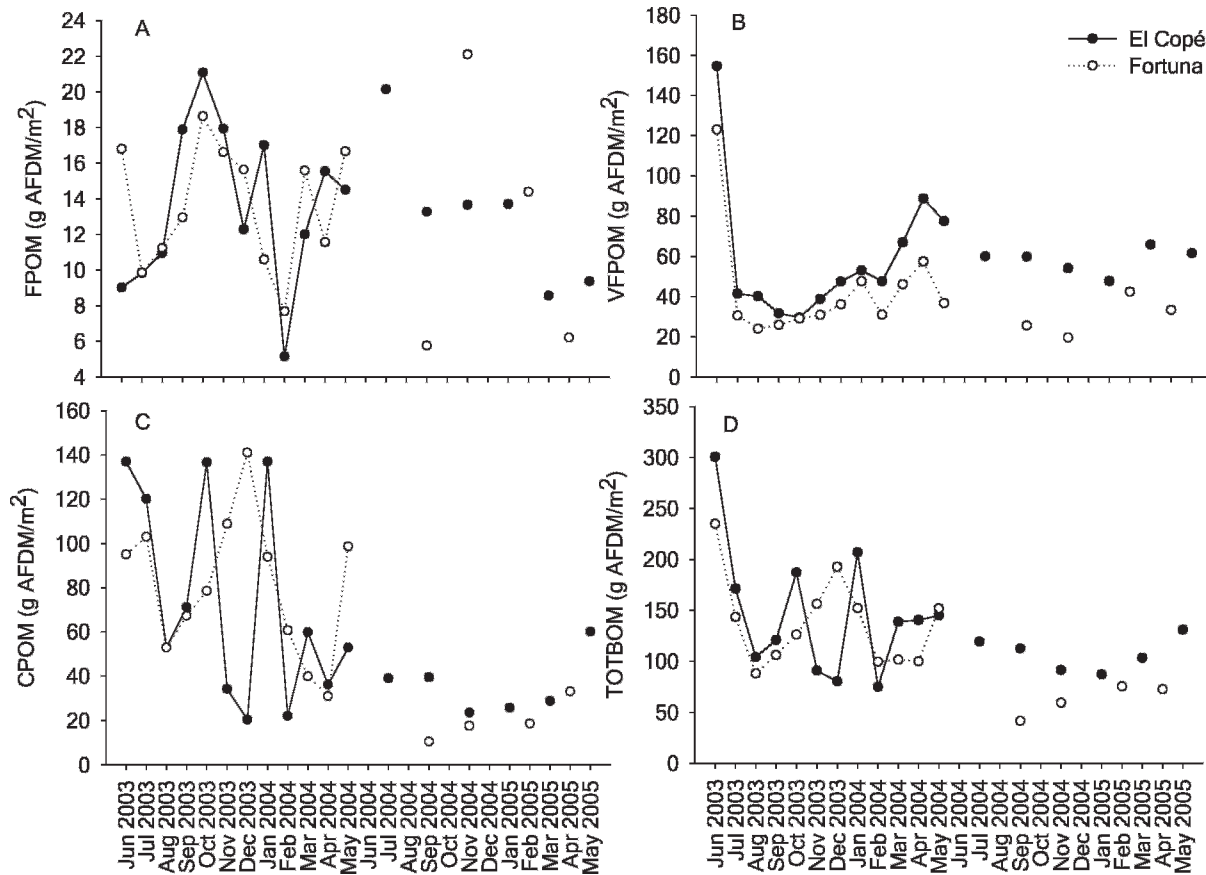


FIG. 1. Mean monthly standing stocks (g ash-free dry mass [AFDM]/m²) of fine particulate (FPOM) (A), very fine particulate (VFPOB) (B), coarse particulate (CPOM) (C), and total benthic organic matter (TOTBOM) (D) in El Copé and Fortuna streams. See text for size distributions for each category. Year 2 values are not connected by lines because samples were collected every other month.

15 mg AFDM/m² during year 2, and no seasonal patterns of density or biomass were found (dry: 2 ± 2 ind./m², 62 ± 18 mg AFDM/m²; wet: 3 ± 2 ind./m², 41 ± 22 mg AFDM/m²). *Hyloscirtus* spp. accounted for most of tadpole biomass during year 2 (53%), followed by Colostethinae (42%), and *L. warszewitschii* (5%).

Only *L. warszewitschii* tadpoles were occasionally observed in Fortuna reaches throughout the duration of our study, and densities were <1 ind./m².

Macroinvertebrate abundance, biomass, and secondary production

Total macroinvertebrate abundance and biomass were similar across study sites and years (range in abundance = 2219–3747 ind./m² and biomass = 198–360 mg AFDM/m² at El Copé; abundance = 2730–3434 ind./m² and biomass = 249–366 mg AFDM/m² at Fortuna; Fig. 3A, B). Gatherers accounted for most of the macroinvertebrate abundance at both study sites throughout the entire study period (Table 2).

Macroinvertebrate biomass was dominated by shredders at El Copé and by filterers and predators at Fortuna. Macroinvertebrate filter-feeder abundance ($F = 9.42, p < 0.01$) and biomass ($F = 14.04, p < 0.01$) were significantly higher at Fortuna than El Copé and significantly increased at both sites during the 2nd study year (abundance: $F = 8.15, p = 0.01$; biomass, $F = 4.90, p = 0.03$). Shredder abundance ($F = 9.88, p < 0.01$) was significantly higher at El Copé during both years of the study, and shredder biomass ($F = 4.43, p = 0.04$) was significantly greater at El Copé during year 1 but slightly decreased at this site during the 2nd y of the study. Grazer abundance ($F = 7.45, p = 0.01$) was significantly greater at Fortuna than El Copé throughout the entire study period. However, grazer biomass did not differ between sites.

