

# Biotic and abiotic effects of flash flooding in a montane desert stream

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With 5 figures and 1 table

**Abstract:** Flash floods in desert streams can be more sudden, brief, and severe compared to floods in mesic streams. To determine their biotic and abiotic effects, substrate composition, organic detritus abundance, and aquatic animal taxonomic richness and abundance were measured 8–16 d before and 7 d after a flash flood in a 122 m reach of a montane desert stream (Chihuahuan Desert, USA). The flash flood severely altered channel morphology by scouring and depositing substrates, but it did not change the overall abundance of any substrate particle size class. The flood removed most coarse detritus from the stream reach, although the quantity of organic particles <2 mm was unchanged. High losses were observed in most animal taxa (95 % overall), and reach-wide taxonomic richness was reduced from 35 to 21 taxa. Ephemeroptera were entirely eliminated from the study reach. The taxon experiencing the lowest percent loss (the belostomatid hemipteran *Abedus herberti*, 14 % loss) is known to possess behavioral mechanisms for flash flood avoidance. Compared to studies of flooding in mesic streams, this study suggests that flash floods in montane desert streams cause greater mortality in animal populations and remove more detritus. Ecologically, these high local mortality rates stress the importance of recolonization mechanisms. Evolutionarily, flash floods provide a strong selection pressure that may influence the genetic structure of populations.

**Key words:** Disturbance, desert streams, flash floods, aquatic invertebrates.

## Introduction

Floods of almost any magnitude and duration affect biotic and abiotic features of streams to some degree, but flash floods in desert streams are defined by their sudden arrivals, short durations, and extensive physical and biological impacts (JOHN 1964, FISHER et al. 1982). These extremes are a consequence of

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the powerful convective thunderstorms that often generate flash floods in desert regions. Desert convective thunderstorms are notorious for their spatial heterogeneity, often saturating one drainage with heavy rainfall while leaving adjacent drainages dry (SELLERS & HILL 1974, FOGEL 1981). Because of this patchiness, individual flash floods are very unpredictable over short time spans (days to several years) but clear patterns of flood regime timing, frequency, and intensity are apparent over longer time spans (several years to centuries) (LYTLE, unpubl.).

Storms typically bring runoff-producing rainfall to small areas (20 to 100 km<sup>2</sup>; OSBORN & LANE 1972) over short time periods (typically <40 min.; FOGEL & DUCKSTEIN 1969, OSBORN & LAURSEN 1973). Rainfall sufficient to produce flash floods, rather than just runoff, occurs over smaller areas and shorter time spans (OSBORN & LANE 1972). The small areal extent of these storms coupled with their brevity accounts for the suddenness of flash floods. Furthermore, thunderstorms in distant upper reaches of a drainage may cause flooding in lower reaches that experience no rain. Flash floods usually dissipate rapidly because most rainfall from large convective thunderstorms results in surface runoff rather than absorption by soils or aquifer recharge (SCHREIBER & KINCAID 1967). Flash floods also carry large amounts of suspended particles. Large boulders, root masses, and sometimes entire trees, in addition to high sediment loads, are carried downstream with the initial pulse of water. Deeply-cut canyons often prevent floods from dissipating laterally into floodplains, which maintains the stream power needed to suspend large substrates (MEFFE 1984, MEFFE & MINCKLEY 1987). After narrowly escaping a flash flood in a canyon, EDWARD ABBEY (1995) observed:

“We couldn’t see anything yet but we could hear it – a freight train rolling full speed down North Wash... there was no rain where we were, and the ground was dry. But we could feel it tremble. From within the flood, under the rolling red waters, we heard the grating of rocks as they clashed on one another, a sound like the grinding of molars in leviathan jaws... we camped that evening while thousands of tons of semiliquid sand, silt, mud, rock, uprooted junipers, logs, a dead cow, rumbled by twenty feet away sometime during the night the flood dropped off and melted away... almost as abruptly as it had come.”

Not surprisingly, these “grinding molars” cause substantial mortality in populations of aquatic organisms. In certain taxa, high mortality rates may have driven the evolution of behavioral, morphological, and life history adaptations. GRIMM & FISHER (1989) suggested that some stream organisms possess traits that impart flood resistance (the ability of individuals to withstand the physical force of floods) or resilience (the ability of populations to recover following floods). Some taxa are able to escape floods either behaviorally or via life history strategies (e.g., LYTLE 1999), which can be interpreted as a form of resistance to floods.

