

Potential functional redundancy and resource facilitation between tadpoles and insect grazers in tropical headwater streams

CHECO COLÓN-GAUD^{*,†}, M. R. WHILES^{*}, R. BRENES^{*,‡}, S. S. KILHAM[§], K. R. LIPS^{*}, C. M. PRINGLE[¶], S. CONNELLY[¶] AND S. D. PETERSON^{*}

^{*}Department of Zoology and Center for Ecology, Southern Illinois University, Carbondale, IL, U.S.A.

[†]Institute for Tropical Ecosystem Studies, University of Puerto Rico – Rio Piedras Campus, San Juan, PR, U.S.A.

[‡]Turtle Mountain Community College, Belcourt, ND, U.S.A.

[§]Department of Biosciences and Biotechnology, Drexel University, Philadelphia, PA, U.S.A.

[¶]Institute of Ecology, University of Georgia, Athens, GA, U.S.A.

SUMMARY

1. We quantified production and consumption of stream-dwelling tadpoles and insect grazers in a headwater stream in the Panamanian uplands for 2 years to assess their effects on basal resources and energy fluxes. At the onset of our study, this region had healthy, diverse amphibian populations, but a catastrophic disease-driven decline began in September 2004, which greatly reduced amphibian populations.
2. Insect grazer production was 348 mg ash-free dry mass (AFDM) m⁻² year⁻¹ during the first year of the study and increased slightly to 402 mg AFDM m⁻² year⁻¹ during the second year.
3. Prior to amphibian declines, resource consumption by grazers (tadpoles and insects) was estimated at 2.9 g AFDM m⁻² year⁻¹ of algal primary production, which was nearly twice the estimated amount available. Insect grazers alone accounted for *c.* 81% of total primary consumption. During the initial stages of the declines, consumption remained at *c.* 2.9 g AFDM m⁻² year⁻¹, but only 35% of the available resource was being consumed and insect grazers accounted for *c.* 94% of total consumption.
4. Production and resource consumption of some insect grazers increased during the second year, as tadpoles declined, indicating a potential for functional redundancy in this system. However, other insect grazer taxa declined or did not respond to tadpole losses, suggesting a potential for facilitation between tadpoles and some insects; differential responses among taxa resulted in the lack of a response by insect grazers as a whole.
5. Our results suggest that before massive population declines, tadpoles exerted strong top-down control on algal production and interacted in a variety of ways with other primary consumers.
6. As amphibian populations continue to decline around the globe, changes in the structure and function of freshwater habitats should be expected. Although our study was focused on tropical headwater streams, our results suggest that these losses of consumer diversity could influence other aquatic systems as well and may even reach to adjacent terrestrial environments.

Keywords: amphibian declines, biodiversity, community structure, ecosystem function, production

Correspondence: Checo Colón-Gaud, Department of Biology, Georgia Southern University, Statesboro, GA 30460, U.S.A. E-mail: checo@ites.upr.edu

Current address: Department of Biology, University of Maryland, College Park, MD 20742, U.S.A.

Introduction

Declining biological diversity and the ultimate consequences of species losses have become topics of increasing interest and debate among ecologists (e.g. Naeem, 2002; Diaz *et al.*, 2006; Laurance, 2007). Evidence suggests that freshwater systems (Malmqvist & Rundle, 2002; Dudgeon *et al.*, 2006) and the tropics (Sala *et al.*, 2000; Laurance, 2007) may be the hardest hit by the loss of biodiversity. The importance of consumer diversity and its effect on food web structure is gaining increasing attention in the light of the ongoing diversity–stability debate (Duffy, 2002, 2003; Worm & Duffy, 2003) and declining biodiversity. In freshwater systems, consumers can regulate, facilitate, and compete for basal resources and, in doing so, influence the complexity of food webs and trophic interactions (Kitchell *et al.*, 1979; Carpenter *et al.*, 1985; Hairston & Hairston, 1993). The rapid rate at which consumer diversity is declining in freshwaters makes studies of the roles of consumers more relevant than ever for understanding the ecological consequences of extinctions and declining biodiversity; however, much current knowledge is based on relatively small-scale studies of assembled communities (Loreau *et al.*, 2001; Petchey *et al.*, 2004; but see Taylor *et al.*, 2006).

Amphibian diversity is highest in the neotropics (Duellman, 1999; Global Amphibian Assessment, 2006), yet relatively little is known about the ecological roles of amphibians in this region compared to other consumer groups. Considering larval stages, only a handful of studies have examined the role of tadpoles in lotic habitats in the neotropics (e.g. Flecker *et al.*, 1999; Ranvestel *et al.*, 2004; Solomon *et al.*, 2004), even though many species in this region breed in streams. Tadpoles can account for a substantial component of consumer biomass in tropical headwater streams and thus have the potential to influence basal resources as well as other consumer communities.

In fact, amphibians have been experiencing well-publicised catastrophic population declines, extirpations and extinctions over the last few decades (Collins & Storfer, 2003; Stuart *et al.*, 2004; Lannoo, 2005; Lips *et al.*, 2006). While much attention has been focused on documenting declines, identifying causes and conserving remaining species, still little is known of the ultimate consequences of these losses. In

Central America, declines associated with a moving disease front provided a unique opportunity to examine the ecological consequences of a sudden loss of consumer diversity in a natural field setting.

As part of the Tropical Amphibian Declines in Streams (TADS) project, we are assessing the ecological effects of amphibian declines in headwater streams in central Panama. For this study, our goal was to estimate grazing insect and tadpole production and consumption in order to quantify the roles of primary consumers in these systems. In doing so, we also examined how the loss of an entire consumer group could alter resource dynamics, particularly algal production and associated flow of autochthonous energy. Prior to our study, we predicted that tadpole production and resource consumption would exceed that of grazing insects and that tadpoles would exert significant top-down control over basal food resources and compete with other primary consumers. We also predicted that a decrease in tadpole productivity and consequent increases in algal resource availability would result in compensatory increases in insect grazer production and consumption.

Methods

Study area

The study was carried out in two 100-m reaches of the headwaters of the Río Guabal in the Parque Nacional Omar Torrijos Herrera, El Copé, Coclé Province, in central Panamá (8°40′04.0″N, 80°35′.6″W). Headwaters of the Río Guabal are high gradient, characterised by distinct riffle and run sequences with pebble and cobble substrates and occasional pools with fine sediments. At the study area (elevation 900 m), Río Guabal is a heavily forested, second-order stream with an average depth of 15 cm and average wetted width of 3.4 m. Two distinct seasons characterise the region, a dry season from January to May and a rainy season from June to December. More detailed descriptions of the study reaches can be found in Colón-Gaud *et al.* (2008) and Connelly *et al.* (2008).

