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Interactions between geomorphology and ecosystem processes in travertine streams: Implications for decommissioning a dam on Fossil Creek, Arizona

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Abstract

Travertine deposits of calcium carbonate can dominate channel geomorphology in streams where travertine deposition creates a distinct morphology characterized by travertine terraces, steep waterfalls, and large pools. Algae and microorganisms can facilitate travertine deposition, but how travertine affects material and energy flow in stream ecosystems is less well understood. Nearly a century of flow diversion for hydropower production has decimated the natural travertine formations in Fossil Creek, Arizona. The dam will be decommissioned in 2005. Returning carbonate-rich spring water to the natural stream channel should promote travertine deposition. How will the recovery of travertine affect the ecology of the creek? To address this question, we compared primary production, decomposition, and the abundance and diversity of invertebrates and fish in travertine and riffle/run reaches of Fossil Creek, Arizona. We found that travertine supports higher primary productivity, faster rates of leaf litter decomposition, and higher species richness of the native invertebrate assemblage. Observations from snorkeling in the stream indicate that fish density is also higher in the travertine reach. We postulate that restoring travertine to Fossil Creek will increase stream productivity, rates of litter processing, and energy flow up the food web. Higher aquatic productivity could fundamentally shift the nature of the stream from a sink to a source of energy for the surrounding terrestrial landscape.

1. Introduction

Projects of decommissioning dams offer an unprecedented opportunity to test how stream ecosystems respond to changes in hydrology and morphology. Dam removals are becoming more common because many dams have outlived usefulness and the public is interested in returning rivers to more natural states (Doyle et al., 2003; Stanley and Doyle, 2003). Treating the removal of dams as large-scale ecological experiments provides a powerful framework for testing how hydrology and geomorphology affect stream ecosystems (Hart et al., 2002).

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In many riparian and aquatic studies, geomorphological processes such as weathering, erosion, or deposition change slowly or sporadically compared to ecological processes, such as population growth, productivity, or nutrient cycling. When significant geomorphic changes occur rapidly, they are often the result of large-scale, intermittent processes (e.g. floods or landslides) that usually occur outside the context of experimental designs (e.g. Schmidt et al., 2001). Thus, stream ecologists often treat stream morphology as static relative to the time scale in which ecological interactions are measured. Decommissioning a dam, which will provide predictable, permanent, large-scale changes to the ecological and geomorphic processes, is a unique opportunity to observe linked geomorphic and ecological changes occurring on the same time scale. Fossil Creek, AZ, provides a compelling system to test, experimentally, the ecosystem and community consequences of changing geomorphology, because increased flow following an upcoming decommissioning of a dam is expected to cause dramatic changes in the physical structure of the stream through increases in stream discharge, sediment load and rate of deposition of travertine.

Before the hydropower dam was built, the formation of travertine in Fossil Creek created large terraces and pools in a distinct reach that extended for roughly 10 km. Historical accounts of Fossil Creek describe a series of travertine terraces and pools with the highest terraces reaching ~ 3 m (Chamberlain, 1904). In 1909, the Arizona Public Service built a diversion dam (8 m high) approximately 0.6 km from the springs. Since then, the majority of base flow ($\sim 1218 \, \mathrm{l \, s^{-1}}$) has been diverted through a flume for the production of hydropower, significantly reducing discharge, precipitation of travertine, and formation of travertine terraces. The actively forming travertine reach is now less than 1 km long and occurs immediately below the Irving Power Plant, where some diverted water ($\sim 150 \, \mathrm{l \, s^{-1}}$) is returned to the natural stream channel.

Little deposition of travertine occurs in the flume because the water moves too quickly through the pipe without enough turbulence for CO_2 outgassing. Geochemists predict that the formation of travertine will increase when flow is restored as dissolved calcium, bicarbonate, turbulence, and CO_2 outgassing increase (Malusa et al., 2003). The rate of deposition of travertine, estimated at 12,000 kg day^{-1} once full flows have been returned to the channel, should restore travertine terraces and pools to the original state. These changes in geomorphology are likely to be far more pronounced than the increases in habitat normally expected with increased flow (Malusa et al., 2003).