The suddenness of flash floods contributes to the high mortality reported in desert stream fish populations (JOHN 1964, MOYLE & NICHOLS 1974, MEFFE 1984, DUDLEY & MATTER 1999). In mesic streams the hydrograph tends to rise less abruptly and flood conditions last longer than in flashy desert streams (RESH et al. 1988, POFF 1996). LOBÓN-CERVIÁ (1996) found, for example, that a series of floods in northern Spain streams did not significantly affect fish populations, although the floods initially increased baseflow by 400 % and maintained flow for several days at 200 %. The floods caused dramatic movement of stream substrates, but fish may have had a chance to strategically change their positions in the water column (RINCÓN & LOBÓN-CERVIÁ 1993, LOBÓN-CERVIÁ 1996), presumably because the flood occurred over several days rather than several hours.

Certain fish taxa native to desert streams exhibit behavioral resistance to floods by rapidly aligning into the current when floods arrive (MEFFE 1984, MINCKLEY & MEFFE 1987). In some cases these adaptations favor the survival of native over introduced taxa (MEFFE 1984, MINCKLEY & MEFFE 1987, DUDLEY & MATTER 1999). Even native taxa don't always survive flash floods, however, and populations can be locally extirpated by large floods (COLLINS et al. 1981).

Invertebrates also experience high mortality from flash floods in both lowland desert streams (GRAY 1981, GRAY & FISHER 1981, FISHER et al. 1982, GRIMM & FISHER 1989, BOULTON et al. 1992, STANLEY et al. 1994) and montane desert streams (MOLLES 1985). Some lowland desert stream taxa show resilience to flash flooding by rapid recolonization (GRAY & FISHER 1981, FISHER et al. 1982, GRIMM & FISHER 1989), primarily via aerial movements and downstream drift. In general, four principal recolonization pathways are possible in streams: aerial movements, downstream drift, upstream movements, and vertical movements from deep substrates (WILLIAMS & HYNES 1976). In montane desert streams, upstream movements can be limited by waterfalls or other barriers, and deep substrate refugia (sensu PALMER et al. 1992) are often precluded by bedrock stream channels. For these reasons downstream drift and aerial movements may be the primary recolonization pathways in montane desert streams. Invertebrates may persist in permanent headwaters where floods occur less frequently because of smaller watershed area, providing a source pool of drifting and aerial colonists to downstream reaches (WILLIAMS & HYNES 1976). Spatial heterogeneity in flash flood occurrence may also allow aerial colonists to immigrate from adjacent non-flooded drainages, which may have important implications for the metapopulation structure of populations.

Some desert stream invertebrates possess behaviors that allow them to resist flash floods and life history adaptations that impart resilience. Adults and juveniles of the giant water bug *Abedus herberti* detect the impact of rainfall

on the stream surface and use this as a cue to abandon streams (LYTLE 1999). GRAY (1981) found that many lowland Sonoran Desert stream mayflies have life history adaptations such as small adult body size, rapid development time, and nearly-continuous reproduction. These life cycles are extreme, with larval development times as low as 8 d for some taxa, the most rapid development known for Ephemeroptera (GRAY 1981). This kind of life cycle ensures that aerial adults are present throughout the flash flood season, and as a consequence stream reaches may be recolonized from local sources rather than from other stream reaches or drainages. Fast life cycles may also facilitate flood resistance, because short residence times in streams reduce the probability of flood encounters.

Relatively little is known about the biotic and abiotic effects of floods in montane desert streams, primarily because the timing of individual flash floods is unpredictable (LYTLE, unpubl.). This makes before-and-after data hard to obtain without careful planning and some amount of luck. The purpose of this study was to characterize a reach of montane desert stream prior to the flood season, and then document the immediate biotic and abiotic changes caused by a flash flood. This was done with three primary objectives in mind. First, measuring mortality would allow the identification of flood-resistant and flood-susceptible taxa. Second, measuring changes in organic detritus would show how floods alter the availability of a food resource that is important for many stream organisms. Third, measuring changes in substrate would show how floods alter the physical environment of these taxa. Taken together, this information provides a foundation for understanding how flash floods shape the ecology and evolution of stream organisms.