Previous surveys reported a total 68 species of amphibians in the study area, with *c.* 40 riparian anurans, 14 of which have a stream-dwelling larval stage (Lips *et al.*, 2003; Whiles *et al.*, 2006). In September 2004, amphibian declines associated with a

disease wave of chytridiomycosis resulted in a rapid, massive die-off of adult amphibians, and larval populations subsequently declined slowly and steadily through the year (Lips *et al.*, 2006; Brem & Lips, 2008). Hence, we considered the sites to be in a transitional phase during year 2 of our study, in that tadpoles were present, but steadily declining in abundance during this period. This situation allowed us to examine ecological responses during the early stages of an amphibian decline.

Consumer biomass

Tadpoles were sampled monthly for the duration of the study using methods based on Heyer *et al.* (1994). On each sampling date, three random samples were taken from each of three major habitat types (riffles, pools and isolated pools) along a stretch of the Rio Guabal (encompassing both study reaches) for a total of nine samples per date. We used 250- μ m mesh 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. Depositional pools were sampled using a stove-pipe benthic corer (22 cm diameter) and isolated pools using exhaustive removal sampling with a dip net until three consecutive scoops produced no tadpoles. For large, deep pools, we made direct observational counts using an underwater viewer (Aqua Scope IITM; Water Monitoring Equipment and Supply, Seal Harbor, ME, USA). We corrected numbers of tadpoles in each sample for area sampled to estimate densities. We estimated biomass by constructing body length versus ash-free dry mass (AFDM) relationships using a range of size classes of dominant taxa following procedures of Benke *et al.* (1999). Grazing tadpoles were represented primarily by three taxa in two genera [two treefrogs, *Hyloscirtus colymba* (Dunn), *Hyloscirtus palmeri* (Boulenger) and one ranid, *Lithobates warszewitschii* (Schmidt)]. The three dominant grazing tadpole taxa occur in these streams throughout the year, with generally higher densities during the dry season.

Aquatic insects were collected monthly from both study reaches from June 2003 to May 2004 [Year 1; Colón-Gaud *et al.* (2009)] and semimonthly from July 2004 to May 2005 (Year 2). On each sampling date, we collected seven replicate samples from dominant habitats (i.e. erosional and depositional); four Surber samples (930 cm², 250- μ m mesh) were collected from

riffles and runs; and three stove-pipe benthic cores (314 cm² sampling area) were collected from pools. We elutriated samples through a 250- μ m mesh sieve in the field and preserved materials remaining on the sieve in *c.* 10% formalin. We removed all macroinvertebrates from coarse fractions of benthic samples; fine fractions were occasionally subsampled (from 1/2 to 1/32 depending on size) using a Folsom plankton splitter.

We classified individual taxa as insect grazers based on the functional feeding groups (FFG) classification established by Merritt *et al.* (2008) or on natural abundance stable isotope data from a concurrent study in nearby streams (Verburg *et al.*, 2007). We identified (usually to genus) and measured (total body length) all insects and estimated taxon- and size-specific AFDM using published length-mass relationships (Benke *et al.*, 1999) or relationships developed with our own specimens. 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 (Colón-Gaud *et al.*, 2009). Insect totals from both reaches were averaged to obtain a representative estimate for the Rio Guabal.

The insect grazer community in the Rio Guabal study reaches consists of 12 insect taxa, representing five orders (Coleoptera, Ephemeroptera, Lepidoptera, Diptera, Trichoptera) and eight families (C. Colón-Gaud, unpublished data). *Ptychophallus* crabs are present in these streams, and these omnivores may also occasionally graze algae. However, we excluded them from our study because they are not properly sampled with the techniques we used and, based on our field observations and stable isotope analyses in our study streams (Verburg *et al.*, 2007), they are not primarily grazers.

Consumer production

Tadpole secondary production was estimated using instantaneous growth rate estimates from individuals reared in *in situ* growth chambers made of clear acrylic tubing following methods of Huryn & Wallace (1986). The use of *in situ* growth chambers has been a standard non-cohort approach for estimating secondary production in streams (see Benke & Huryn, 2006). Chambers ranged in size from 10 to 30 cm in length

and were 8–11 cm in diameter with 500- μm mesh screening on each end. Each chamber contained one tadpole at an intermediate stage of development (e.g. with hind limb buds developing but not yet near metamorphosis; Gosner stages 26–30 [Gosner, 1960]) and rocks and detritus (e.g. leaf pack material) collected from the stream reach. Chambers were positioned and secured horizontally so they would remain entirely submerged and water could flow through them. Chambers were checked weekly, and tadpoles were measured to the nearest mm to estimate growth. All tadpole growth chambers were maintained for a period of approximately 6–8 weeks, until measurable changes in size (c. 2–3 mm) were evident.

We estimated interval production as the product of mean biomass (g AFDM m^{-2}) and growth rates between sampling dates; total production (g AFDM $\text{m}^{-2} \text{year}^{-1}$) was the sum of the interval estimates (Benke & Huryn, 2006). We used the same method to estimate annual production of insect grazer taxa with rapid turnover rates (e.g. Leptophlebiidae, Baetidae and Heptageniidae). Insect growth chambers ranged in size from 10 to 20 cm in length and were 8 cm in diameter with 300- μm mesh screening on each end. We used the size-frequency method (Benke & Huryn, 2006), corrected for cohort production intervals, to estimate annual production for larvae of the water penny beetle *Psephenus* (Coleoptera: Psephenidae) and larvae of the moth *Petrophila* (Lepidoptera: Crambidae). Production of the moth fly *Maruina* (Diptera: Psychodidae), the purse-case caddisfly *Hydroptila* (Trichoptera: Hydroptilidae) and the saddle-case caddisfly *Glossosoma* (Trichoptera: Glossosomatidae) was estimated by applying a P:B of 62 (Diptera) or a P:B of 11 (Trichoptera) to annual mean biomass values based on equations developed by Benke (1993) because individuals of these taxa were rarely collected. More detailed information on methods used for biomass and production estimates is presented in Colón-Gaud et al. (2009).

