The effects of amphibian population declines on the structure and function of Neotropical stream ecosystems

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Amphibians can be important consumers in both aquatic and terrestrial habitats and may represent an important energetic link between the two, particularly in the tropics, where amphibian species richness and abundance are high. In the past 20 years, amphibian populations have declined dramatically around the world; numbers have decreased catastrophically in protected upland sites throughout the neotropics, usually resulting in the disappearance of over 75% of amphibians at a given site, particularly those species that breed in streams. Most studies of amphibian declines have focused on identifying causes and documenting changes in adult abundance, rather than on their ecological consequences. Here, we review evidence for the potential ecological effects of catastrophic amphibian declines, focusing on neotropical highland streams, where impacts will likely be greatest. Evidence to date suggests that amphibian declines will have large-scale and lasting ecosystem-level effects, including changes in algal community structure and primary production, altered organic matter dynamics, changes in other consumers such as aquatic insects and riparian predators, and reduced energy transfers between streams and riparian habitats. Furthermore, because of habitat and functional differences between larvae and adults in most amphibians, the loss of a single species is akin to losing two species.

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Although generally unseen, amphibians can comprise a surprisingly large proportion of the vertebrate abundance and biomass in some temperate wetland and forest systems (eg Burton and Likens 1975b; Stewart and Woolbright 1996), and they are the most abundant land vertebrates in parts of the humid tropics (Stebbins and Cohen 1995). In addition, amphibians may contribute considerably to energy flow because, as ectotherms, ingested energy is efficiently converted to biomass, which then becomes available to higher trophic levels (Pough 1980). Many amphibians also have complex life cycles in which different developmental stages occupy different habitats, usually aquatic and terrestrial, and feed on different food resources. Unfortunately, we are just beginning to understand the ecological significance of amphibians as their populations shrink and they disappear from many regions of the world.

In a nutshell:

- Amphibians probably play a number of important roles in ecosystems, but few studies have quantified their contributions
- Globally, amphibian populations are declining precipitously and species are disappearing without recovery, particularly in remote, montane regions of the tropics
- Most research to date has focused on documenting declines and identifying causes, but we know little about the ecological consequences of these losses
- Ongoing research in Central America, where declines are occurring, suggests that losses of stream-breeding frogs will have wide-ranging consequences for stream ecosystems

The aquatic larval stages of most amphibians feed on algae, detritus, or other animals, depending on species. Tadpoles, many of which are primary consumers, have been shown to influence ecosystem structure and function by altering algal communities, patterns of primary production, and organic matter dynamics in a variety of freshwater habitats (eg Kupferberg 1997; Flecker *et al.* 1999). Insectivorous adults can influence prey communities and related processes in terrestrial habitats (Stewart and Woolbright 1996; Beard *et al.* 2002, 2003). The handful of manipulative field studies to date show that primary production, nutrient cycling, leaf litter decomposition, and invertebrate populations change when tadpoles (Flecker *et al.* 1999; Kiffney and Richardson 2001; Ranvestal *et al.* 2004), frogs (Beard *et al.* 2002), and salamanders (Davic and Welsh 2004) are removed or reduced in numbers. Several investigations suggest that amphibians may be keystone species in some habitats, because they have disproportionately large impacts on ecosystem structure (Holomuzki *et al.* 1994; Wissinger *et al.* 1999).

While few studies have documented the influence of

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amphibians on various components of ecosystems, even fewer have quantified energy flow through amphibian populations (eg amphibian production). In one of the few studies to address this, Burton and Likens (1975a) showed that terrestrial salamanders were an important component of energy and nutrient cycling in a northeastern US forest. More recently, leaf-litter frogs (*Eleutherodactylus coqui*) in Puerto Rico were also shown to be important at the ecosystem level (Stewart and Woolbright 1996). Both of these studies suggest substantial energy flow through amphibians, but the species examined in both studies lacked aquatic stages. Consequently, knowledge of energy flow through amphibians with complex life cycles is lacking.

In addition to their roles in aquatic and terrestrial systems, some amphibians probably subsidize freshwater habitats when they deposit eggs and then transfer energy back to terrestrial habitats when metamorphs (the intermediate stage between larval and adult forms) emerge, but these energy transfers have only rarely been quantified (Davic and Welsh 2004). Some researchers have speculated that metamorphs leaving aquatic habitats might represent the more consequential energy transfer, but recent investigations of pond-breeding salamander assemblages show a consistent net flux of energy into aquatic habitats across a gradient of hydrological conditions and salamander communities (Regester *et al.* in press). These authors estimated an average net flux of 350 g AFDM (ash-free dry mass) yr^{-1} into small forest ponds in southern Illinois, USA and, overall, that the contribution of salamanders to energy flow in these systems, in terms of egg inputs and larval production, was substantial and equal to or higher than many published values for other aquatic groups, such as fish and macroinvertebrates. Adult amphibians can also represent important prey for a variety of terrestrial predators. For example, many snake species are specialists on one or more amphibian life stages, and frog-eating snakes have declined in abundance following amphibian declines (Jennings *et al.* 1992).