## Methods

### Study site

A 122-m reach of the North Fork Cave Creek in the Chiricahua Mountains of southeastern Arizona, USA (31.7° N, 109.2° W), was sampled 8 to 16 d prior to a flash flood on 29 July 1994 and again within 7 d of the flood. The study site consisted of a series of 14 bedrock pools ranging in wetted area from 1.3 to 9.4 m<sup>2</sup> connected by <1 L/sec of baseflow. The North Fork is a permanent, spring-fed, first-order drainage at the study reach (elevation 1935 m) that becomes intermittent below approximately 1700 m. The drainage area upstream of the study site is 5.4 km<sup>2</sup> and contains mixed deciduous and coniferous forest.

### Flash floods

During the summer monsoon season (June–September) of the Sonoran and Chihuahuan deserts of North America, flash floods are caused by brief but intense convective

thunderstorms (SELLERS & HILL 1974, FOGEL 1981). In streams of the Chiricahua Mountains floods recur with a frequency of about 0.8 floods/year (LYTLE, unpubl.). Because the number of floods per season follows a Poisson process, some streams may experience no floods during some years while other streams may experience multiple floods. Although several rainfall events occurred during the two weeks prior to the flood, none of them increased discharge. For the stream reach studied, no large rainfall events (>20 mm) had occurred since the beginning of the dry season, which lasted from early February to mid-July in 1994, so the stream had not been affected by flood disturbance for at least 5 months. Although no observers were present at the study site when the flood began, it was witnessed 5 km downstream at the Southwestern Research Station (American Museum of Natural History) situated at 1580 m elevation. Discharge was estimated 12 h, 24 h, and 5 d after the flash flood by measuring depth and water velocity across a transect in the study reach.

### Pool substrate composition

Each of the 14 pools was mapped before and after the flood. Pools were divided into  $0.5 \times 0.25$  m grids, and a point estimate of substrate type (described in BEVENGER & KING 1995) was made at the center of each grid. Substrate categories were: >20 cm intermediate axis (bedrock), 8–20 cm, 2–8 cm, 0.1–2 cm, and <0.1 cm (silt). Water depth and the presence of organic detritus overlying the substrates were also measured at each mapping point. Substrate composition of pools was expressed as the percentage of pool area covered by a substrate category. Effects of the flood on the five categories of percent substrate composition were tested with MANOVA. Arcsine transformation was not needed to meet test assumptions even though the data were percentages. The individual pools were considered units of replication for making inferences about the stream reach because they were separated during the dry season by 2–10 m of <1 L/sec flow over exposed bedrock, which restricted exchange of detritus and invertebrates among pools.

### Aquatic animals and organic detritus

Aquatic invertebrates were sampled before and after the flood using a  $0.1 \text{ m}^2$  portable invertebrate box sampler (MERRITT et al. 1996). In each pool, the sampler was placed haphazardly on a flat, depositional area and pressed firmly into the substrate. All invertebrates, substrate, and organic detritus were removed during a 5-min. period using a  $63\text{-}\mu\text{m}$  Nitex mesh net. Invertebrates and smaller pieces of detritus were elutriated from the substrate and preserved in 70 % ethanol. Larger pieces of detritus were air dried and saved separately. Because larger taxa were not sampled reliably by the box sampler, belostomatids (*Abedus herberti*), water striders (Gerridae), and fish (*Oncorhynchus mykiss*) were counted visually and by grabbling (tactile search under submerged rock overhangs). Counts were made twice or by two observers and averaged, then expressed as densities (individuals/ $\text{m}^2$ ).

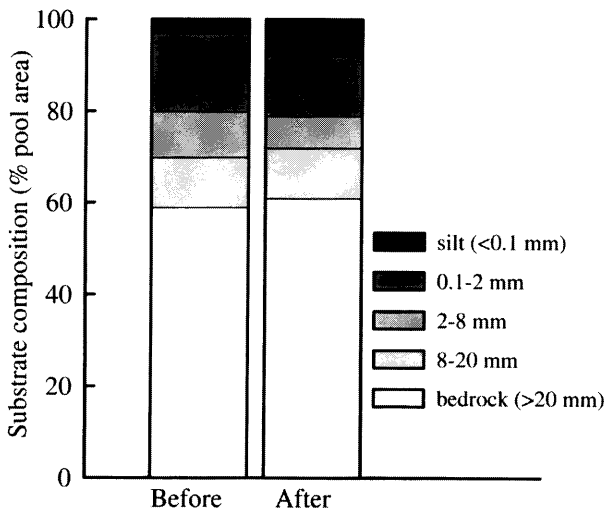
In 10 of the 14 pools, invertebrates were counted and identified to the lowest possible taxonomic unit (genus or species in most cases). Effects of the flood on animal abundance and taxonomic richness were tested with paired *t*-tests comparing counts in