Resource consumption

Resource consumption by grazers was estimated following methods of Benke & Wallace (1980), whereby annual production is divided by the product of the assimilation efficiency (AE) and net production efficiency (NPE) of the consumer for a given food resource. For insect grazers, we used an

AE of 30% and NPE of 50% based on literature estimates (Benke & Wallace, 1980). We used primary production estimates from a previous tadpole exclusion study in our study stream to develop preliminary *in situ* consumption rates for tadpoles (Connelly et al., 2008). Based on these results, we determined that tadpoles removed a total of c. 1 g $\text{m}^2 \text{year}^{-1}$ at undisturbed sites. Because material could either be removed by consumption or bioturbation, we assumed that the material consumed by tadpoles should not exceed the estimated amount.

We determined that diatoms and amorphous detritus formed a large amount of grazing tadpole diets (>80%) based on analyses of gut contents from tadpoles previously collected in our study reaches (Ranvestel et al., 2004). We used estimates of the assimilation efficiencies of these resources by two stream-dwelling omnivores (stoneroller minnows and *Orconectes* crayfishes) from a study by Evans-White et al. (2003) to generate comparable AE estimates for tadpoles. For both of these consumer groups, assimilation efficiencies generally ranged between 10 and 18% of the resource ingested. Based on these calculations, we used an AE of 15% and a predetermined NPE of 50%, based on literature estimates reported for ectothermic vertebrates (Burton & Likens, 1975; Evans-White et al., 2003). We then used these rates to develop an approximate value of gross production efficiency (GPE = AE \times NPE) for tadpoles in these systems.

Statistical analyses

To assess changes in grazer community composition, we used two-way ANOVA and tested for differences in mean monthly biomass of each taxon between sampling seasons (dry versus wet) and study years (year 1 versus year 2). Analyses were conducted using PROC GLM at $\alpha = 0.05$ in SAS version 9.1 (SAS Institute, Cary, North Carolina, U.S.A.). We also constructed non-metric multidimensional scaling (NMDS) ordination plots based on mean grazer biomass using DECODA© (Minchin, 2005) to examine patterns in community structure between the different sampling seasons and years. Dissimilarities were calculated using the Bray–Curtis index (Bray & Curtis, 1957), standardised for unit maxima, and performed the analyses in one to four dimensions using 100 random configurations.

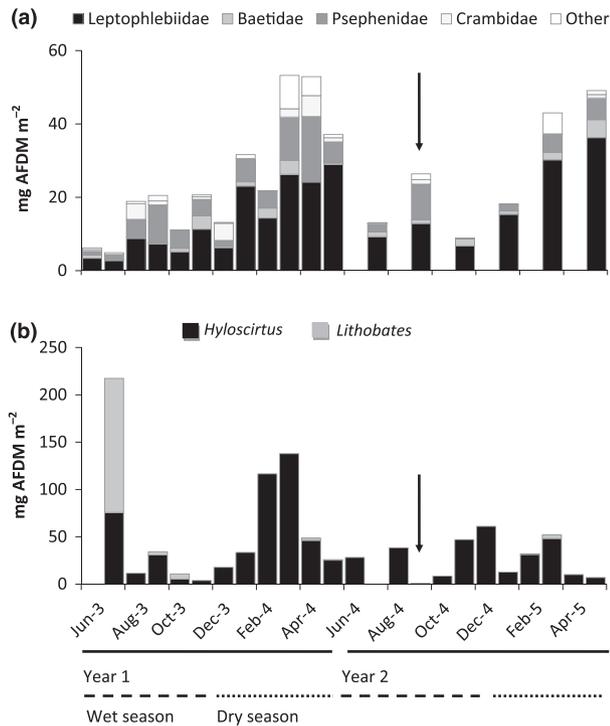


Fig. 1 Mean monthly biomass (mg AFDM m⁻²) of grazing insects (a) and tadpoles (b) in the Rio Guabal reach during year 1 (June 2003–May 2004) and year 2 (June 2004–May 2005) of the study. Dashed lines denote duration of dry (—) and wet (...) seasons. Arrows indicate date (September 2004) of first reports of disease-related amphibian declines in the region. Leptophlebiidae (*Farrodes*, *Hagenulopsis*, *Thraulodes*, *Atopophlebia*); Baetidae (*Baetodes*, *Dactylobaetis*); Psephenidae (*Psephenus*); Crambidae (*Petrophila*); other (*Maruina*, *Stenonema*, *Hydroptila*, *Glossosoma*).

Results

Consumer biomass

During year 1 of the study (June 2003–May 2004), populations of grazing insects and tadpoles peaked during the dry season, particularly during February and March (Fig. 1). Tadpole estimates were also high in July 2003 because of high abundance of *L. warszewitschii* tadpoles. During year 2 (June 2004–May 2005), grazing tadpole populations were relatively lower and showed less seasonal variation.

During year 1 of the study, insect grazers accounted for 24.3 ± 4.7 mg AFDM m⁻² ± SE of mean biomass (31% of total grazer biomass). Insect grazer biomass during year 1 was dominated by *Farrodes* mayflies, followed by *Psephenus* larvae, and *Thraulodes* mayflies (c. 75% of total; Table 1). Grazing tadpoles accounted

Table 1 Mean annual biomasses [mg ash-free dry mass (AFDM) m⁻² ± SE] of insect and tadpole grazers in the Rio Guabal study reach during years 1 (June 2003–May 2004) and 2 (June 2004–May 2005)

Taxa	Year 1	Year 2
Insects		
<i>Psephenus</i>	6.2 ± 1.4	4.1 ± 1.4
<i>Farrodes</i>	8.7 ± 1.9	14.3 ± 3.4
<i>Hagenulopsis</i>	1.0 ± 0.3	0.5 ± 0.4
<i>Thraulodes</i>	3.4 ± 1.2	3.7 ± 1.4
<i>Atopophlebia</i>	0.4 ± 0.1	–
<i>Petrophila</i>	1.7 ± 0.6	0.4 ± 0.2
<i>Baetodes</i>	1.3 ± 0.4	1.9 ± 0.6
<i>Dactylobaetis</i>	<0.1	0.1 ± 0.1
<i>Maruina</i>	0.1 ± 0.01	0.1 ± 0.03
<i>Stenonema</i>	1.6 ± 0.8	1.1 ± 0.8
<i>Hydroptila</i>	0.1 ± 0.02	0.3 ± 0.1
<i>Glossosoma</i>	<0.1	0.1 ± 0.04
Tadpoles		
<i>Hyloscirtus</i>	45.9 ± 13.7	26.7 ± 6.1
<i>Lithobates</i>	14.0 ± 13.4	0.4 ± 0.4
Total insects	24.3 ± 4.7	26.5 ± 6.7
Total tadpoles	54.8 ± 19.4	24.8 ± 6.1

for 54.8 ± 19.4 mg AFDM m⁻² ± SE of mean biomass (69% of total grazer biomass) during year 1.