Total macroinvertebrate production was similar across sites during the 1st y of the study, but was significantly higher at Fortuna during the 2nd y (Fig. 4A). During year 1, shredder production was significantly higher and accounted for most of the production at El Copé sites (34%; Fig. 4B). During this

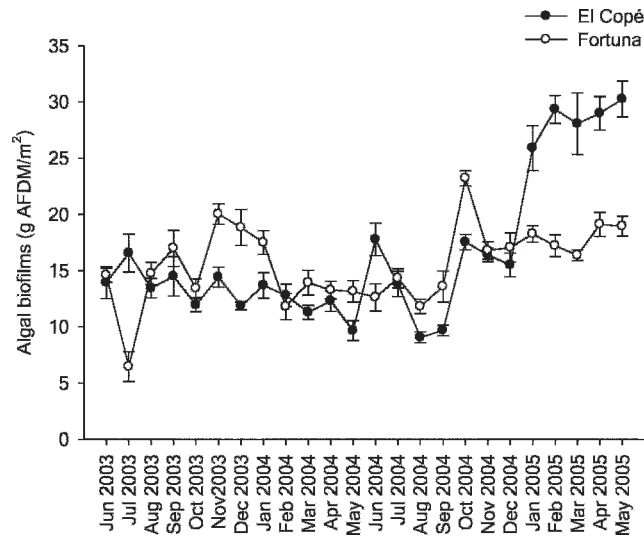


FIG. 2. Mean monthly standing stocks of algal biofilms (g ash-free dry mass [AFDM]/m²) in El Copé and Fortuna streams.

year, filterers (39%) accounted for most of the production at Fortuna sites (Fig. 4C). During year 2, filterers accounted for most production at both sites (31% at El Copé; 65% at Fortuna), and filterer production was significantly higher at Fortuna. Shredder production at El Copé significantly decreased during year 2 to $<1/2$ of year 1 values. Although predator and gatherer production decreased at most study reaches during the 2nd y of the study, none of these shifts were significant (Fig. 4D, E). Grazer production slightly increased in El Copé during the 2nd y of the study (9% vs 16% of total production from year 1 to year 2, respectively), but this change also was not significant (Fig. 4F).

Macroinvertebrate assemblage structure

Nonmetric dimensional scaling based on macroinvertebrate mean monthly abundance and biomass revealed distinct assemblages between Fortuna and El Copé streams during both years of the study (Fig. 5A–D). Furthermore, ANOSIM indicated significant differences in assemblages based on macroinvertebrate abundance during year 1 ($R = 0.14$, $p < 0.01$), but no significant differences during year 2 ($R = 0.13$, $p = 0.07$) (Fig. 5A,B). Moreover, Fortuna and El Copé macroinvertebrate assemblages were not significantly different based on taxon-specific biomass (Year 1: $R = 0.02$, $p = 0.11$; Year 2: $R = 0.4$, $p = 0.27$) (Fig. 5B, D). Ordination plots based on macroinvertebrate production estimates indicated significant differences in assemblages between Fortuna and El Copé (ANOSIM,

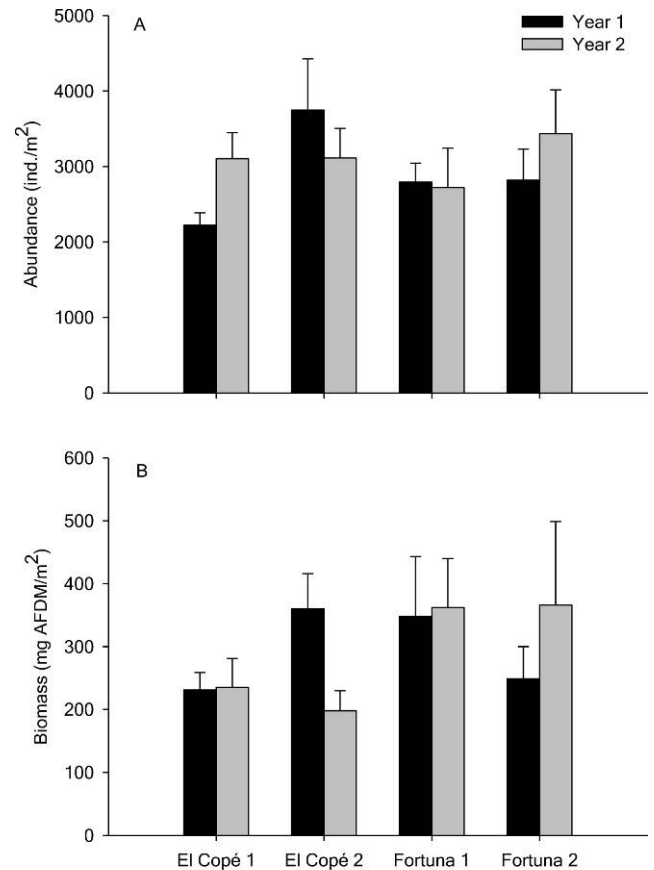


FIG. 3. Mean ($\pm 95\%$ CI) total macroinvertebrate community habitat-weighted abundance (A), and biomass (B) in the El Copé and Fortuna study streams during years 1 and 2. AFDM = ash-free dry mass.

$R = 0.64$, $p = 0.03$), but assemblages did not differ between years (ANOSIM, $R = -0.05$, $p = 0.67$). In addition, vector analysis showed that macroinvertebrate assemblages in El Copé streams (with tadpoles present) were positively associated with increased availability of VFPOM standing stocks during year 1 of the study (Fig. 5). However, only fitted vectors of maximum correlation with amphibians were significant in the year 1 abundance ($R^2 = 0.82$, $p < 0.01$) and biomass ($R^2 = 0.83$, $p < 0.01$) ordinations. In year 2 abundance and biomass ordinations, fitted vectors of maximum correlation with CPOM (abundance: $R^2 = 0.38$, $p = 0.01$; biomass, $R^2 = 0.38$, $p = 0.02$), VFPOM (abundance: $R^2 = 0.50$, $p < 0.01$; biomass: $R^2 < 0.66$, $p = 0.01$), TOTBOM (abundance: $R^2 = 0.59$, $p < 0.01$; biomass: $R^2 = 0.68$, $p < 0.01$), and amphibians (abundance, $R^2 = 0.92$, $p < 0.01$; biomass: $R^2 = 0.83$, $p < 0.01$) were significant. In the production ordination, only fitted vectors of maximum correlation with amphibians were significant ($R^2 = 0.99$, $p = 0.01$).