each pool before and after the flood. Organic detritus from each 0.1-m<sup>2</sup> sample was categorized, dried for 24 h at 60 °C, and massed. Four detritus categories were used: deciduous leaf, coniferous leaf, fine particulate organic matter (FPOM; defined here as particles <2 mm), and woody debris (pine cones, twigs, roots). Effects of the flood on abundance (dry mass) of the four detritus categories was tested with MANOVA, and if significant, effects on individual detritus categories were tested with univariate ANOVAs. Data were ln+1 transformed to stabilize variances.

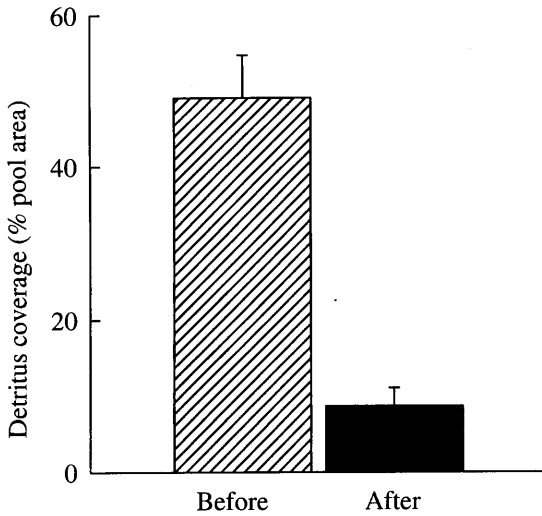
## Results

Viewed from the Southwestern Research Station, the flash flood appeared as a front of mud-saturated water moving down the nearly-dry canyon at a rate of several m/sec. An adjacent tributary (Middle Fork Cave Creek), similar in drainage area to the North Fork, remained at base flow. Much of the leaf litter in the stream channel was either transported downstream or moved laterally to the stream banks. The flood increased stream discharge from <1 L/sec to at least 29 L/sec at the study site. This value was almost certainly an underestimate of peak discharge because it was taken 12 h after the flood began. Scouring was observed 1–2 m above the water level, suggesting that peak discharge had been at least twice the observed amount. Discharge at the study site was down to 8 L/sec within 24 h of the storm and 2 L/sec within 5 days.

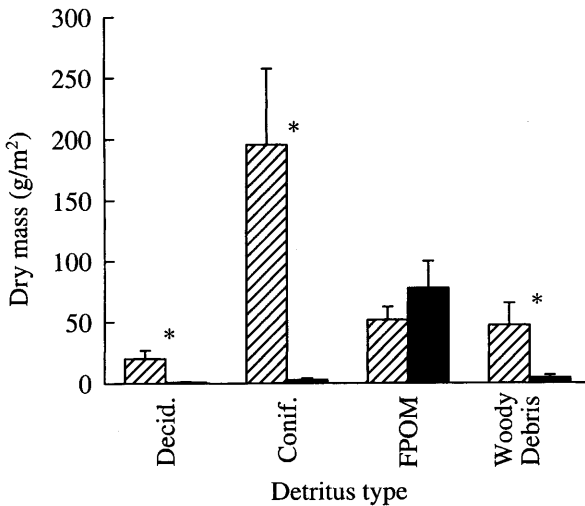
Before the flash flood, the stream pools consisted of exposed bedrock (~60%) and bedrock overlain with smaller particles or silt (Fig. 1). Nearly half



**Fig. 1.** Average pool substrate composition before and after a flash flood ( $N = 14$  pools). The flash flood did not cause significant changes in any of the substrate categories.