During year 2, insect grazer biomass slightly increased (26.5 ± 6.7 mg AFDM m⁻² ± SE; 52% of total grazer biomass). Insect grazer biomass during year 2 was again dominated by *Farrodes*, which at times accounted for nearly all insect grazer biomass, and showed a significant increase ($F = 5.07, P = 0.04$) of 1.6× from year 1 estimates (Tables 2 & 3). *Baetodes*, *Psephenus* and *Thraulodes* combined to account for the majority of the remaining insect grazer biomass (Table 1). Although not accounting for a large amount of grazer biomass, larvae of the purse-case caddisfly *Hydroptila* increased significantly ($F = 9.20, P = 0.01$) to nearly 5× that of year 1. Grazing tadpoles accounted for 24.8 ± 6.1 mg AFDM m⁻² ± SE of mean monthly biomass (48% of total grazer biomass) during year 2.

There were few distinct seasonal patterns in mean biomass of most grazer taxa, with values generally higher during the dry season (Figs 1 & 2). Total insect grazer biomass was significantly higher during the dry season ($F = 17.39; P = 0.001$), with biomass of the leptophlebiid mayflies *Farrodes* ($F = 32.45; P < 0.001$) and *Thraulodes* ($F = 8.86; P = 0.01$) accounting for most of the dry season biomass. The water penny beetle, *Psephenus*, also accounted for a large portion of insect grazer biomass during the dry season (7.4 ± 1.8 mg AFDM m⁻² ± SE; 24% of total), but

Table 2 Seasonal (dry season and wet season) grazer (insects and tadpoles) mean biomasses [mg ash-free dry mass (AFDM) m⁻² ± SE] in the Rio Guabal study reach during years 1 (June 2003–May 2004) and 2 (June 2004–May 2005)

Taxa	Dry season		Wet season	
	Year 1	Year 2	Year 1	Year 2
Insects				
<i>Psephenus</i>	9.3 ± 2.5	4.2 ± 1.3	4.1 ± 1.2	4.0 ± 2.9
<i>Farrodes</i>	15.0 ± 5.1	20.7 ± 3.6	4.2 ± 0.9	7.8 ± 1.8
<i>Hagenulopsis</i>	1.3 ± 0.5	0.9 ± 0.7	0.7 ± 0.3	0.1 ± 0.02
<i>Thraulodes</i>	6.4 ± 2.0	5.7 ± 2.3	1.2 ± 0.6	1.7 ± 0.5
<i>Atopophlebia</i>	0.7 ± 0.2	–	0.2 ± 0.1	–
<i>Petrophila</i>	1.8 ± 1.1	0.3 ± 0.3	1.6 ± 0.8	0.5 ± 0.4
<i>Baetodes</i>	1.6 ± 0.7	2.6 ± 1.2	1.0 ± 0.5	1.2 ± 0.1
<i>Dactylobaetis</i>	<0.1	–	<0.1	0.2 ± 0.2
<i>Maruina</i>	<0.1	0.1 ± 0.1	0.1 ± 0.02	<0.1
<i>Stenonema</i>	3.2 ± 1.7	1.7 ± 1.6	0.4 ± 0.2	0.4 ± 0.4
<i>Hydroptila</i>	<0.1	0.4 ± 0.2	0.1 ± 0.03	0.1 ± 0.1
<i>Glossosoma</i>	<0.1	0.1 ± 0.1	–	<0.1
Tadpoles				
<i>Hyloscirtus</i>	71.9 ± 23.1	21.8 ± 7.8	24.2 ± 11.1	30.7 ± 9.4
<i>Lithobates</i>	0.6 ± 0.5	0.9 ± 0.8	25.1 ± 23.3	–
Total insects	39.3 ± 6.1	36.8 ± 9.5	13.6 ± 2.5	16.1 ± 5.3
Total tadpoles	72.5 ± 22.9	22.8 ± 8.5	42.2 ± 29.5	26.3 ± 9.1

showed no significant differences in seasonal biomass. Tadpole grazer biomass was highly variable and generally highest during the dry season, although no

significant seasonal differences were observed. However, biomass of *Hyloscirtus* tadpoles was generally higher during the dry season in year 1 of the study, but remained constant during year 2 (Table 2).

Two-dimensional ordination plots (Fig. 2) revealed no distinct seasonal patterns in grazer community structure, with frequent overlap of sampled variables between the dry and wet seasons. Furthermore, differences in grazer assemblages were difficult to interpret at this scale despite changes in biomass of individual taxa. Differences in grazer community structure between the study years were apparent over time, with clear differentiation between year 1 (with natural tadpole fluctuations) and year 2 (with tadpole populations declining).

Consumer production

During year 1, insect grazers accounted for 348 mg AFDM m⁻² year⁻¹ of total consumer production, versus 41 mg AFDM m⁻² year⁻¹ by tadpoles (Fig. 3a). Year 1 insect grazer production was dominated by the leptophlebiid mayfly *Farrodes* (34% of total), the water penny beetle *Psephenus* (20%), and the mayflies *Thraulodes* (17%) and *Baetodes* (10%) (Table 4). Tadpole grazer production was dominated by *Hyloscirtus*,

Table 3 Results of two-way ANOVA testing the effects of year (1 versus 2), season (dry season versus wet season) and year × season interactions. Tests are based on grazer taxa mean annual biomasses, except for total insects (total insect mean biomass) and total tadpoles (total tadpole mean biomass). Significant $P > F$ values are in bold. Results are based on type III sum of squares; $\alpha = 0.05$