TABLE 2. Mean (SE) habitat-weighted abundance (individuals/m²) and biomass (mg ash-free dry mass/m²) of macroinvertebrate functional feeding groups (FFG) in the El Copé and Fortuna study reaches during year 1 and 2. Data were analyzed by 2-way analysis of variance (Type III Sums of Squares, $\alpha = 0.05$).

Site/FFG	Year 1		Year 2	
	Abundance	Biomass	Abundance	Biomass
El Copé				
Gatherer	1720 (398)	33 (6)	1522 (444)	29 (6)
Filterer	184 (26) ^{a,b}	58 (17) ^{a,b,c}	325 (81) ^{a,b}	47 (10) ^{a,b,c}
Shredder	350 (56) ^a	123 (33) ^a	254 (95) ^a	83 (23)
Grazer	291 (43) ^a	24 (5)	347 (80) ^a	26 (7)
Predator	658 (99)	58 (12)	865 (196)	41 (14)
Fortuna				
Gatherer	1609 (172)	30 (2)	1190 (68)	23 (1)
Filterer	346 (74) ^{a,b}	89 (26) ^{a,b,c}	760 (281) ^{a,b}	221 (48) ^{a,b,c}
Shredder	112 (16) ^a	36 (7) ^a	119 (37) ^a	50 (16)
Grazer	457 (57) ^a	34 (5)	539 (38) ^a	33 (2)
Predator	515 (60)	132 (33)	546 (77)	56 (18)

^a Statistically significant site effect

^b Statistically significant year effect

^c Statistically significant site \times year effect

Macroinvertebrate taxon-specific responses

Taxon-specific differences in mean monthly abundance, biomass, and annual production were evident across sampling years and between study streams, but were most noticeable as % contribution of particular taxa to total functional group estimates. For example, filterer abundance and production were dominated by the net-spinning caddisflies *Leptonema* and *Macronema* (Hydropsychidae) in El Copé, representing >50% of the total functional group production during both study years (year 1 range = 542–615 mg AFDM m⁻² y⁻¹; year 2 range = 278–648 mg AFDM m⁻² y⁻¹). In contrast, Fortuna filterer abundance was dominated by black fly larvae (Simuliidae; >52% of total), and filterer production in Fortuna streams was codominated by a combination of black flies and *Leptonema* (year 1 range = 849–2017 mg AFDM m⁻² y⁻¹; year 2 range = 2742–2966 mg AFDM m⁻² y⁻¹). Shredder abundance, biomass, and production were dominated by larvae of the beetle *Anchytarsus* (Ptylodactilidae) throughout the entire study period in all 4 streams (i.e., 82–95% of total shredder production at El Copé; 47–97% of total shredder production at Fortuna). However, larvae of the crane fly, *Tipula* (Tipulidae), contributed >20% during year 1 and >40% during year 2 to shredder production in 1 Fortuna reach. Grazer abundance, biomass, and production at El Copé were dominated by the small-bodied mayflies *Farrodes* and *Thraulodes* (Leptophlebiidae; 48–60% of totals) and the water penny beetle *Psephenus* (Psephenidae; 19–33% of

totals) during year 1. However, grazer abundance, biomass, and production were dominated solely by mayflies (e.g., Leptophlebiidae and Baetidae) during year 2 (78–88% of totals). Their numbers generally increased in both El Copé reaches, and *Psephenus* biomass and production decreased. At Fortuna, the grazer community was characterized by the baetid mayflies *Baetodes* and *Dactylobaetis* (Baetidae) and larvae of the lepidopteran *Petrophila* (Crambidae), with leptophlebiid mayflies accounting for >80% of total grazer biomass and production in 1 reach.

Discussion

Understanding how changes in species diversity or species losses affect the integrity and functioning of ecosystems remains a primary focus of ecological research (Cardinale et al. 2000, Loreau et al. 2001, Covich et al. 2004, Greathouse et al. 2006a, b, Hector et al. 2007). Our study provides one of the first quantitative assessments of the effects of the loss of stream-dwelling amphibians from a natural system and the consequent response of remaining consumers. Our study was limited by low replication and sample sizes, but these limitations are frequent in ecosystem-level investigations, particularly for studies in remote locations. Our study represents an intensive, field-based, ecosystem-level study of upland Neotropical streams before and during a massive extirpation event, and thus, our results do not need to be extrapolated. Furthermore, our project is part of a long-term, ongoing effort that will allow us to assess