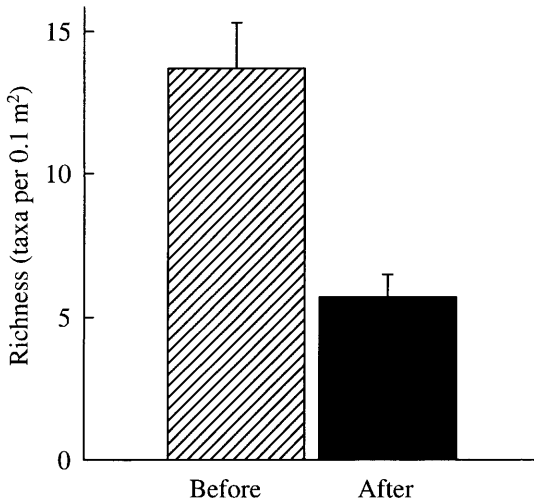


**Fig. 2.** Coverage of pools by organic detritus before and after a flash flood. Bars denote  $\pm 1$  SE ( $N = 14$  pools). The flash flood significantly reduced detritus coverage.



**Fig. 3.** Dry mass of deciduous leaf, coniferous leaf, FPOM (particles  $< 2$  mm), and woody debris (twigs, roots, pine cones) before (hatched bars) and after (solid bars) a flash flood. Bars denote  $\pm 1$  SE ( $N = 10$  pools). “\*” represents a significant difference.

of the pool areas were overlain with some type of organic detritus (Fig. 2). Detritus mass was primarily coniferous leaf litter (nearly  $200 \text{ g/m}^2$ ), followed by FPOM, woody debris, and deciduous leaf litter (Fig. 3).



**Fig. 4.** Average taxonomic richness before and after a flash flood. Bars denote  $\pm 1$  SE ( $N = 10$  pools). The flash flood significantly reduced taxonomic richness.

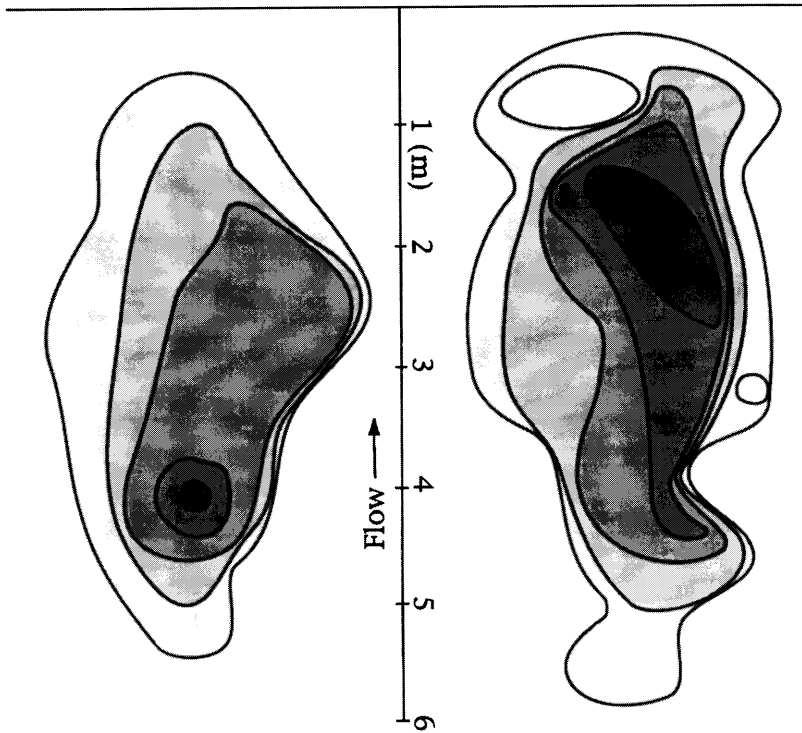
Prior to the flood, aquatic animal richness ranged from 6 to 22 taxa/0.1 m<sup>2</sup> and averaged 14 (Fig. 4). Total taxonomic richness over the entire reach was 35 taxa. Abundances of aquatic animals ranged from over 2500 individuals/m<sup>2</sup> (Chironomidae) to less than one individual/m<sup>2</sup> (the predators *A. herberti* and *O. mykiss*) (Table 1). Diptera clearly dominated the stream in terms of numbers (82 % of all individuals), followed by Trichoptera (6 %), Coleoptera (5 %), and Ephemeroptera (4 %). Total animal abundance averaged 4804 individuals/m<sup>2</sup>, but abundances were highly variable in pools, ranging from 1570 to 9740 individuals/m<sup>2</sup>. Variability in total abundance was driven primarily by differences in chironomid abundance.