The ecological roles of amphibians in temperate regions are probably strongly influenced by pronounced seasonality in breeding and metamorphosis (ie "pulses"). In tropical regions, however, the roles of amphibians in both aquatic and terrestrial habitats are more consistent through time because of their more stable seasonal abundance patterns, high species richness, and diversity of reproductive modes (Crump 1974). Anurans are the dominant group in terms of numbers and diversity in most of the tropics, while salamanders and caecilians are only occasionally abundant. Studies in the neotropics have recorded levels of species richness ranging from 74 species at a mid-elevation site in Panama (Lips *et al.* unpublished) to 81 at a lowland site in Ecuador (Crump 1974). Densities of terrestrial litter frogs may range from 5000–25 000 ha^{-1} (Scott 1976; Stewart and Woolbright 1996). In the tropics, most terrestrial and aquatic habitats are occupied by adult amphibians, while larval stages may be found in most aquatic and even some terrestrial habitats (Altig and Johnston 1989; McDiarmid and Altig 1999). Tropical tadpoles are particularly abundant in ponds and streams (Inger *et al.* 1986; Ranvestal *et al.* 2004). Thus, the ecological roles of neotropical amphibians are evident year-round and operate across many habitats.

History and causes

Stuart *et al.* (2004), reporting on the status of amphibian species around the globe, found that 43% of these species are experiencing some form of population decrease, 32.5% are globally threatened, and 122 species are possibly extinct. Most of those losses are recent, having occurred since 1980. The authors also found that the geographic distribution of rapidly declining species was nonrandom, with neotropical species being the most affected.

Amphibian population declines have been attributed to many factors, including UVB radiation, exotic predators, chemical contaminants, habitat loss, and overexploitation, as well as various combinations of these factors (Wake 1991; Blaustein and Kiesecker 2002). Some declines have also been considered enigmatic, possibly linked to disease or climate change. In particular, a virulent chytrid fungal pathogen of amphibians, *Batrachochytrium dendrobatidis*, has been found at several sites where declines have occurred (Berger *et al.* 1998; Burrowes *et al.* 2004). This fungus kills adult frogs, probably by disrupting homeostasis, and is considered an emerging infectious disease of amphibians (Daszak *et al.* 1999). In the laboratory, *B dendrobatidis* grows best under cool, humid conditions (Piotrowski *et al.* 2004), which might explain its greater impact on montane populations.

Actual die-offs associated with *B dendrobatidis* infections (chytridiomycosis) are rarely witnessed because many of the regions where they have occurred are remote and such declines happen fairly quickly. However, as many as 350 dead adult frogs were found over a 4-month period during a recent outbreak of chytridiomycosis at a site in the Panamanian uplands (Lips *et al.* in press). The dying frogs are generally found in and along streams in a moribund state. Signs of distress include skin sloughing and unnatural postures in adults (Figure 1), and deterioration of mouthparts in tadpoles, which do not appear to succumb until after metamorphosis.

Climate change has also been implicated in declines of some neotropical amphibians (Pounds *et al.* 1999; Burrowes *et al.* 2004). Temperature and moisture influence amphibian ecology, physiology, and behavior because amphibians must maintain moist skin for oxygen and ionic exchange and temperature influences metabolic rates. As a result, scientists have focused on the effects of environmental factors in population declines (Pounds *et al.* 1999; Alexander and Eischeid 2001). While direct links between individual mortality, population declines, and climate change are lacking, interactions between climate change and other agents are likely (Carey and Alexander 2003).

Regardless of the cause, massive declines in amphibian abundance and species richness are occurring in many regions, and recovery of amphibian communities has not been documented for any site, even 15 years post decline. While much effort is directed at documenting declines and identifying causes, we still know very little about the ultimate ecological consequences of these losses (Houlahan *et al.* 2000; Stuart *et al.* 2004), although evidence of tangible effects is mounting.

■ Ecological consequences

Unlike temperate amphibians, a great diversity of neotropical anurans breed or develop in flowing waters. The stream-dwelling tadpoles of these species are primarily grazers and detritivores, but their ecological roles are poorly studied (McDiarmid and Altig 1999). The Tropical Amphibian Declines in Streams (TADS) Project is comparing pre-decline (El Copé) and post-decline (Fortuna) stream sites in the Panamanian highlands, with the goal of quantifying the consequences of the loss of these consumers to stream and riparian ecosystem structure and function. Fortuna experienced catastrophic declines in amphibian species richness and abundance associated with *B dendrobatidis* in 1996 (Lips 1999) and El Copé is directly in the path of the front of declines moving eastward (Lips *et al.* 2003; Figure 2). Both study sites naturally had 30–40 species of riparian anurans, about 20 of which include stream-dwelling tadpole stages; both adults and larvae play different and potentially significant roles in their respective habitats.

Figure 1. *An adult* Eleutherodactylus bufoniformis *dying near an upland stream in Panama. Note the sloughing skin and unnatural posture, which are typical of frogs afflicted with chytridiomycosis.*

Larval stages

Tadpoles in upland Panamanian streams are diverse in morphology, microhabitat, diet, and larval period; these include golden frogs (*Atelopus zeteki*) that graze periphyton on rocks in riffle habitats (Figure 3), ranids (eg *Rana warszewitschii*) and treefrogs (*Hyla* spp) that graze periphyton and fine particulate organic matter from substrates in runs and pools, and glassfrogs (Family Centrolenidae) that feed on fine organic particles while buried in detritus accumulations in pools. Current investigations from the TADS project indicate that densities of these tadpoles range from ~60 *A zeteki* individuals m^{-2} in riffles to ~15 centrolenid individuals m^{-2} in pool sediments during the dry season, when densities peak. Comparison of tadpole communities between decline and healthy sites showed that 8 years post-decline, average habitat-weighted tadpole density in Fortuna streams was 0.0026 m^{-2}. In contrast, El Copé streams had an annual average of 6.16 m^{-2} in 2004, with peak values in the dry season that year of ~30 m^{-2} (Figure 3). Tadpole densities were once as high as 50 m^{-2} at Fortuna (Lips 1999).