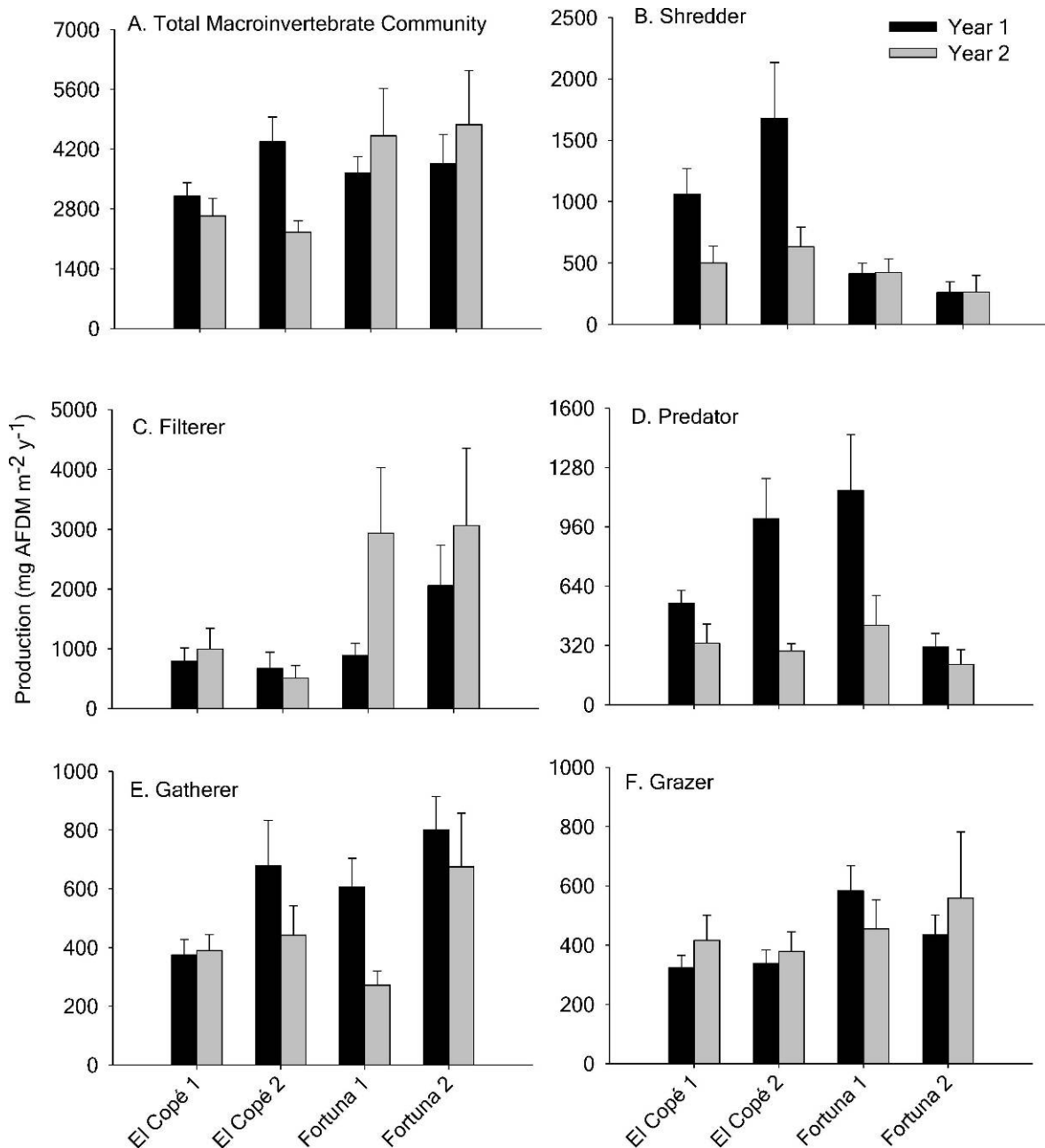


FIG. 4. Mean ($\pm 95\%$ CI) habitat-weighted annual secondary production by total macroinvertebrates (A), and shredder (B), filterer (C), predator (D), gatherer (E), and grazer (F) functional feeding groups in the El Copé (1 and 2) and Fortuna (1 and 2) study streams during years 1 and 2. AFDM = ash-free dry mass.

whether the shifts we observed persist, and to identify both the long- and short-term consequences to ecosystem structure and function.

Tadpole effects on resource standing stocks and fluxes

Autochthonous resources are limited in these headwater streams, and their relative availability appears to increase as amphibians decline (Connelly

at al. 2008). Grazing by primary consumers, particularly when they are at high densities, is likely to translate into top-down effects on producer communities and ultimately to limit periphyton biomass (Rosemond et al. 1993, 2000). At natural densities, tadpoles in our study systems reduce algal standing stocks (Ranvestel et al. 2004, Connelly et al. 2008), enhance primary production per unit biomass (Connelly et al. 2008), and remove accrued sediments from