Stream pool morphology was strongly affected by the flood. Pools were scoured to bedrock in some areas and filled in by substrate in others (Fig. 5). Percent substrate composition per pool was not altered by the flood, however (Fig. 1; MANOVA, Wilks' lambda = 0.753,  $F = 1.444$ ,  $P = 0.248$ ,  $df = 5, 22$ ). This suggests that although substrate was moved within and among pools, the substrate composition of the reach remained constant. The percentage of pool area covered with detritus decreased from nearly 50 % to less than 10 % (Fig. 2; paired  $t$ -test,  $t = 6.396$ ,  $P < 0.0001$ ,  $df = 13$ ). Detritus dry mass also decreased significantly (Fig. 3; MANOVA, Wilks' lambda = 0.0747,  $F = 46.42$ ,  $P < 0.0001$ ,  $df = 4, 15$ ), which was accounted for by significant declines in deciduous leaf, coniferous leaf, and woody debris (significant ANOVAs;  $P < 0.05$ ,  $df = 1, 18$ ). Dry mass of FPOM did not change significantly from the flood.



**Table 1.** Average abundances and percent losses of aquatic taxa after a flash flood. Abundances were estimated from box samples (0.1 m<sup>2</sup>) taken in 10 stream pools before and after a flash flood that occurred on 29 July 1994. Taxa marked with \* were counted visually. All insects were immatures unless noted otherwise.

Taxon	Before flood		After flood		Percent loss
	Mean (m <sup>-2</sup> )	SE	Mean (m <sup>-2</sup> )	SE	
Trichoptera (all taxa)	298	53	19	9	95%
<i>Helicopsyche mexicana</i>	68	38	0	0	100%
<i>Lepidostoma</i>	130	34	0	0	100%
<i>Oecetis</i>	32	10	0	0	100%
<i>Phylloicus aeneus</i>	80	24	3	2	96%
other	21	8	14	9	33%
Plecoptera (early instars)	4	2	7	5	-43%
Odonata (all taxa)	32	13	4	2	87%
<i>Argia</i>	2	1	0	0	100%
<i>Cordulegaster diadema</i>	5	3	0	0	100%
early instars	24	11	4	2	83%
Coleoptera (all taxa)	227	115	48	23	80%
<i>Cleptelmis</i>	8	5	17	11	-53%
<i>Heterolimnius</i>	197	92	22	12	89%
<i>Stictotarsus striatellus</i> (adults)	6	4	2	1	67%
other (juv. & adults)	12	12	3	2	75%
Ephemeroptera (all taxa)	212	94	0	0	100%
<i>Baetis</i>	15	9	0	0	100%
<i>Callibaetis</i>	68	35	0	0	100%
Baetidae: early instars	62	41	0	0	100%
<i>Paraleptophlebia</i>	78	40	0	0	100%
other	4	3	0	0	100%
Hemiptera (all taxa)	11	2.8	1.7	0.3	83%
<i>Abedus herberti</i> * (juv. & adults)	0.34	0.12	0.30	0.14	14%
Gerridae* (juv. & adults)	4.72	0.93	1.43	0.24	70%
<i>Microvelia</i> (adults)	5	2	0	0	100%
Diptera (all taxa)	3938	1030	138	26	97%
Ceratopogonidae	1237	628	28	11	98%
Chironomidae (in part)	2272	554	88	15	96%
Chironomidae: <i>Cricotopus</i>	322	152	2	1	99%
<i>Hexatoma</i>	21	14	5	3	76%
<i>Pericoma</i> or <i>Telmatoscopus</i>	8	8	4	3	50%
early instars	72	72	1	1	99%
other	11	8	8	4	27%
Non-insect invertebrates	21	9	12	5	59%
Trout ( <i>Oncorhynchus mykiss</i> )*	0.26	0.11	0.05	0.04	80%
Total	4804	1057	228	42	95%



**Fig. 5.** Effects of a flash flood on the morphology of a typical stream pool. Scouring and filling of substrate changed general appearance, but overall pool volume and percent substrate composition remained the same. Depth contours represent 7.7 cm increments.