Using electric fence excluders (Pringle and Hamazaki 1997) to regulate tadpole access to experimental tiles in El Copé streams showed that tadpoles significantly reduced organic and inorganic particles and algal diatom biovolume (Ranvestal *et al.* 2004; Figure 4). Diatom biovolume was reduced from 60.51 ± 0.29 mm^3 m^{-2} (mean ± 1 standard error) with no tadpole grazing to 23.92 ± 0.19 mm^3 m^{-2} with tadpole grazing (two-way ANOVA, $F_{1,4} = 9.1$, $P = 0.040$; Ranvestal *et al.* 2004). Tadpole grazing also shifted diatom community structure. In tadpole exclusions, the community was composed of both larger upright diatoms and low-growing diatoms; however, on tiles accessible to the tadpoles, the community was composed primarily of smaller, low-growing diatom taxa.

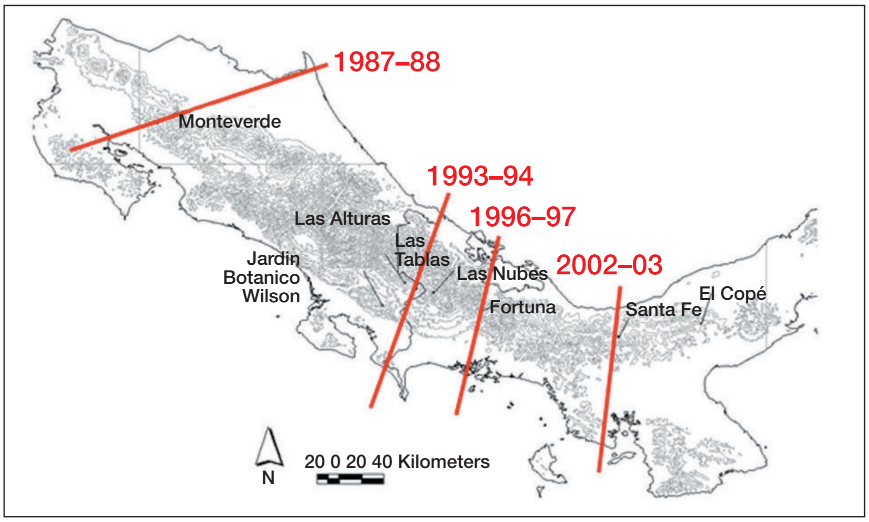

Figure 2. *Map of Costa Rica and Panama indicating sites where recently documented catastrophic declines related to chytridiomycosis have occurred, as well as dates of declines. The TADS (Tropical Amphibian Declines in Streams) project field sites were established at Fortuna (post-decline) and El Copé (pre-decline).*

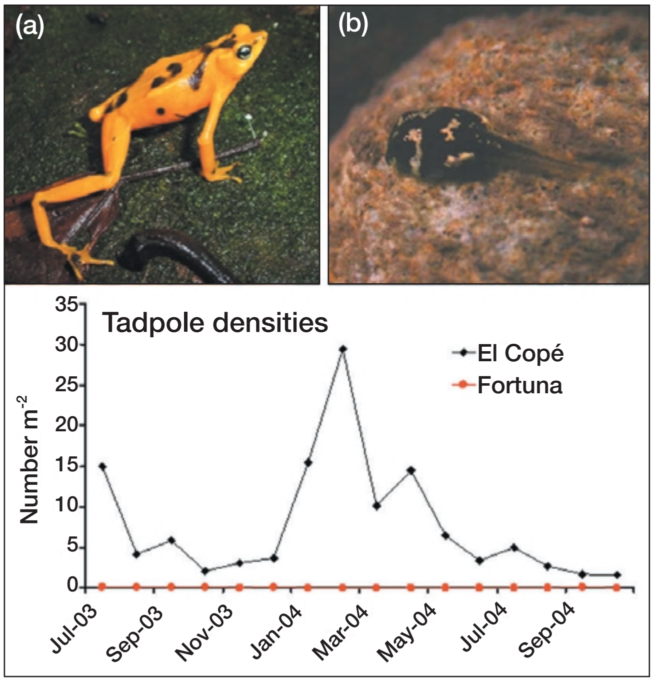

Figure 3. Atelopus zeteki *(a) adult and (b) a tadpole grazing substrates in a Panamanian highland stream with a plot comparing habitat-weighted tadpole densities at El Copé, where declines have not occurred, and Fortuna, where massive declines occurred in the late 1990s. Note that tadpole densities in these same Fortuna streams were up to 50 m*$^{-2}$ *prior to declines (Lips 1999). Note also the seasonal pattern of highest densities during the January–March dry season months.* A zeteki *is a particularly vulnerable stream-dwelling species; tadpoles are found in swift currents and have specialized mouthparts for clinging to substrates.*

Additionally, diatom diversity was approximately 30% higher on tiles without tadpole access compared to tiles with tadpole grazing. These results substantiate patterns reported for other neotropical tadpoles (Flecker *et al.* 1999), as well as other grazers in streams, including fish (Pringle and Hamazaki 1997) and invertebrates (Rosemond *et al.* 1993). Our most recent studies indicate that while grazing tadpoles reduce the standing crop of primary producers, they serve to increase primary production (on a per algal biomass basis). Our continued algal monitoring program in these streams will allow for future comparisons of the primary producer community pre- and post- amphibian decline.