1.1. Travertime geomorphology and ecology

The deposition of travertine occurs when water, supersaturated with CO_2, releases CO_2 to the atmosphere and causes $CaCO_3$ to precipitate out of solution as calcite or aragonite (Barnes, 1965). Travertine can form massive structures, including terraces, tufa mounds, cascade deposits, terrace-mound travertines, and shallow lake fans. These structures can profoundly influence the morphological characteristics of running waters. Travertine terraces can convert the typical morphology of streams into a series of terraced pools. In an extreme example, large travertine terraces completely converted the lotic Korana River in Croatia to the lentic Plitvice Lakes, a series of 16 lakes separated by biogenic travertine terraces. This system is a phenomenal example of the morphological changes caused by biogenic deposition of travertine:

> "The growth, formation and transformation of the Plitvice geomorphology is surprisingly fast. Thirty-five years of the National Park was sufficient to make us witnesses of the dynamics of the system. During this period, the water level rose more than half a meter in places, with all the consequences that this entailed. Any measurements in Plitvice have, almost literally, only momentary worth. The depth, size, shape, and even the number and arrangement of the lakes change all the time and quite quickly. Only life can endow rock with such dynamics" (Brnek-Kostic, Monograph study, Plitvice, 1987).

Algae and bacteria are well known to facilitate the deposition of travertine, both by altering water chemistry and by providing surface area for $CaCO_3$ deposition (Pentecost, 1990; Pedley, 1992; Folk, 1993; Pentecost et al., 1997). Aquatic insect larvae can also promote the formation of travertine. Caddisflies of the genus *Cheumatopsyche* build retreats out of travertine and organic material and construct silken capture nets that promote $CaCO_3$ deposition (Drysdale, 1999). Another caddisfly, *Smicridea travertinera*, builds retreats into travertine deposits and actively manipulates $CaCO_3$ crystals (Paprocki et al., 2003). Other aquatic insects are involved in the biogenesis of freshwater tufa terraces (Humphreys et al., 1995). Fungi can also promote travertine biogenesis through the formation of calcium oxalate crystals (Freytet and Verrecchia, 1995).

Aquatic biota plays a key role in the deposition of travertine, and formations of travertine can alter river

geomorphology. Because structures of travertine create habitat, cement substrates, and promote a distinct biotic assemblage, it is likely that travertine affects many ecological processes directly. For example, deposition of travertine on leaf litter can retard colonization by macroinvertebrates, slowing rates of decomposition, and cause fungi to be relatively more important agents of decomposition (Casas and Gessner, 1999). Such 'armoring' of the substrate in river ecosystems has been postulated as a mechanism through which deposition of travertine depresses biological activity, particularly of stream invertebrates (Casas and Gessner, 1999). On the other hand, the close association between the travertine substrate and microorganisms suggests that travertine may promote photosynthesis and bacterial activity, as has been observed in some marine travertine deposits (Riding, 2000).

These direct effects of travertine are almost certainly important. Because travertine structures can so profoundly alter the morphology of running waters, we submit that these mediate large changes in ecosystem processes, and that these indirect effects may well outweigh the direct ones. Here, we present the initial investigations of ecosystem processes in travertine and riffle/run reaches of Fossil Creek, Arizona. Specifically, we compare water quality, algal accrual, the decomposition of leaf litter, macroinvertebrate densities and species compositions, and fish densities. Based on these

findings we present a conceptual model for how the formation of travertine alters ecosystem processes. We also describe how we plan to test this conceptual model by using the pending decommissioning of the Fossil Creek dam as a large-scale experiment integrating geomorphology and ecology.