Aquatic animal taxonomic richness declined from an average of 14 to 6 taxa/0.1 m<sup>2</sup> (Fig. 4; paired *t*-test,  $t = 6.461$ ,  $P = 0.0001$ ,  $df = 9$ ), and reach-wide taxonomic richness declined from 35 to 21 taxa. The flash flood reduced aquatic animal abundance by 95 %, from 4804 to 228 individuals/m<sup>2</sup> (Table 1; paired *t*-test,  $t = 4.276$ ,  $P = 0.0021$ ,  $df = 9$ ). Most taxa experienced greater than 80 % reductions in numbers. All Ephemeroptera were eliminated from the reach (100 % loss). Diptera experienced losses of 97 %, with abundances changing from 3938 to 138 individuals/m<sup>2</sup>. Trichoptera were reduced by 95 %, Odonata by 87 %, Coleoptera by 80 %, and rainbow trout by 80 %. Early instar Plecoptera and the riffle beetle *Cleptelmis* actually increased in abundance, but in both cases this increase was driven by a high post-flood count in only one sample. Other taxa with low percent losses in all stream pools were the hemipterans Gerridae (70 % loss) and *A. herberti* (14 % loss), and the crane fly *Hexatoma* (76 % loss).

## Discussion

### Mortality and removal of resources

Most of the biotic and abiotic effects of the flash flood, including movement of substrate, loss of organic detritus, and removal of most aquatic animals, probably occurred during the first few minutes. The flood was observed pushing leaf litter downstream and to the edges of the flood plain. The “grinding molars” of moving substrates may have been responsible for converting some of this detritus into FPOM, which was the only class of detritus that did not decline significantly from the flood. This wholesale removal of detritus from the system may be peculiar to flash floods, which, unlike floods in mesic streams, often scour stream bottoms down to bedrock. ANGRADI (1997), for example, found that an 18-year flood event in a mesic Appalachian headwater stream reduced invertebrate abundances by 70–95 %, but instream structures such as debris dams, interstitial habitats, leaf detritus, and FPOM were relatively unaffected by flooding.

The high loss rates of invertebrates in this study (95 %) were comparable to those reported after flash floods in a lowland Sonoran Desert stream (86 %, GRAY 1981; 98 %, FISHER et al. 1982) and from a flash flood in a montane desert stream in New Mexico (94 %, MOLLES 1985). Many of the stream animals were probably removed in a way similar to the removal of organic detritus: stranded laterally in the flood plain, carried downstream to reaches that would desiccate within days, or ground into FPOM by moving substrates. Because most taxa were present as obligately-aquatic juveniles during the flood, any one of these fates could cause mortality.

Some of these stranded individuals, especially case-building Trichoptera, may have been able to survive in terrestrial habitats for short periods of time before desiccating, but the low numbers observed 5 d after the flood (Table 1) suggest that stranded individuals did not return to the stream. One organism that may be able to persist outside of the stream is the chironomid *Cricotopus*, which was always found in symbiosis with colonies of the cyanobacterium *Nostoc*. Filaments of *Nostoc* are held together by a gelatinous matrix, forming a flat, translucent case that completely encloses the several-mm long larva. The cases have a flexible, rubbery texture that is resistant to tearing or crushing by forceps. BROCK (1960) noted that encased *Cricotopus* may be able to survive periods of drought because *Nostoc* cases retain moisture, in addition to serving as the larva's only food source. It is possible that encased *Cricotopus* may be also be able to survive flash floods, and then resist desiccation in the terrestrial environment for the 5 to 9 days (BROCK 1960) required for pupation.

## Implications for behavioral and life history strategies

The giant water bug *A. herberti* probably avoided mortality (only 14 % loss) by abandoning the stream in response to heavy rainfall prior to the flash flood. Because not all individuals abandon streams in response to rainfall cues (LYTLE 1999), it is possible that the 14 % loss resulted from individuals that failed to respond to rainfall prior to the flood. A similar behavioral mechanism may account for the low reductions in abundance observed in another hemipteran group, the Gerridae (70 %), although this remains to be demonstrated. It is also not clear what *A. herberti* use as food after floods have removed most prey, but cannibalism is well-documented in this taxon (SMITH 1974, VELASCO & MILLAN 1998).

