Ecosystem responses to restored flow in a travertine river

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Abstract: Disruptions of natural flow impair rivers and streams worldwide. Those conducting restoration efforts have rarely explored how and when stream ecosystems can recover after reinstating natural flows. We quantified responses of ecosystem metabolism and N dynamics to the decommissioning and removal of a 100-y-old diversion dam in a desert stream, Fossil Creek, Arizona. Fossil Creek is a travertine river, meaning that $CaCO_3$ concentrations in water in the springs that feed Fossil Creek are high enough to precipitate out of the water to form travertine terraces and deep pools. The majority of flow was diverted for power generation, so travertine deposition rates were significantly reduced and travertine terraces were smaller and less frequent compared to pre-dam historical records. Flow restoration enabled the recovery of the geochemical process of travertine deposition and increased gross primary production and N uptake to rates comparable to those measured in an upstream, reference reach. Reinstating a river's natural flow regime can result in rapid and near-complete recovery of fundamental ecosystem processes that reshape the aquatic food web.

Key words: restoration, natural flow regimes, ecosystem function, nitrogen uptake, metabolism, travertine, stream ecology, nutrient cycles

Habitat: stream/river
Climate: arid/dry
Country: USA

Human degradation of Earth's ecosystems is extensive and alters biogeochemical cycles and biotic interactions (Scheffer et al. 2001). Degraded ecosystems can be resistant to restoration, which requires addressing ultimate rather than proximate drivers of degradation (Palmer et al. 2014). In rivers, one ultimate driver is water flow, considered a *master variable* (Poff et al. 1997) that influences geomorphological processes, habitat, disturbance, and temperature regimes that, in turn, determine the distributions, abundances, and activities of freshwater and riparian organisms.

Disruptions to river flow (e.g., by impoundments, diversions, and altered watershed surface cover) are a primary cause of river degradation worldwide (Nilsson et al. 2005). Reinstating natural flow regimes is essential to restoring freshwater ecosystems, and flow restoration projects are predicted to succeed in cases where other forms of river restoration fall short, such as channel design, riparian enhancement, and pollution reduction (Palmer et al. 2014). Ecologists' ability to establish the conditions under which restoring natural flow regimes will lead to functional re-

covery of rivers has been hindered by the failure to include functional metrics and the lack of defined goals and monitoring necessary to measure restoration success (Palmer et al. 2014). Assessing the effectiveness of flow restoration requires estimating the extent to which biological processes rebound in rivers with restored flow regimes and identifying the ecological and geomorphic factors that promote or limit such recovery.

We tested whether restoring a river's natural flow regime results in the recovery of ecosystem metabolism and N uptake dynamics after a century of water withdrawals and flow regulation. Fossil Creek is a travertine-forming stream, and reaches with travertine terraces have high biological and biogeochemical activity (Malusa et al. 2003, Fuller et al. 2011). Travertine (or tufa) forms in waters that are supersaturated in $CaCO_3$ as CO_2 degasses causing $CaCO_3$ to precipitate out of the water and deposit in the stream channel (Barnes 1965, Stumm and Morgan 1970, Hoffer-French and Herman 1989). Historical accounts of Fossil Creek describe a series of travertine terraces and pools with the high-

est terraces reaching 3 m (Chamberlain 1904). From 1909–2005, most of the base flow (~1200 L/s) was diverted outside the stream channel for hydropower production, which significantly reduced discharge, travertine precipitation, and travertine dam formation.

We hypothesized that flow restoration in Fossil Creek would alter ecosystem processes, but that responses would vary with geomorphic response to flow. We measured 4 ecosystem processes: gross primary production (GPP), ecosystem respiration (ER), N uptake, and net Ca^{2+} removal before and after flow restoration. We predicted that restored stream flow would increase GPP, ER, the production to respiration ratio (P : R), and NO_3^- uptake at all restored sites, but that responses would be more pronounced in areas where travertine deposition rates were high enough to create a terrace–pool geomorphology (Malusa et al. 2003, Marks et al. 2006, Carter and Marks 2007, Fuller et al. 2011). These predictions were based on observations before restoration in Fossil

Creek and from studies in the Plitvice Lakes (Croatia) that demonstrated increases in primary productivity and decomposition with $CaCO_3$ deposition (Carter and Marks 2007, Belančić et al. 2009, Miliša et al. 2010)