2. Materials and methods

Perennial flow in Fossil Creek ($\sim$1218 l s^{-1}) originates from a series of seven springs 22.4 km above the confluence with the Verde River (Fig. 1). The springs are near the town of Strawberry, in Gila County, Arizona. We compared species distributions and ecosystem processes in two reaches of Fossil Creek. The first reach, the travertine terrace reach, is below the Irving Power Plant and extends for less than 1 km. At Irving, a portion of the water that was diverted for the production of hydropower is returned to the natural stream channel immediately below the Irving Power Plant at a rate of 150 l s^{-1} (Fig. 1). The remaining flow is re-diverted to a second power plant (Childs Power Plant) on the Verde River above the confluence with Fossil Creek. The water has high concentrations of dissolved calcium and carbonate held in solution by dissolved carbon dioxide (CO_2) (Malusa et al., 2003). As CO_2 outgasses from the water, with exposure to the atmosphere, the saturation level of $CaCO_3$ is lowered
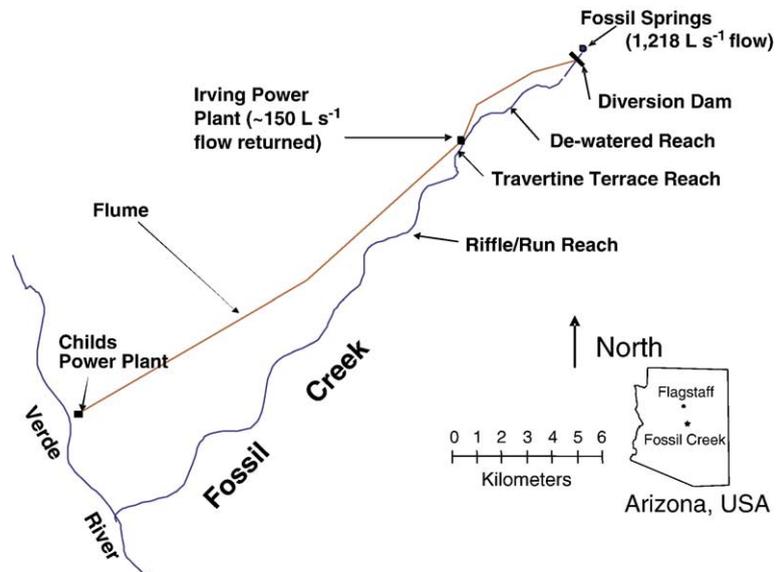

Fig. 1. Map of Fossil Creek, Arizona. Water originates from a series of springs less than 1 km above the diversion dam. Most of the base flow (>95%) is diverted through the flume to the Irving Power Plant. Approximately 150 l s^{-1} of flow is returned to the river at Irving, and the remainder is re-diverted through a second flume to the Childs Power Plant. The travertine terrace reach begins at Irving and extends approximately 1 km downstream. A transition area occurs below this where travertine terraces are present but scarce. The formation of travertine terraces ceases by 2 km below Irving where the river has a riffle/run morphology from this point to its confluence with the Verde River.

and $CaCO_3$ precipitates out of solution to form solid travertine. Travertine deposits on solid surfaces and forms terraces. The formation of travertine terraces begins to dwindle approximately 1 km downstream from the Irving Power Plant (Fig. 1) and ceases approximately 2 km downstream from the Irving Power Plant. The active travertine terrace forming reach is in stark contrast with the rest of the perennial stretch that extends downstream to the Verde River (Fig. 1). The remainder of the river has a riffle/run/pool morphology. Widely scattered deep pools exist, but most of the reach is made up of shallow riffles and runs. The deposition of travertine occurs intermittently in the lower reach but does not form terraces. Discharge in both reaches is $\sim 150\,l\,s^{-1}$. For simplicity, in this paper, we refer to the two sample reaches as the "travertine terrace reach" and the "riffle/run reach". We sampled the travertine terrace reach beginning 20 m below the Irving Power Plant extending approximately 1 km downstream. This entire reach has travertine terraces. Terraces are spread approximately 15–20 m apart. The riffle/run sample reach began approximately 3 km below the Irving Power Plant, and extended approximately 1.5 km downstream, and had no travertine terraces.

We measured water temperature (°C), pH, dissolved oxygen (DO, mg l^{-1}), specific conductivity (SpC, µS cm^{-1}), and concentrations of ammonium (NH_4^+), phosphate (PO_4^{-3}), nitrate (NO_3^-), calcium (Ca^{+2}), magnesium (Mg^{+2}), sodium (Na^+), potassium (K^+), chloride (Cl^-), and sulfate (SO_4^{-2}). Water quality data were collected in August 2002, December 2002, and May 2003. Water samples were collected within 100 m of each other across sample periods. Temperature, pH, DO, and SpC were measured at three randomly picked sites within each reach using a Hydrolab Datasonde 4a. Three replicate water samples were collected in 250 ml plastic bottles for nutrient and ionic composition, filtered through a 0.4 µm glass microfibre filter, and acidified to a pH <2.0 with either nitric or sulfuric acid. Water analyses were conducted in the laboratory using a Technicon Auto Analyzer II (PO_4^{-3}, NO_3^-, NH_4^+), a Perkin-Elmer Flame Atomic Absorption Spectrophotometer Model 560 (Mg^{+2}, Ca^{+2}, Na^+, K^+), and a Dionex DX 100 Ion Chromatograph (Cl^- and SO_4^{-2}).