Ephemeroptera were locally extirpated from the study site by the flash flood, so recolonization from outside the stream reach is critical for maintaining populations of this group. Because downstream drift is common in mayflies (ALLAN 1995) and serves as the most important recolonization pathway for lowland desert stream Ephemeroptera (GRAY & FISHER 1981), it is likely that montane desert streams are also recolonized by individuals drifting from upstream refugia.

Drift from upstream refugia may also be responsible for maintaining populations of introduced rainbow trout, as illustrated by changes in fish distributions in the North Fork Cave Creek (LYTLE 2000). In the early 1960s only native speckled dace (*Rhinichthys osculus*) occurred in the North Fork, but by the time of this study in 1994 these had been replaced by introduced rainbow trout. Flooding in late 1994, exacerbated by recent forest fires in the area, reduced trout to a remnant population approximately 1 km upstream of the study reach in a series of non-flooding, spring-fed pools. Following the removal of trout by flooding, native dace populations returned to the lower reaches of the North Fork below the study reach. By 1999, the remnant trout population had re-invaded downstream into the study reach. It remains to be seen if the trout population will move further downstream and again exclude native speckled dace from these streams (presumably via direct predation), if flooding will favor the flood-adapted speckled dace over the trout, or if both populations remain in a dynamic flood-mediated balance (sensu HEMPHILL & COOPER 1983, MEFFE 1984).

Higher-elevation flood refugia are not a good habitat for leaf-shredding taxa such as the caddisfly *P. aeneus* because individuals are excluded from these areas by the lack of deciduous detritus (LYTLE, unpubl.). *P. aeneus* is one of the few invertebrate taxa in this stream that has only one generation per year (WIGGINS 1996), and this univoltine cycle may be reinforced by the flood-driven cycling of detritus as well as the seasonal timing of floods. Late-instar larvae depend on deciduous leaf litter both as a food source and as a case-

building material (WIGGINS 1996), but this resource is almost entirely removed from the stream by flash floods (Fig. 3). Leaf litter does not enter the stream in large amounts until leaf abscission of live oaks occurs at the beginning of the dry season in February or March (DICK-PEDDIE 1993). Early instar larvae, on the other hand, feed on and build cases from FPOM (LYTLE 2000) which is abundant in streams following floods (Fig. 1). Because most *P. aeneus* emerge at the beginning of the monsoon season in June and July (LYTLE, unpubl.), mature individuals becoming aerial adults at this time avoid the post-flood lack of deciduous detritus, while their progeny utilize FPOM until whole leaves become available the following spring. This emergence strategy also facilitates flood avoidance because it occurs just before the long-term mean date of the first monsoon season flash flood (around Aug. 5th; LYTLE, unpubl.). Because the observed flash flood occurred only a week before the long-term mean date, many individuals may have avoided mortality as aerial adults. Thus, flash floods may reinforce a particular life history both directly by imposing mortality and indirectly by controlling a limiting resource.

### Implications for population dynamics and evolution

The data presented here show that flash floods can extirpate or severely reduce abundances of aquatic taxa at the scale of the individual stream pool (1–20 m) and at the scale of the reach (>100 m), which suggests montane desert stream taxa have low resistance to flash flooding. As a result, population bottlenecks may occur when in-stream populations are reduced to low numbers or when reaches are recolonized by small numbers of individuals (VRIJENHOEK 1985). Population bottlenecks can reduce heterozygosity, allowing genetic drift to fix deleterious alleles within populations (CROW & KIMURA 1970). In some desert stream fishes population bottlenecks result from drought disturbance, and the resulting reduction in heterozygosity (VRIJENHOEK et al. 1985, MEFFE & VRIJENHOEK 1988) causes a reduction in fitness as measured by survival, fecundity, growth rate, and bilateral asymmetry (QUATTRO & VRIJENHOEK 1989). Disturbances such as flash floods can also impose strong selection of favorable traits (VRIJENHOEK 1985), however, and may even favor adaptation to local disturbance regimes. Severe floods can, in theory, drive the evolution of adaptive strategies for flood avoidance (LYTLE, unpubl.), but the degree to which this favors adaptations to local flood regimes remains to be determined empirically.

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