Gut analyses of tadpoles collected from El Copé streams revealed that they fed on organic sediments and periphyton, and experimental results also indicated that physical disturbance associated with their feeding activities influenced sediment dynamics. Bioturbation associated with the foraging activity of various grazers alters sediment dynamics and algal communities, such that snails (Harvey and Hill 1991), tadpoles (Kiffney and Richardson 2001), and fish (Flecker 1992) have all been referred to as "bulldozers" of the benthic world. Indeed, tadpoles observed feeding on tiles and natural substrates during our experiments at El Copé left obvious feeding trails in the sediments (Ranvestal *et al.* 2004; Figure 4). In addition to direct consumption of organic sediments, bioturbation by tadpoles is a mechanism for resuspension of sediments in streams. Tadpoles can therefore represent a link between deposited and entrained particulates.

Along with altering sediment and periphyton dynamics, manipulative experiments at El Copé indicated that tadpoles influence other grazers, particularly mayflies. During tadpole exclusion experiments, mayflies of the family Baetidae were four times more abundant on grazed tiles compared to exclusions, indicating tadpoles were facilitating these invertebrate grazers (Ranvestal *et al.* 2004). This was probably related to tadpoles removing overlying sediments through feeding and bioturbation, exposing algal resources for mayflies to graze. This positive response of mayflies to the activities of larger grazers has also been observed in Puerto Rican streams, where atyid shrimp have been observed to facilitate the exploitation of algal resources by Baetid mayflies (Pringle *et al.* 1993; March *et al.* 2002). However, these findings are in contrast to some other studies that have shown antagonistic interactions between large and small-bodied grazers (eg McAuliffe 1984; Flecker 1992).

The organic seston (fine particulate matter) exported from El Copé streams, where tadpoles are still abundant, is consistently higher in percent nitrogen than that from Fortuna streams, where tadpoles have disappeared (Figure 5). We hypothesize that this reflects increased feces, periphyton, and organic sediments in the water column, associated with tadpole feeding activities. Recent estimates from the TADS project indicate that individual tadpoles

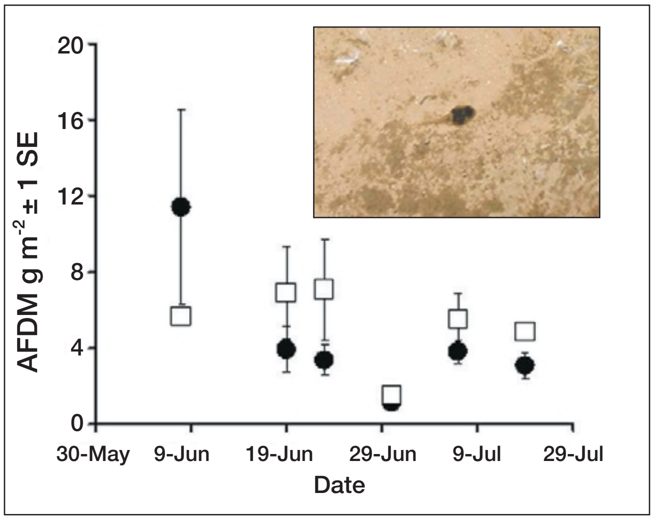

Figure 4. *An experimental tile in a Panamanian highland stream with a* Rana warszewitschii *tadpole grazing the surface, and a plot of total organic material (ash-free dry mass = AFDM) through time on tadpole grazed (black circles) and ungrazed (squares) tiles during a 52-day experiment that commenced on 24 May 2001. Differences between grazed and exclusion tiles are significant (repeated measures ANOVA:* $F_{1,8} = 10.3$, $P = 0.013$). *Low values on July 1 were the result of a scouring flood. Data are from Ranvestal* et al. *(2004).*

ranging in size from 30–50 mm egest an average of 0.34 ± 0.04 mg hr^{-1} (mean ± 1 standard error) of organic material (AFDM) and 1.5 ± 0.1 mg hr^{-1} of inorganic material. Based on dry season 2004 tadpole densities, this equates to 10 mg m^{-2} hr^{1} AFDM and 43 mg m^{-2} hr^{-1} ash, not including particles resuspended through bioturbation but not ingested. If, as these various lines of evidence suggest, tadpoles are influencing the quantity and quality of suspended particles, this has implications for downstream communities, as seston exported from headwaters represents an important source of energy for downstream reaches (eg Vannote *et al.* 1980).

In addition to particulate dynamics, tadpoles may also influence dissolved nutrients in neotropical streams, particularly in the dry season when densities are high and flow is relatively low. Ammonium excretion rates for individual tadpoles from El Copé streams range from 0.15 µg hr^{-1} for small (8–16 mm total length) individuals to 3.6 µg hr^{-1} for large (46–60 mm) tadpoles. Based on densities measured during the 2004 dry season, and dry season estimates of ammonium uptake, tadpole excretion represents ~7% of bulk uptake for these systems.

Although much of the evidence is still circumstantial, stable isotope analyses from El Copé and Fortuna streams further demonstrate the importance of amphibians in these systems. Stable isotopes are useful tools for elucidating food webs because fractionation of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotopes provide information about trophic transfers. For many aquatic systems, fractionation per trophic step is about 1‰ $\delta^{13}C$ and 3.4‰ $\delta^{15}N$ (Vander Zanden and Rasmussen 2001). However, Kilham and Pringle (2000) and our current studies show trophic fractionation is only about 2 ‰ $\delta^{15}N$ in tropical upland streams. Figure 6 illustrates the positions of the major consumers in the food web in El Copé streams and riparian habitats, and the expected generalized trend of increasing $\delta^{13}C$ and $\delta^{15}N$ (Figure 6a). The $\delta^{13}C$ increases by approximately 4‰ between the basal and first trophic levels, rather than by 1‰ per trophic step as has been previously documented.