We compared the decomposition rates of leaf litter for alder, *Alnus oblongifolia*, in the travertine and riffle/run reaches. We measured litter decomposition using litterbags. Naturally senesced leaves were sewn into 6-mm mesh bags and secured in the stream in both reaches. Litterbags were attached to rebar and randomly placed along a 0.5 km length of the travertine terrace reach, and a 1.5 km length of the riffle/run reach at an

approximate depth of 1 m. The experiment began on December 16, 2002 and ended on February 10, 2003.

At each site, 10 litterbags were harvested at 7, 14, 21, 28, and 56 days. Litterbags were transported to the laboratory, rinsed with distilled water to remove invertebrates and algae. The collected material was oven-dried to constant weight (70 °C), weighed, ashed for a minimum of 1 h at 500 °C, and re-weighed to calculate ash-free dry mass (AFDM). Rates of decomposition were determined as the slope of the line derived by regressing ln(AFDM) against time. We used Analysis of Covariance to test for differences in the rates of decomposition between the two reaches with ln(AFDM) as the dependent variable, reach a categorical variable and time a continuous variable. A significant interaction term (site × time) indicates a significant difference in the rate of decomposition (slope) between the reaches.

We monitored algal biomass using clay flowerpots as artificial substrates, as described in Fairchild and Lowe (1984). Twenty replicate substrates were placed in the river in each reach on November 4, 2002, for a total of 40 substrates. Substrates were randomly placed along a 0.5 km length of the travertine terrace reach, and a 1.5 km length of the riffle/run reach at an approximate depth of 1 m. Ten replicates were collected from each reach after 14 and 35 days (December 11, 2002). Algae were scraped from a 179 cm^2 area on the outer surface of each substrate. Ash-free dry mass was determined as described above. We express the accumulation of algal biomass as g AFDM per substrate.

Assemblages of macroinvertebrates were collected in August 2002 and January 2003 using Surber (929 cm^2; 250 µm mesh size) samplers in riffles, and core (10 cm diameter) samplers in pools, in the reaches described above. Five replicates were taken in riffles and pools in each reach, at each sampling period and were processed by elutriating the sample five times. The elutriate was filtered through a 250 µm net and preserved in 95% ethanol. Samples were sorted in the laboratory and identified to the lowest level feasible using current North American taxonomic keys (e.g. Merritt and Cummins, 1996). Diversity indices were calculated using PC-ORD version 4.02 (McCune and Mefford, 1999). The richness of species was calculated by combining quantitative samples with survey samples taken in 2001. Combining these samples provides the most comprehensive list of all taxa collected at the two sites (Dinger and Marks, 2002).

Fish densities were estimated by counting and identifying fish during snorkel surveys, conducted in August 2003 and May 2004. Conditions in late summer and spring are most conducive for snorkel surveys

because water clarity is high during these periods of low precipitation. Although these sample dates do not coincide with the food base experiments, the long-term fish surveys show little temporal variation in fish composition and indicate that these samples, taken before and after the food base experiments, yield accurate estimates of fish densities throughout this period (Marks et al., 2005). Seventeen sub-sites were chosen where all native and non-native species occur sympatrically. Nine sub-sites were located in the travertine terrace portion of the stream and eight sites were located downstream in the riffle/reach. Each sub-site was approximately 100 m long and included riffle and pool habitats, although riffle habitats are proportionally less frequent in the travertine terrace reach. Sites were sampled by three independent observers and the results were averaged to estimate densities and community structure. The number and species identification of each fish were recorded. We tested for differences in fish density between sites using a Student's t-test.