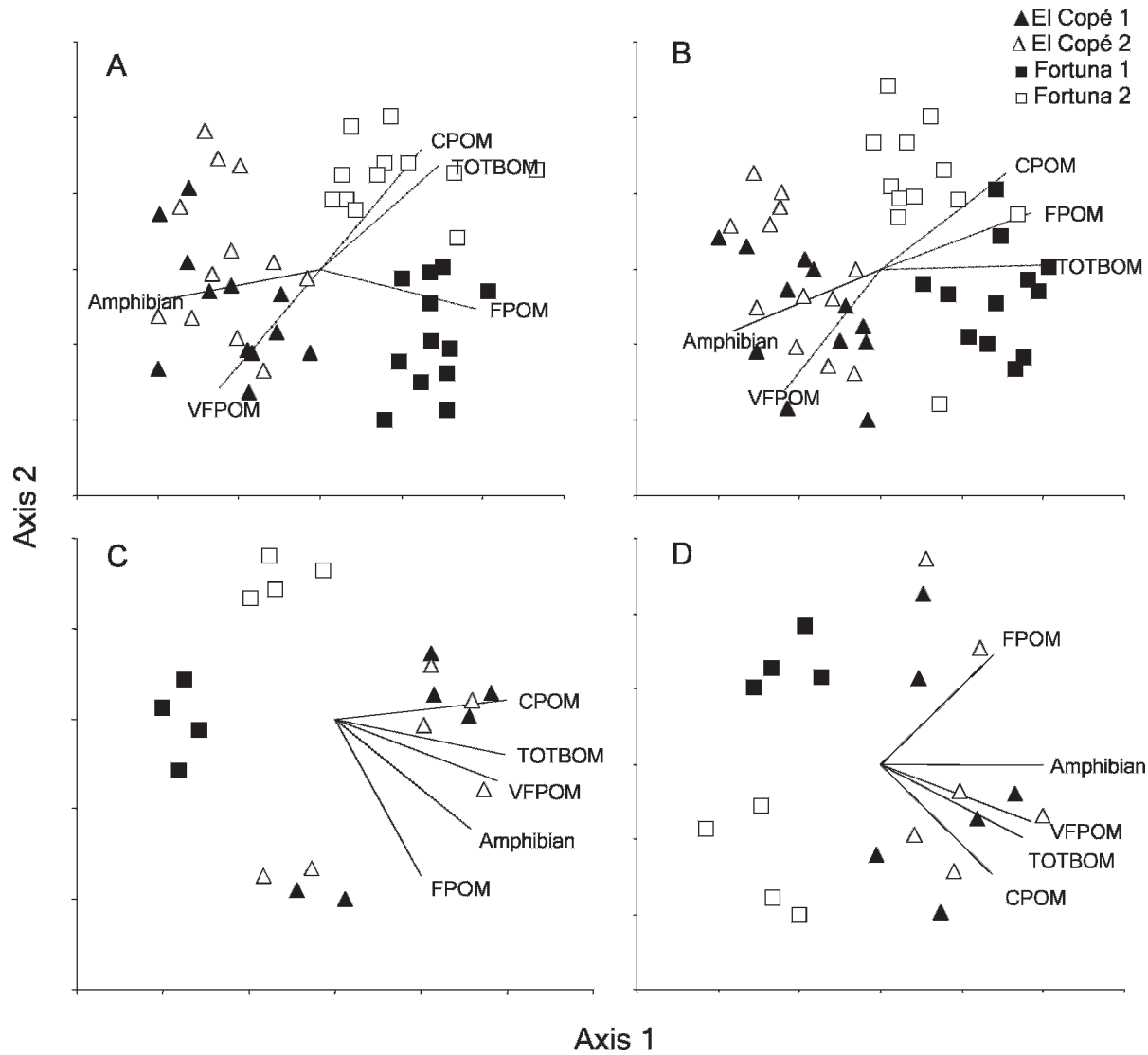


FIG. 5. Nonmetric dimensional scaling ordinations of the El Copé (1 and 2) and Fortuna (1 and 2) study streams based on macroinvertebrate abundance (A, C) and biomass (B, D) during years 1 (A, B) and 2 (C, D). Variables of maximum correlation are shown as vectors (CPOM = coarse particulate organic matter; FPOM = fine particulate organic matter; VFPOM = very fine particulate organic matter; TOTBOM = total benthic organic matter; Amphibian = presence or absence of tadpoles). Significant vectors are presented as full lines, and nonsignificant vectors are presented as dashed lines.

substrates (Ranvestel et al. 2004, Connelly et al. 2008). As tadpole numbers declined in the 2nd y of our study, algal mass, measured as AFDM and as chlorophyll *a*, increased rapidly (Connelly et al. 2008), periphyton became a less limited resource, and production of some macroinvertebrate grazer taxa increased (Colón-Gaud et al. 2010).

The availability of autochthonous resources in neotropical streams can be directly affected by grazers (e.g., Power 1990, Pringle et al. 1993, Flecker et al. 1999, Taylor et al. 2006). Moreover, high densities of

primary consumers, such as the tadpole assemblages that once inhabited our study sites, can influence the cycling of nutrients through excretion or bioturbation, and can ultimately enhance the quality and quantity of exported materials (Covich et al. 1999, Cross et al. 2007, Colón-Gaud et al. 2008) and maintain the supply rates and ratios within local habitats (Kitchell et al. 1979, Vanni 2002). As such, effects of the loss of the tadpole assemblage might extend well beyond the ability of other grazers (with which they compete for algal resources) to mitigate.

Macroinvertebrate functional and taxon-specific responses

Our results indicate that responses of macroinvertebrates to amphibian declines are not apparent in some coarser-scale metrics (e.g., abundance and biomass). Tadpoles once accounted for an appreciable amount of biomass in these systems, particularly during the dry season when biomass sometimes reached ~ 140 mg AFDM/m² (Ranvestel et al. 2004, KRL, unpublished data). Nonetheless, we saw no major changes in total macroinvertebrate abundance and biomass as tadpoles declined precipitously during the 2nd y of our study. However, total macroinvertebrate production did change during year 2. This pattern is consistent with other studies suggesting that secondary production can be a more sensitive response variable for perturbation studies than abundance and biomass (Lugthart and Wallace 1992, Whiles and Wallace 1995).

The significant drop in shredder production in El Copé streams during year 2, as tadpoles declined, is consistent with evidence from our earlier studies suggesting that tadpoles might influence CPOM quality, and thus ultimately, shredders. CPOM standing stocks at El Copé decreased significantly as shredders decreased, but this resource also decreased significantly at Fortuna, where shredder production remained constant. Therefore, the reduction in shredder production probably was not caused by a reduction in available resources. Furthermore, shredder biomass and production were significantly higher in predecline El Copé streams than in postdecline Fortuna streams, and shredders consumed only a small portion of the available CPOM resource in these systems (Colón-Gaud et al. 2009). Colón-Gaud et al. (2009) hypothesized that the higher shredder production in predecline streams was linked to increased nutritional quality of CPOM from nutrient remineralization by centrolenid (glass frog) tadpoles that congregate in leaf packs. Centrolenids were the only dominant group that was not present in samples during year 2, further supporting our hypothesis that tadpoles might indirectly influence macroinvertebrate shredders. This hypothesis is further supported by results of a recent study in which tadpole feeding activities reduced C:N ratios of senescent leaves (Iwai and Kagaya 2007). Iwai and Kagaya (2007) also found that invertebrate detritivore growth rates (a major component of secondary production) increased when they were fed leaf litter conditioned with tadpoles.

The decline in shredder production in our study was mostly caused by reduced production of the beetle, *Anchytarsus*, the dominant shredder in these systems. Based on patterns at Fortuna, where shred-

der production in any year or reach during our study was never >500 mg AFDM m⁻² y⁻¹, shredder production could continue to decline in the El Copé streams. As is the case for many other tropical streams (e.g., Ramírez and Pringle 1998, Boyero et al. 2009), shredders are poorly represented in these systems despite high litter inputs (Colón-Gaud et al. 2008). Hence, $>50\%$ reductions in shredder production, which we observed within a year after declines started, could have significant consequences for litter decomposition, a vital ecosystem process in forested headwaters. Iwai et al. (2009) found that leaf-litter decomposition rates in streamside experimental channels in Australia were higher when invertebrate shredders and tadpoles occurred together in leaf packs. Their study suggests that facilitation does occur among these groups, and thus, the loss of tadpoles could have negative impacts on litter processing.

Predators, like shredders, declined at El Copé in year 2, and this decline was a result of decreases in most of the common predator taxa. Linking this result with tadpole declines is difficult because the tadpoles are unlikely to have been an important prey item for many of the predatory taxa that declined, such as Tanyptodinae midges and turbellarians. However, we have observed some invertebrate predators, such as belostomatids and naucorids, feeding on tadpoles in these streams, and these and other aquatic Hemiptera commonly feed on smaller freshwater vertebrates (Merritt et al. 2008). Some decreases, even in small predatory taxa, might have been related to shifts in the availability of specific types of prey. Invertebrate predators in predecline streams probably benefited from tadpole feeding activities that removed organic sediments, senescent algae, and overlying materials from substrata (e.g., Ranvestel et al. 2004) and exposed prey, such as small dipterans and beetles (e.g., *Psephenus*). Predator decreases in our study might indicate a transitional shift from smaller predatory taxa (i.e., midges and flatworms) in predecline streams to larger, more mobile predators (e.g., odonates and plecopterans) in postdecline streams because of changes in the accessibility of small prey.