Coarse particulate organic materials, periphyton, and seston appear to be the dominant organic matter sources assimilated by primary consumers in this system. Tadpoles are, on average, in the same trophic level as most stream insects. The difference in $\delta^{13}C$ of the tadpoles and adult anurans indicate differences in the source of their diets; tadpoles reflect the aquatic signal while the adults reflect a terrestrial signal. There is also significant variation in the $\delta^{15}N$ among tadpole species (Figure 6d). For example, glassfrog (Centrolenidae) tadpoles, which are usually buried in organic deposits, have $\delta^{15}N$ values lower than that of the fine benthic organic matter they live in, indicating that they are probably assimilating bacteria. The $\delta^{15}N$ values also indicate that rocket frog (*Colostethus* spp) tadpoles may be more omnivorous than *Hyla* spp and *R warszewitschii* tadpoles.

Comparisons between El Copé and Fortuna show consistently higher $\delta^{15}N$ values in organic matter resources such as FBOM in El Copé stream pools, suggesting greater internal recycling of N in streams with tadpoles. Isotope analyses of all food web components in these same systems also show a higher degree of change from basal resources to predators in streams with tadpoles (El Copé = 4.9‰) compared to those without (Fortuna = 3.5‰), suggesting that the food web is truncated in streams without tadpoles.

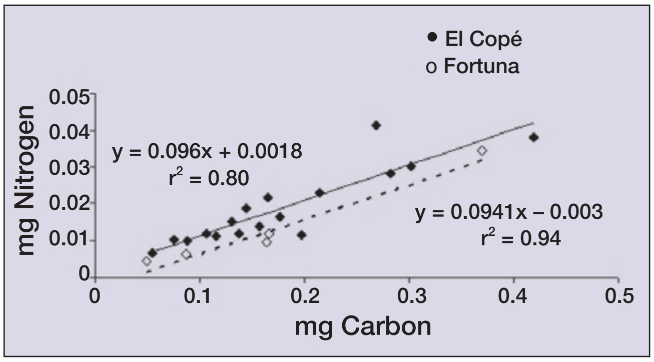

Figure 5. *Relationship between nitrogen and carbon content in fine seston from two streams with tadpoles (El Copé) and two without (Fortuna). Values are mg N and C in fine seston samples (98–754 µm) collected from streams during baseflow or near baseflow conditions. Slopes for the sites are similar (ANCOVA* $_{F1,19}$ *= 0.01, P=0.93) but the amount of nitrogen per unit carbon differs significantly between the sites (ANCOVA* $_{F1,20}$ *= 53.2, P = 0.02).*

Terrestrial stages

Adult anurans may be more conspicuous than their larvae, but we know comparatively little about their ecological importance in the tropics. For example, *A zeteki*, a large and brightly colored anuran that is common in El Copé streams, has small and cryptically colored larvae (Figure 3). It may be surprising that we know relatively little about the ecological significance of the adults of *A zeteki* compared to their larvae, which have been documented to be important grazers in this system (Ranvestal *et al.* 2004). Potentially significant roles of adult anurans include contributing energy in the form of egg masses to streams, controlling or otherwise influencing riparian insect prey, and serving as prey themselves.

Ten species of anurans breed throughout the year at El Copé and as many as 20 species deposit egg masses in or near streams during the rainy season. Inputs from leaf-breeding species such as glassfrogs are especially abundant and easy to quantify; we have found as many as 0.64 egg masses m^{-2} of stream transect during a 3-month period of the breeding season (Figure 7). Upon hatching, these egg masses subsidize benthic food webs. A reciprocal export occurs in the form of juvenile biomass that emerges from the stream at metamorphosis. Quantifying amphibian metamorph emergence and abundance has always been problematic, but especially so for the variety of species found in the complex riparian environments of the Panamanian uplands. Ongoing research as part of the TADS Project is generating estimates of tadpole biomass and secondary production in these streams that can then