Taxa	Model		Year		Season		Year × Season	
	F value	P	F value	P	F value	P	F value	P
Insects								
<i>Psephenus</i>	1.85	0.18	1.49	0.24	1.67	0.22	1.40	0.26
<i>Farrodes</i>	13.90	<0.001	5.07	0.04	32.45	<0.0001	0.25	0.62
<i>Hagenulopsis</i>	1.52	0.25	1.71	0.21	3.08	0.10	0.10	0.76
<i>Thraulodes</i>	3.64	0.04	0.01	0.94	8.86	0.01	0.15	0.70
<i>Atopophlebia</i>	3.23	0.05	6.25	0.03	1.48	0.24	1.48	0.24
<i>Petrophila</i>	0.66	0.59	1.96	0.18	0.00	0.99	0.05	0.83
<i>Baetodes</i>	1.00	0.42	0.78	0.39	2.06	0.17	0.28	0.61
<i>Dactylobaetis</i>	1.77	0.20	1.76	0.21	1.80	0.20	2.72	0.12
<i>Maruina</i>	0.70	0.59	0.00	0.95	1.05	0.32	1.67	0.22
<i>Stenonema</i>	1.57	0.24	0.36	0.56	3.00	0.11	0.38	0.55
<i>Hydroptila</i>	5.88	0.01	9.20	0.01	3.42	0.09	7.81	0.01
<i>Glossosoma</i>	1.36	0.29	2.05	0.17	1.77	0.21	0.55	0.47
Tadpoles								
<i>Hyloscirtus</i>	2.79	0.07	2.56	0.13	2.04	0.17	4.33	0.05
<i>Lithobates</i>	1.04	0.40	1.00	0.33	0.91	0.35	1.06	0.32
Total Insects	7.04	<0.01	0.00	0.99	17.39	<0.001	0.21	0.66
Total Tadpoles	1.04	0.40	2.42	0.14	0.40	0.53	0.64	0.43

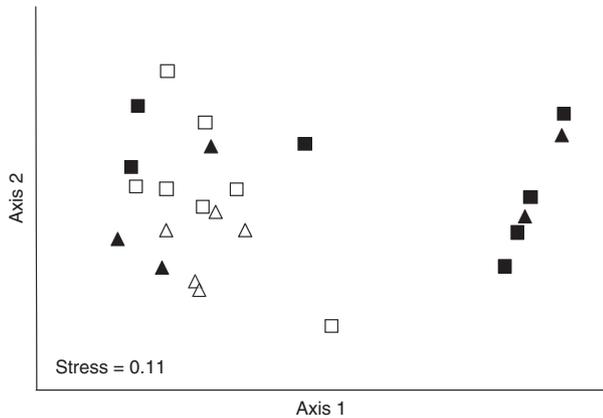


Fig. 2 Two-dimensional NMDS ordination plots of grazer community structure based on consumer mean monthly biomass in the Guabal stream study reach during year 1 (open symbols) and year 2 (filled symbols). Squares represent wet season estimates (June–December) and triangles represent dry season estimates (January–May).

which accounted for >90% of total tadpole production (Table 4).

During year 2, total insect grazer production increased slightly to $402 \text{ mg AFDM m}^{-2} \text{ year}^{-1}$, as tadpole production decreased to $13 \text{ mg AFDM m}^{-2} \text{ year}^{-1}$ (Fig. 3b). Year 2 insect grazer production was dominated by *Farrodes* mayflies, which accounted for *c.* 53% of total production during the year, representing a $1.8\times$ increase in production from the previous year. The mayflies *Thraulodes*, *Baetodes*, and the water penny beetle *Psephenus*, accounted for the majority of the remaining insect grazer production (38% combined) during year 2 (Table 4). Tadpole production was dominated by *Hyloscirtus*, which accounted for over 99% of total tadpole production, despite a *c.* $3\times$ decrease in production from the previous year (Table 4).

Resource consumption

During year 1, all grazers combined consumed an estimated $2865 \text{ mg AFDM m}^{-2} \text{ year}^{-1}$ of algal primary production, with insect grazers accounting for *c.* 81% of total consumption. Total grazer consumption during year 1 exceeded the estimated availability of periphyton resources by $>1.9\times$, with insect grazers alone consuming $>1.6\times$ of the available amount (Fig. 3a). *Hyloscirtus* tadpoles consumed the highest amount of algal production among all grazers during

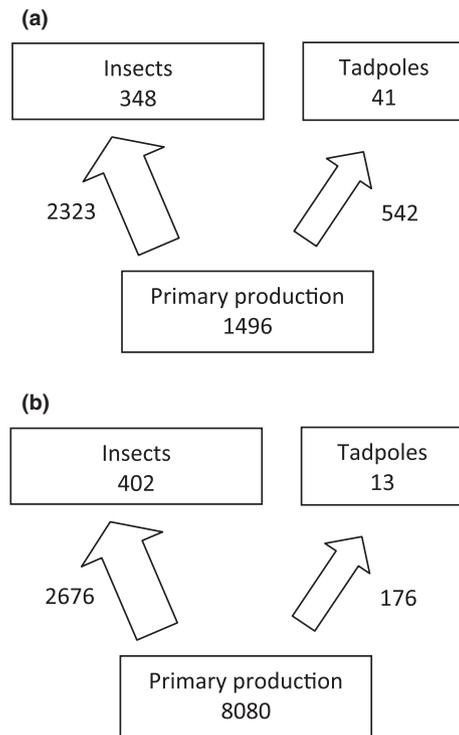


Fig. 3 Primary consumer food webs and energy flow pathways of the Rio Guabal study reach (a) prior to amphibian declines and (b) during the transitional stage of amphibian declines in the region. Values in boxes represent annual secondary production [$\text{mg ash-free dry mass (AFDM) m}^{-2} \text{ year}^{-1}$] for consumers and net primary production ($\text{mg AFDM m}^{-2} \text{ year}^{-1}$). Arrows directed at consumer boxes indicate consumption ($\text{mg AFDM m}^{-2} \text{ year}^{-1}$). Values next to arrows represent amounts of the resource consumed by each group. Primary production estimates are derived from algal biofilms accumulated on artificial substrates (unglazed tiles) in a concurrent grazer exclusion study by Connelly *et al.* (2008).

the first year (Table 4). Resource consumption by insect grazers during this year was highest among the mayflies *Farrodes* and *Thraulodes*, and the beetle *Psephenus*, accounting for $>1.6 \text{ g AFDM m}^{-2} \text{ year}^{-1}$ of total consumption.