Total grazer production did not change significantly, but grazers were the only group in El Copé that tended to increase from year 1 to year 2, and production of some individual grazer taxa, such as leptophlebiid and baetid mayflies did increase in year 2 (Colón-Gaud et al. 2010). We previously documented tadpole facilitation of grazing mayflies in small-scale manipulation experiments in these same streams whereby tadpoles exposed periphyton resources by

removing overlying sediments while feeding (Ranvestel et al. 2004). However, the patterns we observed in this and other concurrent studies in the same streams suggest that, at larger spatial scales, tadpoles and some invertebrate grazers, such as mayflies, compete for limited periphyton resources in these shaded headwaters (Colón-Gaud et al. 2010). These results support other observations that small-scale manipulations are not always accurate predictors of larger-scale patterns and processes (Kohler and Wiley 1997, Taylor et al. 2002, Greathouse et al. 2006a, McNeely and Power 2007).

Our results, combined with results of our prior investigations, indicate that the loss of tadpoles in these streams affects basal resources and some aspects of assemblage and functional structure of remaining consumers. Given the major roles of macroinvertebrate functional groups in stream ecosystems (e.g., Wallace and Webster 1996), these responses probably translate into changes in ecosystem processes and function, even during the early stages of amphibian declines. However, despite the loss of an entire consumer group, these systems did not yet show signs of a complete collapse. Long-term studies, which are ongoing in our study sites, will allow for further quantitative assessments of the ultimate consequences of the functional and taxonomic shifts we observed. Predicting the consequences of declining biodiversity remains one of the great challenges in ecology. Results of our study add to mounting evidence that losses of biodiversity will affect the structure and function of freshwater ecosystems through a variety of direct and indirect mechanisms (see Taylor et al. 2006, Whiles et al. 2006, Vaughn 2010). Some of the changes documented in our study and others appear subtle at short time scales, but long-term consequences remain to be seen.

Acknowledgements

This work was supported by National Science Foundation grants DEB #0234386 and DEB #0234149. We thank The Smithsonian Tropical Research Institute, Autoridad Nacional del Ambiente (ANAM), and Parque Nacional General de División Omar Torrijos Herrera for providing logistical support in Panamá. We also thank S. Arce, C. Espinosa, J. L. Bonilla, F. Quezada, H. Ross, and A. Colón for field assistance. A. D. Huryn, J. Reeve, S. G. Baer, H. M. Rantala, A. Rugenski, W. Clements, and 2 anonymous referees provided valuable advice and suggestions during the development of this manuscript. All the research complies with the current laws of the

Republic of Panamá, as stated in the scientific permits SE/A-49-04, SE/A29-05, and SE/A-108-04. All animal handling and sacrifices followed the animal care protocols established by Southern Illinois University (Protocol 06-008).

Literature Cited

- ALTIG, R., M. R. WHILES, AND C. L. TAYLOR. 2007. What do tadpoles really eat? Assessing the trophic status of an understudied and imperiled group of consumers in freshwater habitats. *Freshwater Biology* 52:386–395.
- BENKE, A. C., AND A. D. HURYN. 2006. Secondary production of macroinvertebrates. Pages 691–709 in F. R. Hauer and G. A. Lamberti (editors). *Methods in stream ecology*. 2nd edition. Academic Press, San Diego, California.
- BENKE, A. C., A. D. HURYN, L. A. SMOCK, AND J. B. WALLACE. 1999. Length–mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. *Journal of the North American Benthological Society* 18:308–343.
- BOYERO, L., A. RAMÍREZ, D. DUDGEON, AND R. G. PEARSON. 2009. Are tropical streams really different? *Journal of the North American Benthological Society* 28:397–403.
- BRAY, J. R., AND J. T. CURTIS. 1957. An ordination of upland forest communities of southern Wisconsin. *Ecological Monographs* 27:325–349.
- BREM, F. M. R., AND K. R. LIPS. 2008. Patterns of infection by *Batrachochytrium dendrobatidis* among amphibian species, habitats and elevations during epizootic and enzootic stages. *Diseases of Aquatic Organisms* 81: 189–202.
- CARDINALE, B. J., K. NELSON, AND M. A. PALMER. 2000. Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos* 91: 175–183.
- CHADWICK, M. A., AND A. D. HURYN. 2005. Responses of stream macroinvertebrate production to atmospheric nitrogen deposition and channel drying. *Limnology and Oceanography* 50:228–236.
- CHADWICK, M. A., AND A. D. HURYN. 2007. Role of habitat in determining macroinvertebrate production in an intermittent-stream system. *Freshwater Biology* 52:240–251.
- CHAPIN, F. S., E. S. ZAVALA, V. T. EVINER, R. L. NAYLOR, P. M. VITOUSEK, H. L. REYNOLDS, D. U. HOOPER, S. LAVOREL, O. E. SALA, S. E. HOBBI, M. C. MACK, AND S. DIAZ. 2000. Consequences of changing biodiversity. *Nature* 405: 234–242.
- CLARKE, K. R. 1993. Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.
- COLÓN-GAUD, C., S. PETERSON, M. R. WHILES, S. S. KILHAM, K. R. LIPS, AND C. M. PRINGLE. 2008. Allochthonous litter inputs, organic matter standing stocks, and organic seston dynamics in upland Panamanian streams: potential effects of tadpoles on organic matter dynamics. *Hydrobiologia* 603:301–312.