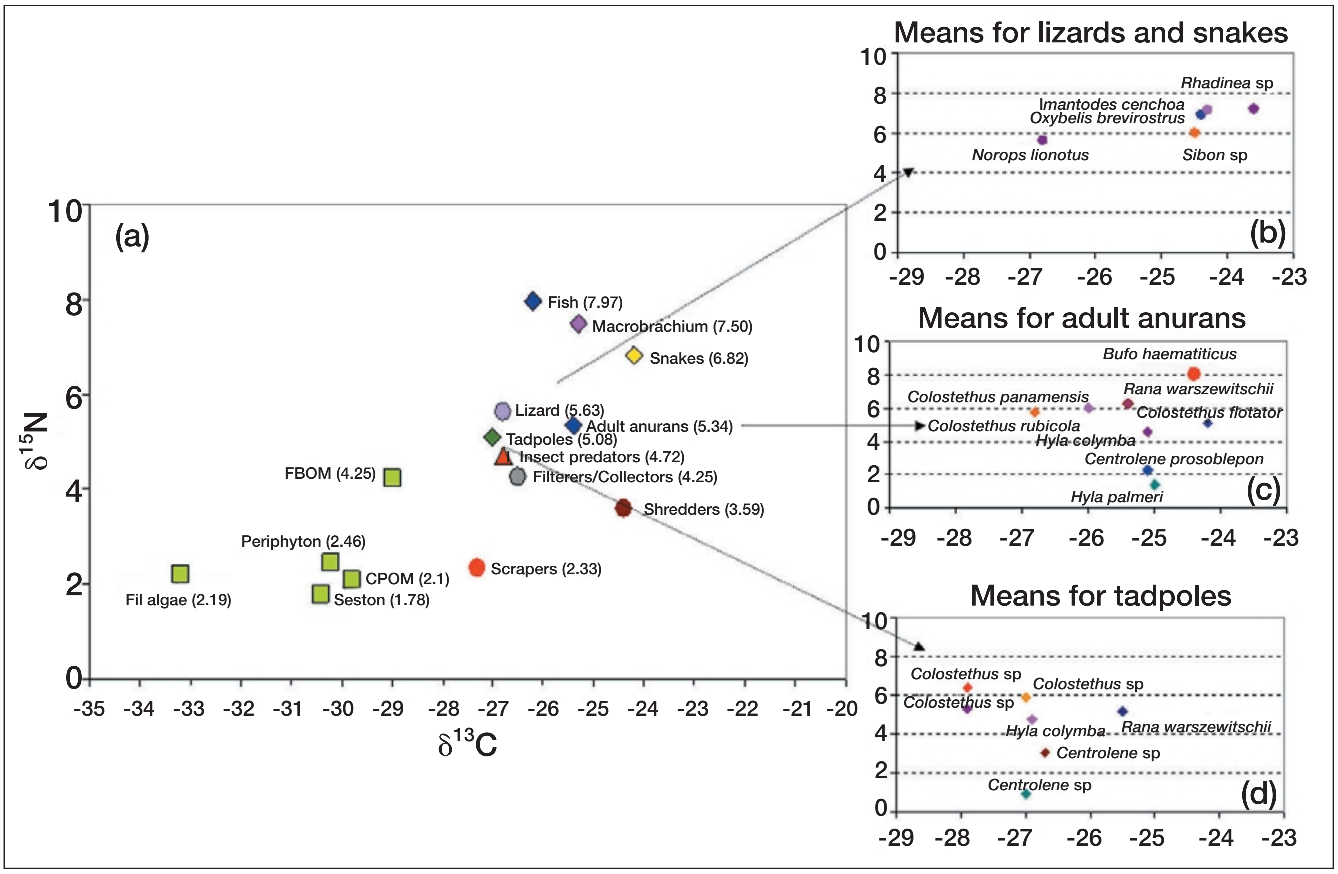

Figure 6. *Stable isotopes of nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) in the food web of a stream at El Copé, Panama, based on samples collected during May through August, 2000; (a) mean values of basal resources and consumers; (b) mean values for riparian snakes and lizards; (c) mean values for adult anurans; and (d) mean values for tadpoles. Each value in panels b, c, and d is the mean of three replicate samples. For basal resources, FBOM = fine benthic organic material, CPOM = coarse particulate organic material, and seston = suspended particles. For consumers, scrapers = invertebrates that feed by scraping materials from substrates (eg many mayflies), shredders = invertebrates that shred coarse organic materials such as leaf litter (eg many caddisflies), and filterers/collectors = invertebrates that feed on seston and/or FBOM (eg most midges and net-spinning caddisflies).*

be used to estimate metamorph emergence biomass.

Stable isotope analyses of adult anurans at El Copé show a wide range in $\delta^{15}N$ signals, and thus diets (Figure 6c). There appears to be systematic variation in diet, even between species within the same genera. For example, the $\delta^{15}N$ signals are very similar among species of *Colostethus*, indicating that they are feeding at the same level within the riparian food web. However, variation in the $\delta^{13}C$ signal among species indicates that sources of prey insects vary. For example, *Colostethus flotator* has a $\delta^{13}C$ signal that is closer to terrestrial compared with the $\delta^{13}C$ signal of the other *Colostethus* species, suggesting it may be feeding further away from the riparian zone. The leaf litter toad (*Bufo haematiticus*) is feeding higher on a trophic scale than other anurans in this system.

There are a number of abundant riparian snake species that specialize on frogs and their eggs at El Copé (Figure 8). Stable isotope analyses from El Copé show expected patterns; riparian snakes such as snail-eating snakes (*Sibon* spp), blunt-headed tree snakes (*Imantodes cenchoa*), yellow-lipped snakes (*Rhadinea vermiculaticeps*), and vine snakes (*Oxybelis brevirostrus*) all have $\delta^{13}C$ and $\delta^{15}N$ signatures that are consistent with feeding on adult frogs (Figure 6b).

Obviously, at Fortuna and other sites where declines have already occurred, any energy exchanges associated with metamorphs and adults have been eliminated. Historically, adult amphibian species richness and density were similar between Fortuna and El Copé, with at least 54 amphibian species present at both sites and adult densities as high as 0.2 individuals m^{-2} of riparian habitat. Following extensive declines, adult densities at Fortuna are now an order of magnitude lower and species richness is < 50% that of healthy sites (Lips 1999).

■ What does the future hold?