During year 2, grazers consumed an estimated $2853 \text{ mg AFDM m}^{-2} \text{ year}^{-1}$ of algal primary production, only a *c.* $10 \text{ mg AFDM m}^{-2}$ decrease from the year 1 estimate but now only 35% of the estimated resources available (Fig. 3b). Insect grazers accounted for the majority of resource consumption (*c.* 94%) during year 2, with *Farrodes* accounting for $>1.4 \text{ g AFDM m}^{-2} \text{ year}^{-1}$ of total consumption, $1.8\times$ the amount consumed by this taxon during year 1 (Table 4). *Baetodes* also showed a noticeable increase in resource consumption, accounting for *c.* 388 mg

Taxa	Year 1		Year 2	
	Production	Consumption	Production	Consumption
Insects				
<i>Psephenus</i>	68.3	455.3	36.9	246.7
<i>Farrodes</i>	118.1	787.2	214.7	1431.0
<i>Hagenulopsis</i>	16.4	109.5	7.5	49.7
<i>Thraulodes</i>	59.3	395.3	59.4	395.8
<i>Atopophlebia</i>	7.1	47.1	0	0
<i>Petrophila</i>	24.7	165.0	9.8	65.1
<i>Baetodes</i>	34.1	227.1	58.2	387.8
<i>Dactylobaetis</i>	0.2	1.6	0.9	6.6
<i>Maruina</i>	2.9	19.8	3.9	26.6
<i>Stenonema</i>	16.4	109.3	6.6	44.0
<i>Hydroptila</i>	0.7	4.7	2.9	19.6
<i>Glossosoma</i>	0.1	0.6	0.6	4.1
Tadpoles				
<i>Hyloscirtus</i>	37.5	500.5	12.9	172.7
<i>Lithobates</i>	3.1	41.9	0.2	3.2

Table 4 Production [mg ash-free dry mass (AFDM) m⁻² year⁻¹] and resource consumption (mg AFDM m⁻² year⁻¹) by insect and tadpole grazers in the Rio Guabal study reach during year 1 (June 2003–May 2004) and year 2 (June 2004–May 2005); consumption = production ÷ gross production efficiency (GPE); GPE = assimilation efficiency (AE) × net production efficiency (NPE). Insects GPE = 0.15; tadpoles GPE = 0.075; AE and NPE are based on literature values or our own estimates (see Methods)

AFDM m⁻² year⁻¹ of resource consumed (1.7× the amount consumed during year 1), while *Psephenus* consumption declined to *c.* 1/2 the amount consumed during the previous year. Tadpole grazer consumption declined to *c.* 1/3 the amount consumed the previous year, with *Hyloscirtus* tadpoles accounting for nearly all of the resource consumption by this group (*c.* 98%).

Discussion

Our results indicate that insect grazer communities undergo subtle shifts in assemblage and structure following amphibian declines, which partially compensate for amphibian losses. These shifts indicate potential redundancy in these systems among some insect grazers and grazing tadpoles. However, the overall functional roles of amphibians in these systems and the degree of functional redundancy among primary consumers are not completely understood, and thus the degree of redundancy is difficult to assess. Long-term monitoring of community structure in these systems will allow us to assess whether these changes persist, and for how long, following amphibian losses.

Consumer biomass

Although biomass of some insect grazers increased in year 2 of the study, particularly during the dry season as tadpole biomass remained constant, total insect

grazer biomass did not change during the study years. This suggests that the entire consumer community does not compensate for amphibian losses, but that particular taxa are more directly affected by amphibian declines. These different responses probably reflect the strength of interactions between the once abundant consumer group (tadpoles) and those consumers that remain (e.g. Brönmark *et al.*, 1991; Feminella & Resh, 1991; Kohler & Wiley, 1997). Previous studies on stream grazer communities also found differential responses to decreases in dominant grazer abundance, with some taxa increasing while others decreased or were unaffected (McAuliffe, 1984; Kohler & Wiley, 1997; Jonsson & Malmqvist, 2003). These and similar studies suggested that a dominant consumer could reduce the populations of other consumers with similar resource needs via competition, while increasing populations of others via facilitation.

Negative responses to amphibian declines by some smaller-bodied insect grazers suggest they may benefit from the presence of tadpoles, either through reductions in populations of other competitors or via facilitation. A previous exclusion study by Ranvestel *et al.* (2004) in these same streams also suggested that tadpole grazing could facilitate smaller insect grazers by removing sediments deposited on substrata and exposing underlying periphyton. Our results, combined with the experimental manipulations of Ranvestel *et al.* (2004), indicate that tadpoles, when present, compete with larger grazing insects (i.e. larvae of Lepidoptera and Trichoptera, and later instars of

some Ephemeroptera), but also make periphyton resources more available to smaller insects.

Consumer production and resource consumption

Although most dominant insect grazers (e.g. mayflies) responded positively to declining tadpole production and consumption, others did not, and this in part explains the lack of an overall significant positive response by grazers. The lack of response by the water penny beetle, *Psephenus*, suggests that these relatively small-bodied grazers do not compete directly with tadpoles for periphyton resources, possibly because they generally inhabit the undersides of stones in the substrata during the day and graze on the surfaces at night. Alternatively, the lack of a strong positive response by *Psephenus* may be because tadpoles and *Psephenus* feed on different components of the periphyton. Connelly *et al.* (2008) found that grazing tadpoles reduced the abundance of larger diatom taxa and shifted periphyton communities to smaller forms, which could favour smaller taxa such as *Psephenus*. Our small-scale experimental manipulations in these same streams also indicated that tadpole-grazed periphyton assemblages, although lower in biomass, are more productive per unit biomass (Connelly *et al.*, 2008), which, again, could favour grazers that feed on smaller components of the periphyton.

Although we document some positive responses in production and consumption by grazing mayflies, it is not clear if mayfly grazing has the same effect on periphyton community structure, biomass and productivity as tadpole grazing. Additional dietary studies are needed to determine whether mayflies and tadpoles feed on the same species of diatoms, or whether these two groups partition algal resources. Furthermore, studies that examine long-term changes in insect grazer diets would provide more detailed estimates of the effects of amphibian declines in these systems; the long-term consequences of increased insect grazing and decreased tadpole grazing on algal resources in these streams remain to be seen.

Our results suggest that tadpoles can be more efficient per unit biomass at consuming periphyton than insect grazers as a whole. Even at the early stages of declining tadpole production, the rate of periphyton consumption by insect grazers does not appear to have the same effect as tadpole consumption did in previous years (Connelly *et al.*, 2008). For example,

tadpoles consumed 13.5 g of resource per gram of consumer production, whereas insect grazers consumed only 6.7 g. Such differences in consumption rates would have produced a surplus of unconsumed periphyton that probably resulted in increased resource availability. Additionally, our results may underestimate the overall effects of tadpoles on periphyton resources because we did not account for non-consumptive losses such as bioturbation.

Our study attests to the importance of considering multiple response variables and over different taxonomic scales when examining the effects of biodiversity losses on ecosystem processes. While estimates at the total community or functional (e.g. grazer) level did not reveal a clear distinction between study years, genus-level estimates revealed significant responses. Hence, investigations of biodiversity losses at coarse taxonomic scales may be confounded by differential responses of individual taxa.