- COLÓN-GAUD, C., M. R. WHILES, R. BRENES, S. S. KILHAM, K. R. LIPS, C. M. PRINGLE, S. CONNELLY, AND S. D. PETERSON. 2010. Potential functional redundancy and resource facilitation between tadpoles and insect grazers in tropical headwater streams. *Freshwater Biology* (in press).
- COLÓN-GAUD, C., M. R. WHILES, S. S. KILHAM, K. R. LIPS, C. M. PRINGLE, S. CONNELLY, AND S. D. PETERSON. 2009. Assessing ecological responses to catastrophic amphibian declines: patterns of macroinvertebrate production and food web structure in upland Panamanian streams. *Limnology and Oceanography* 54:331–343.
- CONNELLY, S., C. M. PRINGLE, R. J. BIXBY, R. BRENES, M. R. WHILES, K. R. LIPS, S. KILHAM, AND A. D. HURYIN. 2008. Changes in stream primary producer communities resulting from large-scale catastrophic amphibian declines: can small scale experiments predict effects of tadpole loss? *Ecosystems* 11:1262–1276.
- COVICH, A. P., M. C. AUSTEN, F. BÄRLOCHER, E. CHAUVET, B. J. CARDINALE, C. L. BILES, P. INCHAUSTI, O. DANGLES, M. SOLAN, M. O. GESSNER, B. STATZNER, AND B. MOSS. 2004. The role of biodiversity in the functioning of freshwater and marine benthic ecosystems. *BioScience* 54:767–775.
- COVICH, A. P., M. A. PALMER, AND T. A. CROWL. 1999. The role of benthic invertebrate species in freshwater ecosystems. *BioScience* 49:119–127.
- CROSS, W. F., A. RAMÍREZ, A. SANTANA, AND L. SILVESTRINI-SANTIAGO. 2007. Toward quantifying the relative importance of invertebrate consumption and bioturbation in Puerto Rican streams. *Biotropica* 40:477–484.
- DAVIC, R. D., AND H. H. WELSH. 2004. On the ecological roles of salamanders. *Annual Review of Ecology, Evolution and Systematics* 35:405–434.
- DUPELLMAN, W. E. 1999. Global distribution of amphibians: patterns, conservation, and challenges. Pages 1–30 *in* W. E. Duellman (editor). *Patterns of distribution of amphibians: a global perspective*. John Hopkins University Press, Baltimore, Maryland.
- EFFRON, B., AND R. TIBSHIRANI. 1993. An introduction to the bootstrap. *Monographs on Statistics and Applied Probability* 57. Chapman and Hall, New York.
- FLECKER, A. S., B. P. FEIFAREK, AND B. W. TAYLOR. 1999. Ecosystem engineering by a tropical tadpole: density-dependent effects on habitat structure and larval growth rates. *Copeia* 2:495–500.
- GREATHOUSE, E. A., C. M. PRINGLE, AND W. H. McDOWELL. 2006a. Do small-scale enclosure/enclosure experiments predict effects of large-scale extirpation of freshwater migratory fauna? *Oecologia* (Berlin) 149:709–717.
- GREATHOUSE, E. A., C. M. PRINGLE, W. H. McDOWELL, AND J. G. HOLMQUIST. 2006b. Indirect upstream effects of dams: consequences of migratory consumer extirpation in Puerto Rico. *Ecological Applications* 16:339–352.
- GRUBAUGH, J. W., J. B. WALLACE, AND E. S. HOUSTON. 1996. Longitudinal changes of macroinvertebrate communities along an Appalachian stream continuum. *Canadian Journal of Fisheries and Aquatic Sciences* 53:896–909.
- HAUER, F. R., AND A. C. BENKE. 1987. Influence of temperature and river hydrograph on black fly growth rates in a subtropical blackwater river. *Journal of the North American Benthological Society* 6:251–261.
- HECTOR, A., J. JOSHI, M. SCHERER-LORENZEN, B. SCHMID, E. M. SPEHN, L. WACKER, M. WEILENMANN, E. BAZELEY-WHITE, C. BEIERKUHNLIN, M. C. CALDEIRA, P. G. DIMITRAKOPOULOS, J. A. FINN, K. HUSS-DANELL, A. JUMPPONEN, P. W. LEADLEY, M. LOREAU, C. P. H. MULDER, C. NÉBHÖVER, C. PALMBORG, D. J. READ, A. S. D. SIAMANTZIOURAS, A. C. TERRY, AND A. Y. TROUMBIS. 2007. Biodiversity and ecosystem functioning: reconciling the results of experimental and observational studies. *Functional Ecology* 21:998–1002.
- HEYER, W. R., M. A. DONNELLY, R. W. MCDIARMID, L. C. HAYEK, AND M. S. FOSTER (EDITORS). 1994. *Measuring and monitoring biological diversity. Standard methods for amphibians*. Smithsonian Institution Press, Washington, DC.
- HURYIN, A. D., AND J. B. WALLACE. 1986. A method for obtaining *in situ* growth rates of larval Chironomidae (Diptera) and its application to studies of secondary production. *Limnology and Oceanography* 31:216–222.
- IWAI, N., AND T. KAGAYA. 2007. Positive indirect effect of tadpoles on a detritivore through nutrient regeneration. *Oecologia* 152:685–694.
- IWAI, N., R. G. PEARSON, AND R. A. ALFORD. 2009. Shredder-tadpole facilitation of leaf litter decomposition in a tropical stream. *Freshwater Biology* 54:2573–2580.
- KITCHELL, J. F., R. V. O'NEIL, D. WEBB, G. W. GALLEPP, S. M. BARTELL, J. F. KOONCE, AND B. S. AUSMUS. 1979. Consumer regulation of nutrient cycling. *BioScience* 29:28–34.
- KOHLER, S. L., AND M. J. WILEY. 1997. Pathogen outbreaks reveal large-scale effects of competition in stream communities. *Ecology* 78:2164–2176.
- KUPFERBERG, S. 1997. Facilitation of periphyton production by tadpole grazing: functional differences between species. *Freshwater Biology* 37:427–439.
- LIPS, K. R. 1999. Mass mortality and population declines of anurans at an upland site in western Panama. *Conservation Biology* 13:117–125.
- LIPS, K. R., F. E. BREM, R. BRENES, J. D. REEVE, R. A. ALFORD, J. VOYLES, C. CAREY, L. LIVO, A. P. PESSIER, AND J. P. COLLINS. 2006. Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proceedings of the National Academy of Sciences of the United States of America* 103:3165–3170.
- LIPS, K. R., J. DIFFENDORFER, J. R. MENDELSON, AND M. W. SEARS. 2008. Riding the wave: reconciling the roles of disease and climate change in amphibian declines. *PLoS Biology* 6:441–454.
- LOEB, S. L. 1981. An *in situ* method for measuring the primary productivity and standing crop of the epilithic periphyton community in lentic systems. *Limnology and Oceanography* 26:394–399.
- LOREAU, M., S. NAEEM, P. INCHAUSTI, J. BENGTTSSON, J. P. GRIME, A. HECTOR, D. U. HOOPER, M. A. HUSTON, D. RAFFAELLI, B. SCHMID, D. TILMAN, AND D. A. WARDLE. 2001. Ecology – biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* 294:804–808.
- LUGTHART, G. J., AND J. B. WALLACE. 1992. Effects of disturbance on benthic functional structure and pro-