Over the past 15 years, amphibian faunas have sequentially declined from upland sites in Costa Rica and Panama in a pronounced NW to SE direction (Lips *et al.* 2003; Figure 2). Our choice of El Copé as a healthy site for the TADS Project was based on the prediction that this front of declines would continue to move eastward and would eventually affect this site. Unfortunately for the frogs, our predictions were correct; adult amphibians recently began to die in large numbers at El Copé. As a result, adult and larval populations have already crashed to < 50% of previous levels, egg masses are reduced by 50%, and already a few species of frog-eating riparian snakes are no longer seen during routine surveys. Based on mounting evidence for the importance of amphibians in these systems, we expect measurable changes in stream and riparian ecosystem structure and function over the next several years. Monitoring ecosystem components and processes at El Copé before and after this catastrophic event provides us with a rare, if disturbing opportunity to quantify the ecological consequences of a sudden and dramatic loss of an entire group of consumers. Furthermore, given the differences in the habitat and ecological roles of larvae and adults, the loss of each anuran species is akin to the loss of two species.

Data from the TADS project and other studies on the ecological roles of amphibians indicate that, along with the inherent tragedy of these losses, amphibian declines will likely result in measurable changes to aquatic and riparian ecosystems in regions where they are, or were, abundant. In streams and other freshwater habitats, important grazers and detritivores are being lost, with probable impacts on algal community structure and primary production, sediment dynamics and seston quality, and populations of other grazers. In riparian habitats, once abundant consumers of invertebrates, and food for snakes and other predators, are disappearing. Finally, energy and nutrient subsidies associated with the complex life cycles of many amphibians are becoming diminished. How all of these changes will ultimately alter ecosystem structure and function remains to be seen.

In order to understand the "big picture" significance of these losses and put them in context, there is a need for more quantitative information on the ecological roles of amphibians. Surprisingly, there is also still a need for even basic information such as life cycle length, diet, microhabitat use, assimilation and production efficiencies, and digestive physiology for many species, particularly those that live in the tropics; this need is becoming more urgent as species disappear. Beyond this basic information, there is still much to be learned about how amphibians contribute to energy flow and nutrient cycling in freshwater and terrestrial habitats. As an example, we know of only a handful of published production estimates for amphibian populations, yet production estimates are one of the best ways to link consumers to ecosystem processes (Benke 1993). More detailed or long-term studies of amphibians in food webs using stable isotopes and/or fatty acids profiles could also provide additional insight into the trophic status and food web interactions of adult and larval amphibians. Finally, monitoring of sites after declines, such as the current TADS project efforts at El Copé, should have a long-term component after population crashes, to detect potentially subtle and delayed responses, as ecosystem responses to changes can sometimes be slow (eg Slavik *et al.* 2004; Hooper *et al.* 2005).

Figure 7. *Developing embryos in an egg mass of a centrolenid frog overhanging a stream in the Panamanian uplands. Egg masses are present year-round along streams and during the peak breeding season occur at densities of ~0.6 masses per linear meter of stream.*

Acknowledgments

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Figure 8. *A young eyelash pit viper (*Bothriechis schlegelii*) eating an adult golden-groined rain frog (*Eleutherodactylus cruentus*).*

References

Alexander MA and Eischeid JK. 2001. Climate variability in regions of amphibian declines. *Conserv Biol* **15**: 930–42.

Altig RA and Johnston GF. 1989. Guilds of anuran larvae: relationships among developmental modes, morphologies, and habitats. *Herpetol Monogr* **3**: 81–109.

Beard KH, Eschtruth AK, Vogt KA, *et al.* 2003. The effects of the frog *Eleutherodactylus coqui* on invertebrates and ecosystem processes at two scales in the Luquillo Experimental Forest, Puerto Rico. *J Trop Ecol* **19**: 607–17.

Beard KH, Vogt KA, and Kulmatiski A. 2002. Top-down effects of a terrestrial frog on forest nutrient dynamics. *Oecologia* **133**: 583–93.

Benke AC. 1993. Concepts and patterns of invertebrate production in running waters. *Verh Int Vereinigung Limnol* **25**: 15–38.

Berger L, Speare R, Daszak P, *et al.* 1998. Chytridiomycosis causes amphibian mortality associated with population declines in the rain forests of Australia and Central America. *P Natl Acad Sci–Biol* **95**: 9031–36.

Blaustein AR and Kiesecker JM. 2002. Complexity in conservation: lessons from the global decline of amphibian populations. *Ecol Lett* **5**: 597–608.

Burrowes PA, Joglar RL, and Green DE. 2004. Potential causes for amphibian declines in Puerto Rico. *Herpetologica* **60**: 141–54.

Burton TM and Likens GE. 1975a. Energy flow and nutrient cycling in salamander populations in the Hubbard Brook Experimental Forest, New Hampshire. *Ecology* **56**: 1068–80.

Burton TM and Likens GE. 1975b. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. *Copeia* **1975**: 541–46.

Carey C and Alexander MA. 2003. Climate change and amphibian declines: is there a link? *Divers Distrib* **9**: 111–21.

Crump ML. 1974. Reproductive strategies in a tropical anuran community. *Univ Kans Mus Nat Hist Misc Publ* **61**: 1–68.

Daszak P, Berger L, Cunningham AA, *et al.* 1999. Emerging infectious diseases and amphibian population declines. *Emerg Infect Dis* **5**: 735–48.

Davic RD and Welsh HH. 2004. On the ecological roles of salamanders. *Annu Rev Ecol Syst* **35**: 405–34.

Flecker AS. 1992. Fish trophic guilds and the structure of a tropical stream: weak vs strong indirect effects. *Ecology* **73**: 927–40.

Flecker AS, Feifarek BP, and Taylor BW. 1999. Ecosystem engineering by a tropical tadpole: density-dependent effects on habitat structure and larval growth rates. *Copeia* **1999**: 495–500.