Loss of consumer diversity

Species diversity has been linked to ecosystem stability (Johnson *et al.*, 1996; McCann, 2000). Even if grazing mayflies compensate to some degree for the loss of tadpoles, severely reduced grazer diversity may alter the long-term stability of these systems. The loss of an entire consumer group in these systems will quite likely lead to changes beyond those of the remaining grazer community and may ultimately alter organic matter dynamics and rates of material processing (Whiles *et al.*, 2006; Colón-Gaud *et al.*, 2008, 2009; Connelly *et al.*, 2008). Such changes could translate to differences in overall function and ultimately influence resistance and resilience to other perturbations such as invasive species, disease, pollution and climate change.

Given the connections among streams and the landscapes they drain, responses to amphibian declines are likely to transcend stream boundaries. For example, larval amphibians can be an important energetic link between aquatic and terrestrial environments (Regester *et al.*, 2006) and in this region serve as the primary food source for some riparian predators such as snakes (Whiles *et al.*, 2006). Although some grazing consumers in our study systems, particularly mayflies, can also serve as an important food source for riparian predators as they emerge into terrestrial environments (e.g. Jackson &

Fisher, 1986; Baxter *et al.*, 2005), they are prey for different groups of predators such as spiders, bats and birds and are of little value to amphibian specialists.

Our initial predictions regarding the overall contributions of tadpoles to grazer production and consumption were not supported, as insect grazer contributions exceeded those of tadpoles. However, the effects of tadpoles on algal production appear to go far beyond removal and depletion of the food resource and clearly have consequences on organic matter dynamics (Colón-Gaud *et al.*, 2008; Connelly *et al.*, 2008). Although there were no distinct changes in grazer production and consumption at the community level, it is clear that the structure of the grazer community in these streams shifted. Thus, the absence of pronounced changes in total consumer biomass and material fluxes, or even the absence of a total ecosystem collapse, should not be misinterpreted as a lack of functional change in the system. Furthermore, it is unknown whether these changes are representative of a new stable community or simply a transitional stage during the early stages of declines and consequent changes will follow.

In a similar field-based study of the loss of a dominant fish from a tropical river, Taylor *et al.* (2006) found an increase in primary production and respiration, and disruption of energy flow and carbon transport. Unlike our study, Taylor *et al.* (2006) found a lack of redundancy, despite a high diversity of consumers in their study system. Similar to the results of Taylor *et al.* (2006), tadpole declines ultimately resulted in large amounts of unconsumed basal resource that will either: (i) increase downstream exports (probably during wet seasons) or (ii) contribute to the detritus pool, increasing in-stream respiration. Whether the changes in consumer community and potential redundancy found in our study persist or eventually shift towards patterns observed by Taylor *et al.* (2006) remains to be seen. However, evidence to date indicates that amphibian communities that experience catastrophic disease-driven declines in this region do not recover (Lips *et al.*, 2003). In the light of this, we hypothesise that freshwater systems that experience amphibian declines will (i) continue to experience shifts in grazer community structure until a stable assemblage of dominant grazers persists (such as larger mayfly taxa), thus decreasing food web complexity; (ii) experience increases in autochthonous production

and changes in production to respiration ratios (P:R); and (iii) experience changes in fluxes (rates and ratios) of energy, exported materials and available nutrients with consequent alterations to material storage, downstream transport and nutrient cycling.

In conclusion, our results show the potential ramifications of the loss of an entire group of consumers and its consequent effects on the structure and functioning of these ecosystems. Our study was limited by low spatial and temporal replication, which is a common limitation of ecosystem level studies. Also, our estimates of availability of autochthonous resources were based on small-scale exclusion studies using artificial substrata, and these probably underestimated variability in algal resource availability in these hydrologically flashy systems (Connelly *et al.*, 2008). These issues limit the statistical inference and robustness of our results. However, our approach also has its merits. In particular, our results and assessments are based on field studies of natural communities, rather than manipulations of assembled communities. Thus, our results do not need to be extrapolated. Further, our study represents an intensive, quantitative examination of a stream system.

Amphibian population declines are ongoing in this region and continue to extend to nearby regions in South America and other parts of the globe. Continued studies of these declines should provide us with a greater understanding of the ultimate consequences of consumer biodiversity losses.

Acknowledgments

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, A. Rugenski, T. Frauendorf and H. Rantala 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 killings

followed the animal care protocols established by Southern Illinois University (Protocol 06-008).

References

- Baxter C.V., Fausch K.D. & Saunders W.C. (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology*, **50**, 201–220.
- Benke A.C. (1993) Concepts and patterns of invertebrate production in running waters. *Verhandlungen Internationale Vereinigung für theoretische und angewandte Limnologie*, **25**, 15–38.
- Benke A.C. & Huryn A.D. (2006) Secondary production of macroinvertebrates. In: *Methods in Stream Ecology* (Eds F.R. Hauer & G.A. Lamberti), pp. 691–709. Academic Press, San Diego.
- Benke A.C. & Wallace J.B. (1980) Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. *Ecology*, **78**, 108–118.
- Benke A.C., Huryn A.D., Smock L.A. & Wallace J.B. (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.
- Bray J.R. & Curtis J.T. (1957) An ordination of upland forest communities of southern Wisconsin. *Ecological Monographs*, **27**, 325–349.
- Brem F.M.R. & Lips K.R. (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.
- Brönmark C., Rundle S.D. & Erlandsson A. (1991) Interactions between freshwater snails and tadpoles: competition and facilitation. *Oecologia*, **87**, 8–18.
- Burton T.M. & Likens G.E. (1975) Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest. *Ecology*, **56**, 1068–1080.
- Carpenter S.R., Kitchell J.F. & Hodgson J.R. (1985) Cascading trophic interactions and lake productivity. *BioScience*, **35**, 634–639.
- Collins J.P. & Storer A. (2003) Global amphibian declines: sorting the hypothesis. *Diversity and Distributions*, **9**, 89–98.
- Colón-Gaud C., Peterson S., Whiles M.R., Kilham S.S., Lips K.R. & Pringle C.M. (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., Whiles M.R., Kilham S.S., Lips K.R., Pringle C.M., Connelly S. & Peterson S.D. (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., Pringle C.M., Bixby R.J., Brenes R., Whiles M.R., Lips K.R., Kilham S. & Huryn A.D. (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.
- Diaz S., Fargione J., Chapin F.S. III & Tilman D. (2006) Biodiversity loss threatens human well-being. *PLoS Biology*, **4**, 1300–1305.
- Dudgeon D., Arthington A.H., Gessner M.O. *et al.* (2006) Freshwater biodiversity: importance, threats, status, and conservation challenges. *Biological Reviews*, **81**, 163–182.
- Duellman W.E. (1999) Global distribution of amphibians: patterns, conservation, and challenges. In: *Patterns of Distribution of Amphibians: A Global Perspective* (Ed. W.E. Duellman), pp. 1–30. The John Hopkins University Press, Baltimore.
- Duffy J.E. (2002) Biodiversity and ecosystem function: the consumer connection. *Oikos*, **99**, 201–219.
- Duffy J.E. (2003) Biodiversity loss, trophic skew, and ecosystem functioning. *Ecology Letters*, **6**, 680–687.
- Evans-White M.A., Dodds W.K. & Whiles M.R. (2003) Ecosystem significance of crayfishes and stonerollers in a prairie stream: functional differences between co-occurring omnivores. *Journal of the North American Benthological Society*, **22**, 423–441.
- Feminella J.W. & Resh V.H. (1991) Herbivorous caddisflies, macroalgae, and epilithic microalgae: dynamic interactions in a stream grazing system. *Oecologia*, **87**, 247–256.
- Flecker A.S., Feifarek B.P. & Taylor B.W. (1999) Ecosystem engineering by a tropical tadpole: density-dependent effects on habitat structure and larval growth rates. *Copeia*, **2**, 495–500.
- Global Amphibian Assessment (2006) IUCN, Conservation International and NatureServe. www.globalamphibians.org, version 1.1
- Gosner K.L. (1960) A simplified table for staging anuran embryos and larvae with notes on identification. *Herpetologica*, **16**, 183–190.
- Hairston N.G. & Hairston N.G. (1993) Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. *The American Naturalist*, **142**, 379–411.