3. Results

Water temperature was similar at the two reaches in August and May but was higher at the travertine site in December (Table 1). Water entering the stream below the power plant is relatively warm and cools off downstream during the winter when air temperatures are low. NO_3^- and Ca^+ were consistently higher in the travertine reach, as was conductivity. All other variables for water chemistry were similar across sites and seasons (Table 1). The water quality of the travertine terrace reach is similar to the water quality at the springhead, which indicates that the hydropower operation does not change water quality (Marks et al., 2003). We collected additional data for water quality through March 2004, as part of an ongoing monitoring program, and found that the reaches differed in temperature from October through May, but did not differ from June through September. In contrast, differences in NO_3^-, Ca^+, and conductivity persisted throughout the year (Marks et al., 2005).

Decomposition was significantly faster at the travertine terrace site than at the riffle/run site (Fig. 2). Differences in decomposition between the two sites became apparent and persisted after 14 days. The decomposition coefficient (k) was 0.176 day^{-1} in the travertine reach, and 0.066 day^{-1} in the riffle/run reach. This threefold increase in decomposition rate at the travertine terrace reach indicates that allochthonous energy in the travertine terrace reach is used more quickly compared to the riffle/run reach.

Table 1
Water quality data collected at the travertine terrace reach and the reach in summer, winter, and spring

	Temperature (°C)	pH	DO	DO%	Cond	PO₄	NO₃	Mg	Ca	Na	K	Cl	SO₄	CO₂
Travertine terrace reach														
8/15/2002	23.04 (0.05)	7.8 (0.04)	7.39 (0.06)	111 (0.9)	749 (1.7)	0.047 (0.01)	0.09 (0.01)	42 (0.17)	100.8 (3.2)	12.2 (0.3)	2.1 (.06)	5.7 (0.2)	24.4 (0.3)	
12/5/2002	20.04 (0.7)	7.81 (0.03)	8.1 (0.02)	114 (0.5)	730 (0.5)	0.043 (0.005)	0.46 (0.05)	35 (0.5)	85 (0.8)	10.5 (0.24)	1.5 (0.12)	9.1 (0.57)	24.6 (0.2)	19.3 (1.5)
5/6/2003	20.3 (0.06)	8.15 (0.01)	6.98 (0.07)	100 (0.81)	679 (0.2)	0.1 (0.04)	0.11 (0.006)	35 (0.52)	85.8 (0.26)	10.8 (0.15)	1.6 (0.06)	8.1 (0.25)	23.5 (0.2)	
Riffle/run reach														
8/15/2002	22.8 (0.02)	8.33 (0.01)	7.4 (0.05)	110 (0.65)	514 (.3)	<0.04	<0.02	41 (0.2)	22.7 (1.2)	12.9 (0.12)	2.2 (0.1)	6.5 (1.07)	23.8 (0.05)	
12/5/2002	12.5 (0.01)	8.23 (0.04)	9.43 (0.03)	113 (0.4)	564 (.2)	<0.02	0.21 (0.06)	36 (0.3)	51.2 (0.4)	10.7 (0.12)	1.5 (0.12)	8.5 (0.12)	24.4 (0.17)	30.7 (1.15)
5/6/2003	19.2 (0.02)	8.50 (0.01)	7.95 (0.13)	111 (1.95)	501 (0.2)	<0.02	<0.02	35 (0.06)	46.5 (0.3)	11.2 (0.12)	1.7 (0.1)	8.13 (0.12)	24 (0.2)	

NH₃ concentrations were also determined, but were below detection limits in all cases (<0.02 mg N l⁻¹). Mg, Ca, Na, K and Cl are reported in mg l⁻¹. DO, PO₄, NO₃, SO₄, and CO₂ are reported in mg O, P, N, S, and C l⁻¹, respectively. Mean values are reported with standard deviations in parentheses below the mean, $n=3$.
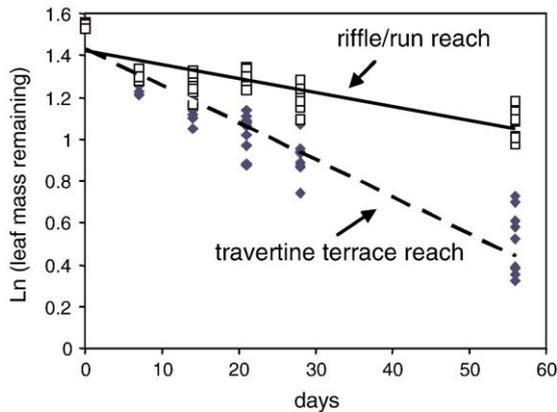
Fig. 2. Decomposition of leaf litter in the travertine terrace reach and downstream in the riffle/run reach plotted as the natural logarithm of mass remaining at each harvest period. Rates of decomposition were significantly higher in the travertine terrace reach.