Harvey BC and Hill WR. 1991. Effects of snails and fish on benthic invertebrate assemblages in a headwater stream. *J N Am Benthol Soc* **10**: 263–70.

Holomuzki JR, Collins JP, and Brunkow PE. 1994. Trophic control of fishless ponds by tiger salamander larvae. *Oikos* **71**: 55–64.

Hooper DU, Chapin FS, Ewel JJ, *et al.* 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* **75**: 3–35.

Houlahan JE, Findlay CS, Schmidt BR, *et al.* 2000. Quantitative evidence for global amphibian population declines. *Nature* **404**: 752–55.

Inger RF, Voris HK, and Frogner KJ. 1986. Organization of a community of tadpoles in rain forest streams in Borneo. *J Trop Ecol* **2**: 193–205.

Jennings WB, Bradford DF, and Johnson DF. 1992. Dependence of the garter snake *Thamnophis elegans* on amphibians in the Sierra Nevada of California. *J Herpetol* **26**: 503–05.

Kiffney PM and Richardson JS. 2001. Interactions among nutrients, periphyton, and invertebrate and vertebrate (*Ascaphus truei*) grazers in experimental channels. *Copeia* **2001**: 422–29.

Kilham SS and Pringle CM. 2000. Food webs in two neotropical stream systems as revealed by stable isotope ratios. *Verh Int Vereinigung Limnol* **27**: 1768–75.

Kupferberg S. 1997. Facilitation of periphyton production by tadpole grazing: functional differences between species. *Freshwater Biol* **37**: 427–39.

Lips KR. 1999. Mass mortality and population declines of anurans at an upland site in western Panama. *Conserv Biol* **13**: 117–25.

Lips KR, Brem F, Brenes R, *et al.* Emerging infectious disease and the loss of biodiversity in a neotropical amphibian community. *P Natl Acad Sci Biol.* In press.

Lips KR, Reeve JD, and Witters LR. 2003. Ecological traits predicting amphibian population declines in Central America. *Conserv Biol* **17**: 1078–88.

March JG, Pringle CM, Townsend MJ, and Wilson AI. 2002. Effects of freshwater shrimp assemblages on benthic communities along an altitudinal gradient of a tropical island stream. *Freshwater Biol* **47**: 377–90.

McAuliffe JR. 1984. Resource depression by a stream herbivore: effects on distributions and abundances of other grazers. *Oikos* **42**: 327–33.

McDiarmid RW and Altig RA. 1999. Tadpoles: the biology of anuran larvae. Chicago, IL: University of Chicago Press.

Piotrowski JS, Annis SL, and Longcore JE. 2004. Physiology of *Batrachochytrium dendrobatidis*, a chytrid pathogen of amphibians. *Mycologia* **96**: 9–15.

Pough FH. 1980. The advantages of ectothermy for tetrapods. *Am Nat* **115**: 92–112.

Pounds JA, Fogden MPL, and Campbell JH. 1999. Biological response to climate change on a tropical mountain. *Nature* **398**: 611–15.

Pringle CM, Blake GA, Covich AP, *et al.* 1993. Effects of omnivorous shrimp in a montane tropical stream: sediment removal, disturbance of sessile invertebrates and enhancement of understory algal biomass. *Oecologia* **93**: 1–11.

Pringle CM and Hamazaki T. 1997. Effects of fishes on algal response to storms in a tropical stream. *Ecology* **78**: 2432–42.

Ranvestel AW, Lips KR, Pringle CM, *et al.* 2004. Neotropical tadpoles influence stream benthos: evidence for the ecological consequences of decline in amphibian populations. *Freshwater Biol* **49**: 274–85.

Regester KJ, Lips KR, and Whiles MR. Energy flow and subsidies associated with the complex life cycle of ambystomatid salamanders in ponds and adjacent forest in southern Illinois. *Oecologia*. In press.

Rosemond AD, Mulholland PJ, and Elwood JW. 1993. Top-down and bottom-up control of stream periphyton: effects of nutrients and herbivores. *Ecology* **74**: 1264–80.

Scott NJ. 1976. The abundance and diversity of the herpetofaunas of tropical forest litter. *Biotropica* **8**: 41–58.

Slavik K, Peterson BJ, Deegan LA, *et al.* 2004. Long-term responses of the Kuparuk River ecosystem to phosphorus fertilization. *Ecology* **85**: 939–54.

Stebbins RC and Cohen NW. 1995. A natural history of amphibians. Princeton, NJ: Princeton University Press.

Stewart MM and Woolbright LL. 1996. Amphibians. In: Reagan DP and Waide RP (Eds). The food web of a tropical rainforest. Chicago, IL: University of Chicago Press.

Stuart SN, Chanson JS, Cox NA, *et al.* 2004. Status and trends of amphibian declines and extinctions worldwide. *Science* **306**: 1783–86.

Vander Zanden MJ and Rasmussen JB. 2001. Variation in δ^{15}N and δ^{13}C trophic fractionation: implications for aquatic food web studies. *Limnol Oceanogr* **46**: 2061–66.

Vannote RL, Minshall GW, Cummins KW, *et al.* 1980. The river continuum concept. *Can J Fish Aquat Sci* **37**: 130–37.

Wake DB. 1991. Declining amphibian populations. *Science* **253**: 860.

Wissinger SA, Whiteman HH, Sparks GB, *et al.* 1999. Foraging tradeoffs along a predator-permanence gradient in subalpine wetlands. *Ecology* **80**: 2102–16.