- Heyer W.R., Donnelly M.A., McDiarmid R.W., Hayek L.C. & Foster M.S. (1994) *Measuring and Monitoring Biological Diversity. Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, DC.
- Hurny A.D. & Wallace J.B. (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.
- Jackson J.K. & Fisher S.G. (1986) Secondary production, emergence, and export of aquatic insects of a Sonoran desert stream. *Ecology*, **67**, 629–638.
- Johnson K.H., Vogt K.A., Clark H.J., Schmitz O.J. & Vogt D.J. (1996) Biodiversity and the productivity and stability of ecosystems. *Trends in Ecology and Evolution*, **11**, 372–377.
- Jonsson M. & Malmqvist B. (2003) Importance of species identity and number for process rates within different stream invertebrate functional feeding groups. *Journal of Animal Ecology*, **72**, 453–459.
- Kitchell J.F., O'Neil R.V., Webb D., Gallepp G.W., Bartell S.M., Koonce J.F. & Ausmus B.S. (1979) Consumer regulation of nutrient cycling. *BioScience*, **29**, 28–34.
- Kohler S.L. & Wiley M.J. (1997) Pathogen outbreaks reveal large-scale effects of competition in stream communities. *Ecology*, **78**, 2164–2176.
- Lannoo M. (2005) *Amphibian Declines: The Conservation Status of United States Species*. University of California Press, Berkeley.
- Laurance W.F. (2007) Have we overstated the tropical biodiversity crisis? *Trends in Ecology and Evolution*, **22**, 65–70.
- Lips K.R., Reeve J.D. & Witters L.R. (2003) Ecological traits predicting amphibian population declines in Central America. *Conservation Biology*, **17**, 1078–1088.
- Lips K.R., Brem F., Brenes R., Reeve J.D., Alford R.A., Voyles J., Carey C., Livo L., Pessier A.P. & Collins J.P. (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.
- Loreau M., Naeem S., Inchausti P. *et al.* (2001) Ecology – Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, **294**, 804–808.
- Malmqvist B. & Rundle S. (2002) Threats to the running water ecosystems of the world. *Environmental conservation*, **29**, 134–153.
- McAuliffe J.R. (1984) Resource depression by a stream herbivore: effects on distribution and abundances of other grazers. *Oikos*, **42**, 327–333.
- McCann K.S. (2000) The diversity-stability debate. *Nature*, **405**, 228–233.
- Merritt R.W., Cummins K.W. & Berg M.B. (2008) *An Introduction to the Aquatic of North America*. Kendall/Hunt Publishing, Dubuque.
- Minchin P.R. (2005) *Database for Ecological Community Data (DECODA), Version 3.00 b38*. Southern Illinois University, Edwardsville.
- Naeem S. (2002) Ecosystem consequences of biodiversity loss: the evolution of a paradigm. *Ecology*, **83**, 1537–1552.
- Petchey O.L., Downing A.L., Mittelbach G.G., Persson L., Steiner C.F., Warren P.H. & Woodward G. (2004) Species loss and the structure and functioning of multitrophic aquatic systems. *Oikos*, **104**, 467–478.
- Ranvestel A.W., Lips K.R., Pringle C.M., Whiles M.R. & Bixby R.J. (2004) Neotropical tadpoles influence stream benthos: evidence for the ecological consequences of decline in amphibian populations. *Freshwater Biology*, **49**, 274–285.
- Regester K.J., Lips K.R. & Whiles M.R. (2006) Energy flow and subsidies associated with the complex life cycle of ambystomatid salamanders in ponds and adjacent forest in southern Illinois. *Oecologia*, **147**, 303–314.
- Sala O.E., Chapin F.S. III, Armesto J.J. *et al.* (2000) Global biodiversity scenarios of the year 2100. *Science*, **287**, 1770–1774.
- Solomon C.T., Flecker A.S. & Taylor B.W. (2004) Testing the role of sediment mediated interactions between tadpoles and armored catfish in a neotropical stream. *Copeia*, **3**, 610–616.
- Stuart S.N., Chanson J.S., Cox N.A., Young B.E., Rodrigues A.S.L., Fischman D.L. & Waller R.W. (2004) Status and trends of amphibian declines and extinctions worldwide. *Science*, **306**, 1783–1786.
- Taylor B.W., Flecker A.S. & Hall R.O. (2006) Loss of a harvested fish species disrupts carbon flow in a diverse tropical river. *Science*, **313**, 833–836.
- Verburg P., Kilham S.S., Pringle C.M., Lips K.R. & Drake D.L. (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.
- Whiles M.R., Lips K.R., Pringle C.M. *et al.* (2006) The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems. *Frontiers in Ecology*, **4**, 27–34.
- Worm B. & Duffy J.E. (2003) Biodiversity, productivity and stability in real food webs. *Trends in Ecology and Evolution*, **18**, 628–632.

(Manuscript accepted 8 May 2010)

This document is a scanned copy of a printed document. No warranty is given about the accuracy of the copy. Users should refer to the original published version of the material.