No difference existed in algal growth after 14 days. At day 35, however, algal growth was five times higher on substrates incubated in the travertine terrace reach compared to the riffle/run reach (Fig. 3). Additional experiments conducted in the late winter and early summer also showed significantly more algal growth in the travertine terrace reach which indicates that this result is independent of the temperature differences between the two reaches in the winter (Carter, unpublished). Experimental results are consistent with field observations that show extensive algal blooms in the travertine terrace reach. These blooms were dominated by large growths of filamentous green algae, including *Spirogyra* sp., *Zygnema* sp., and *Mougeotia* sp., members of the Zygnematales, which form large blooms in lentic areas of the river. In addition, long filaments of the green alga, *Cladophora glomerata*, and its associated epiphyte assemblage are found growing on the travertine terraces in addition to *Vaucheria* sp., a filamentous Xanthophyceae. In contrast, the riffle/run

reach was characterized by short filaments of *C. glomerata*.

Assemblages of macroinvertebrates were significantly different between the two reaches (Table 2). In contrast to other southwestern travertine streams, the travertine terrace sites contained the highest richness of species. This indicates that the pre-dam conditions possibly supported diverse communities and suggested that richness has been reduced in areas by flow regulation. The densities of insects were similar in travertine and riffle/run reaches, but travertine sites promote a unique insect fauna with specialized adaptations to travertine deposition.

Sites with travertine terraces were often characterized by insects not found in the riffle/run reach, including two taxa of caddisflies, *Wormaldia* sp. (Trichoptera: Philopotamidae) and *Ochrotrichia* sp. (Trichoptera: Hydroptilidae). Other insects also found primarily in travertine zones include Dipterans—*Forcipomyia* sp. (Diptera:Ceratopogonidae), *Pericoma* sp. (Diptera:Psychodidae), and *Dixa* sp. (Diptera:Dixidae), Coleopterans—*Octhebius* sp. (Coleoptera:Hydraenidae), and Hemiptera—*Belostoma* sp. (Hemiptera:Belostomatidae). In addition to the suite of taxa that were associated with travertine terraces, the following taxa were present in other stream reaches but at significantly lower densities than in the travertine terrace reach: the caddisfly *Hydropsyche* sp. (Trichoptera:Hydropsychidae), the mayflies *Caenis* sp. (Ephemeroptera:Caenidae), *Tricorythodes* sp. (Ephemeroptera:Tricorythodidae), and lastly the dipterans *Simulium* sp. (Diptera:Simuliidae) and *Caloparyphus* sp. (Diptera:Stratiomyidae).

Fish densities were four times higher in the travertine reach relative to the riffle/run reach ($T=3.841$, $p=0.0008$, Fig. 4). At both sites, approximately half the fish were exotic. We observed significantly more round tail chub (*Gila robusta*), a native fish of special concern, however, in the travertine reach than the riffle/run reach. Round tail chub are only found in roughly 18% of their historical range, making Fossil Creek an important site for conservation of this species (Voeltz, 2002). In contrast, the majority of the native fish
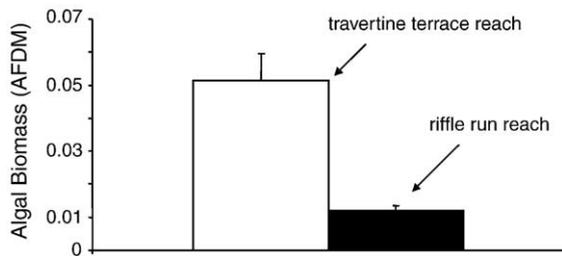

Fig. 3. Primary productivity, measured as accrual of algae on artificial substrates, is higher in the travertine terrace reach relative to the riffle/run reach.