- duction in mountain streams. *Journal of the North American Benthological Society* 11:138–164.
- McCUNE, B., AND J. B. GRACE (EDITORS). 2002. *Analysis of ecological communities*. MjM Software Design, Glenden Beach, Oregon.
- MCNEELY, C., AND M. E. POWER. 2007. Spatial variation in caddisfly grazing regimes within a northern California watershed. *Ecology* 88:2609–2619.
- MERRITT, R. W., K. W. CUMMINS, AND M. B. BERG (EDITORS). 2008. *An introduction to the aquatic insects of North America*. 4th edition. Kendall/Hunt Publishing, Dubuque, Iowa.
- MINCHIN, P. R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69: 89–107.
- MINCHIN, P. R. 1989. Montane vegetation of the Mt. Field massif, Tasmania: a test of some hypotheses about properties of community patterns. *Vegetatio* 83:97–110.
- MÜLLER, F., R. HOFFMAN-KROLL, AND H. WIGGERING. 2000. Indicating ecosystem integrity – theoretical concepts and environmental requirements. *Ecological Modelling* 130:13–23.
- NAEEM, S. 1998. Species redundancy and ecosystem reliability. *Conservation Biology* 12:39–45.
- PACALA, S., AND A. P. KINZIG. 2002. Introduction to theory and the common ecosystem model. Pages 169–174 in A. P. Kinzig, S. W. Pacala, and D. Tilman (editors). *Functional consequences of biodiversity: empirical progress and theoretical extensions*. Princeton University Press, Princeton, New Jersey.
- PETCHEY, O. L., A. L. DOWNING, G. G. MITTELBACH, L. PERSSON, C. F. STEINER, P. H. WARREN, AND G. WOODWARD. 2004. Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos* 104:467–478.
- POWER, M. E. 1990. Resource enhancement by indirect effects of grazers: armored catfish, algae, and sediment. *Ecology* 71:897–904.
- PRINGLE, C. M., G. A. BLAKE, A. P. COVICH, K. M. BUZBY, AND A. FINLEY. 1993. Effects of omnivorous shrimp in a montane tropical stream: sediment removal, disturbance of sessile invertebrates, and enhancement of understory algal biomass. *Oecologia (Berlin)* 93:1–11.
- RAMÍREZ, A., AND C. M. PRINGLE. 1998. Structure and production of a benthic insect assemblage in a neotropical stream. *Journal of the North American Benthological Society* 17:443–463.
- RANVESTEL, A. W., K. R. LIPS, C. M. PRINGLE, M. R. WHILES, AND R. J. BIXBY. 2004. Neotropical tadpoles influence stream benthos: evidence for the ecological consequences of decline in amphibian populations. *Freshwater Biology* 49:274–285.
- REGISTER, K. J., K. R. LIPS, AND M. R. WHILES. 2006. Energy flow and subsidies associated with the complex life cycle of ambystomatid salamanders in ponds and adjacent forest in southern Illinois. *Oecologia (Berlin)* 147:303–314.
- ROSEMOND, A. D., P. J. MULHOLLAND, AND S. H. BRAWLEY. 2000. Seasonally shifting limitation of stream periphyton: response of algal populations and assemblage biomass and productivity to variation in light, nutrients, and herbivores. *Canadian Journal of Fisheries and Aquatic Sciences* 57:66–75.
- ROSEMOND, A. D., P. J. MULHOLLAND, AND J. W. ELWOOD. 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology* 74: 1264–1280.
- SOLOMON, C. T., A. S. FLECKER, AND B. W. TAYLOR. 2004. Testing the role of sediment mediated interactions between tadpoles and armored catfish in a Neotropical stream. *Copeia* 3:610–616.
- SRIVASTAVA, D. S., AND M. VELLEND. 2005. Biodiversity and ecosystem function research: is it relevant to conservation? *Annual Review of Ecology, Evolution, and Systematics* 36:267–294.
- TAYLOR, B. W., A. S. FLECKER, AND R. O. HALL. 2006. Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science* 313:833–836.
- TAYLOR, B. W., A. R. MCINTOSH, AND B. L. PECKARSKY. 2002. Reach-scale manipulations show invertebrate grazers depress algal resources in streams. *Limnology and Oceanography* 47:893–899.
- TILMAN, D. 1996. Population versus ecosystem stability. *Ecology* 77:350–363.
- VANNI, M. J. 2002. Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics* 33:341–370.
- VAUGHN, C. C. 2010. Biodiversity losses and ecosystem function in freshwaters: emerging conclusions and research directions. *BioScience* 60:25–35.
- VERBURG, P., S. S. KILHAM, C. M. PRINGLE, K. R. LIPS, AND D. L. DRAKE. 2007. A stable isotope study of a neotropical stream food web prior to the extirpation of its large amphibian community. *Journal of Tropical Ecology* 23: 643–653.
- WALLACE, J. B., AND J. R. WEBSTER. 1996. The role of macroinvertebrates in stream ecosystem function. *Annual Review of Entomology* 41:115–139.
- WHILES, M. R., K. R. LIPS, C. M. PRINGLE, S. S. KILHAM, R. J. BIXBY, R. BRENES, S. CONNELLY, J. C. COLÓN-GAUD, M. HUNTE-BROWN, A. D. HURYN, C. MONTGOMERY, AND S. PETERSON. 2006. The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. *Frontiers in Ecology* 4:27–34.
- WHILES, M. R., AND J. B. WALLACE. 1995. Macroinvertebrate production in a headwater stream during recovery from anthropogenic disturbance and hydrologic extremes. *Canadian Journal of Fisheries and Aquatic Sciences* 52: 2402–2422.

Received: 3 August 2009

Accepted: 16 June 2010