Table 2
The richness (R) of macroinvertebrates, evenness (E), and diversity according to the Simpson's (H) and Shannon-Wiener (D') indices

Site	R	E	H	D'
Travertine terrace reach	69	0.446	1.678	0.6639
Riffle/run reach	46	0.337	1.277	0.4878

All measures indicate a more diverse community of macroinvertebrates in the travertine reach of Fossil Creek relative to the riffle/run reach.
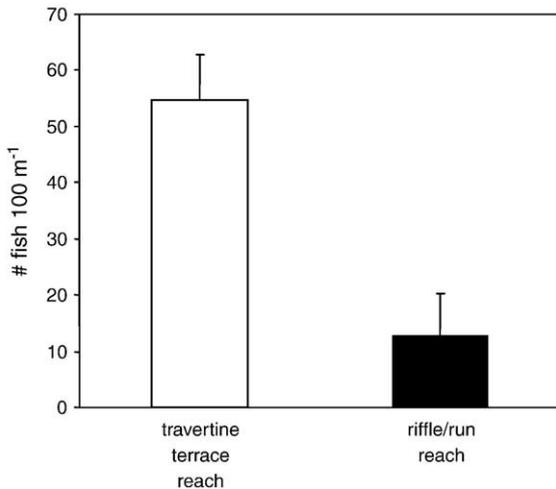
Fig. 4. Fish densities, estimated from snorkel surveys, indicated significantly higher fish densities in the reach with travertine terraces relative to the riffle/run reach.

observed in the riffle/run reach were desert and Sonoran suckers, which are still found in other headwater streams in the Verde watershed. Exotic bass and sunfish were the dominant invasive species at both sites.

4. Discussion

The food base of most southwestern streams is a combination of benthic algae and leaf litter entering the stream from the riparian zone. Stable isotope food webs in Fossil Creek indicate that macroinvertebrates and fish depend on algae and leaf litter as important food sources (Marks et al., 2005). Increases in algal productivity and faster processing of leaf litter are both indicators of a more productive food base—energy that will be available to higher trophic levels. The observed differences in decomposition and algal growth are likely driven by multiple mechanisms, including increased temperature and nutrient availability in the travertine zone. Algal growth experiments were repeated in the spring and fall with similar results, and suggest that the seasonal differences between sites in temperature were not driving the differences in productivity of algae. Algal growth within the travertine reach also correlated positively with calcium concentrations in a prior study in Fossil Creek (Malusa et al., 2003). Ongoing studies are investigating whether retention of nutrients and microbial activity are higher in the travertine terrace reach relative to the riffle/run reach. Although densities of invertebrates were not higher in the travertine terrace reach, snorkel surveys indicate that fish are more abundant in the travertine terrace reach compared to

the riffle/run reach, which we attribute to increased food resources and complexity of habitat associated with this morphological feature of Fossil Creek. The fish may also be suppressing macroinvertebrate standing crops, masking differences in secondary productivity.

These results differ from other studies that have shown decreased decomposition and macroinvertebrate diversity in travertine streams (Robinson et al., 1996; Casas and Gessner, 1999; Oberlin et al., 1999). In systems such as Fossil Creek, where calcium carbonate concentrations are high, travertine preferentially deposits on terraces, as shown by artificial substrate work by Malusa (1998) and Strength (1999). This preferential deposition creates a positive feedback where deposition is stimulated by the complex structure of the terraces themselves. This formation creates distinct travertine terraces and large pools with extensive riparian vegetation, providing high quality habitats for macroinvertebrates and fish. Other streams maintain a riffle/run morphology because the travertine does not form terraces but deposits uniformly on the streambed and causes armoring of the substrate. Field observations of these types of streams (Travertine Grotto and Travertine Springs, Arizona) compared to terrace-depositing systems, like Fossil Creek and the Little Colorado River, lead us to conclude that non-terrace deposits are primarily $CaCO_3$ with a lower proportion of organic matter than in travertine terraces, though these observations have not yet been quantified. As established by Malusa et al. (2003), a strong correlation exists between large travertine terraces and productivity on these terraces: larger terraces provide faster, shallower flow, providing algae with greater nutrient fluxes and better light penetration.

We suggest that the insects dominating travertine zones either have mechanisms to cope with travertine deposition or may benefit from travertine formation. Examples of insects that may cope with deposition better than other organisms include the two dominant mayflies, *Caenis* and *Tricorythodes*. Their gills are modified so that a hard, enlarged gill operculum covers the remaining gills, possibly preventing travertine deposition directly upon their respiratory surfaces. *Caloparyphus*, however, may benefit from travertine —these Stratiomyidae soldier flies incorporate calcite minerals into their integument, possibly to toughen their skin as a predatory defense. Both the filter-feeders, *Simulium* and *Hydropsyche*, may benefit from the hydrology of travertine terraces, in that the terraces provide flat areas with continual flow which are ideal substrates for filter feeders. Although none of the insect species found in Fossil Creek overlap with those
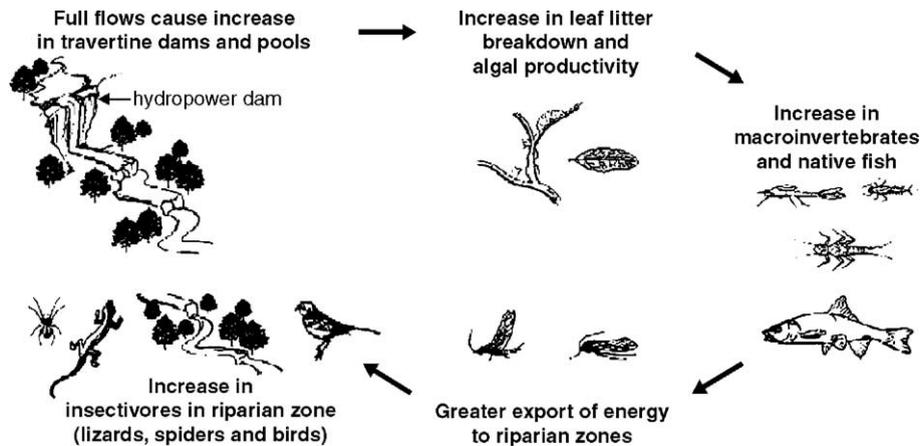
Fig. 5. Conceptual model of how increased travertine formation following restoration of flow in Fossil Creek will affect productivity, abundance of species, and stream–riparian interactions.

described in the Introduction, *Hydropsyche* sp., a dominant caddisfly in travertine reaches in Fossil Creek, may benefit in the same manner as *Smicridea travertina* (Paprocki et al., 2003), by using travertine to strengthen its silk net which is used to capture food particles.

4.1. Fossil Creek: a model system for testing experimental interactions between geomorphology and ecology

Fossil Creek provides an unprecedented opportunity to study how geomorphology affects ecosystem processes in real time. We have a developed a conceptual model of how restoration of flow will affect ecosystem processes—effects which could cascade into the adjacent riparian forest (Fig. 5). The observed differences between the travertine and riffle/run sites motivate this overarching conceptual framework for how the stream will respond to full flows: stream restoration will alter geomorphology by increasing travertine formation, causing non-linear changes in ecosystem productivity and community structure, shifting the stream from a sink to a source of organic carbon in the watershed, with cascading effects on the riparian terrestrial community (Fig. 5).

This model is based on the differences between the travertine terrace and riffle/run sites reported herein, data from on-going studies, and a healthy dose of speculation. We predict that travertine terraces and pools will re-establish once flows are returned, fundamentally changing the geomorphology of this stream. We anticipate the changes in geomorphology will stimulate productivity of the ecosystem above levels predicted by the increase in aquatic habitat, driven by higher

productivity in travertine areas (Fig. 3). This increase in non-linear productivity will in turn enhance species diversity and native fish densities following return of full flows (Table 2, Fig. 4). These increases may be substantial enough that the river will become a major source of energy for associated riparian animals including lizards, spiders, and birds (Jackson and Resh, 1989; Nakano and Murakami, 2001; Sanzone et al., 2003).

One of the side effects of removing dams is the release of sediments stored behind the dam (Stanley and Doyle, 2003). We know of no study that addresses how sediments affect travertine deposition. In Fossil Creek, managers and policy makers are still negotiating whether to remove or lower the diversion dam. This decision has been delayed until 2007 to protect a population of lowland leopard frogs that is concentrated above the dam. If the dam will ultimately be removed, then it will be important to determine how sediment loads affect travertine deposition.

This study shows that by taking a comparative approach towards understanding how geomorphology affects ecological systems can yield predictions about how systems will respond to changes in geomorphology. Ongoing research will capitalize on the decommissioning of dams in Fossil Creek to test these predictions and build a more refined model that couples geomorphology and ecology.

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