METHODS
Site description
Fossil Creek originates from a series of 7 springs (UTM Zone 12: 3809309 N, 447275 E; elevation 1304 m asl) and flows 22.4 km to its confluence with the Verde River (Figs 1A–E, 2A, B). Base flow is 1218 L/s with high concentrations of Ca^{2+} and HCO_3^- (Table S1; Malusa et al. 2003). CO_2 outgassing creates super-saturation of Ca^{2+}, causing calcite deposition and the formation of travertine (Fig. 1C, D; Malusa et al. 2003, Fuller et al. 2011). In 1909, an 8-m-high dam (Fig. 1E) was built to divert almost the entire base flow of the stream (>90%; cf. Fig. 1A, B) to 2 down-
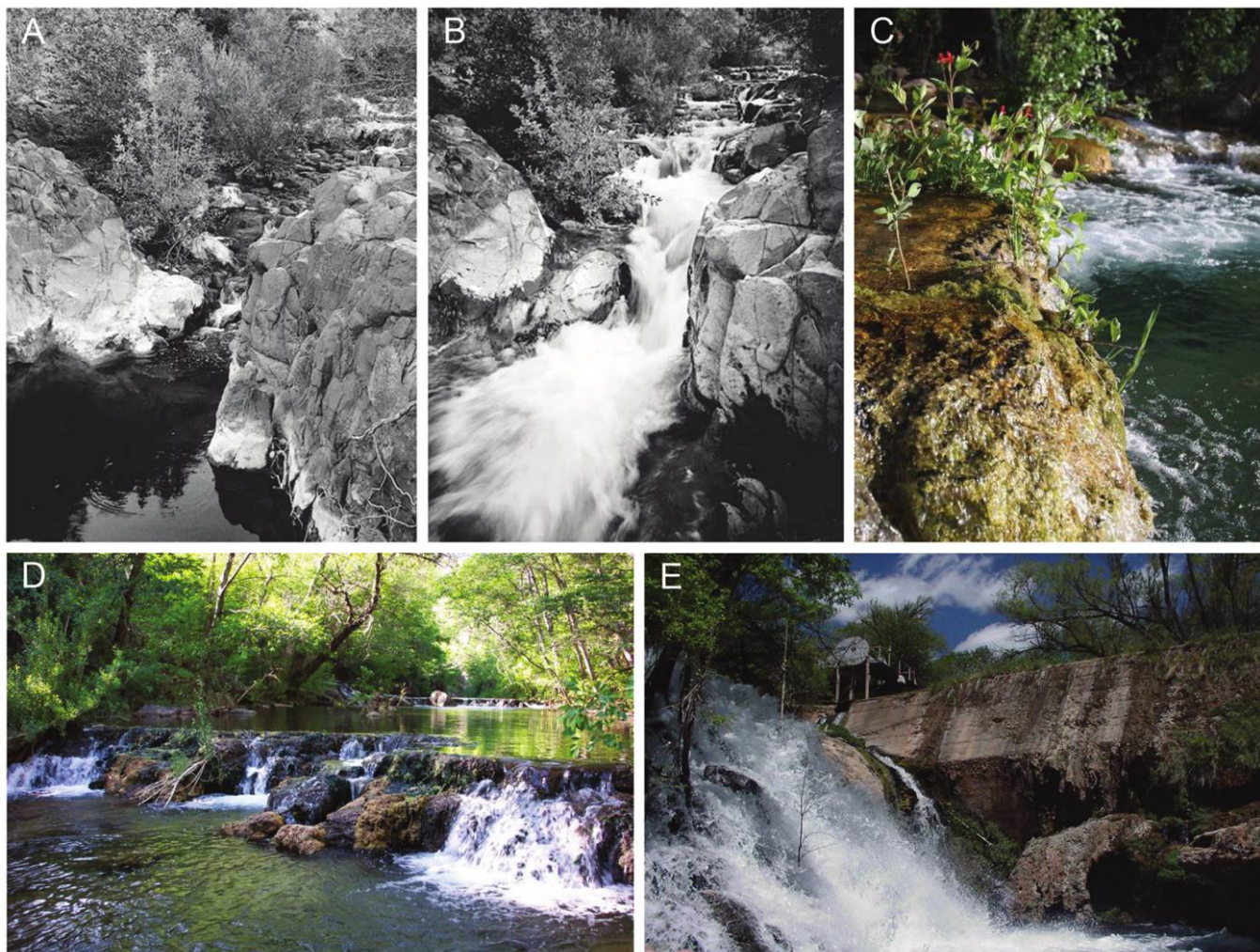

Figure 1. Photographs before (A) and after (B) flow restoration showing change in water flow below the Irving Power Plant (photo credit: N. Berezenko), travertine dam structures in close-up (C) and showing channel-spanning morphology (D), and the diversion dam after flow restoration but before the dam was actually removed (E).
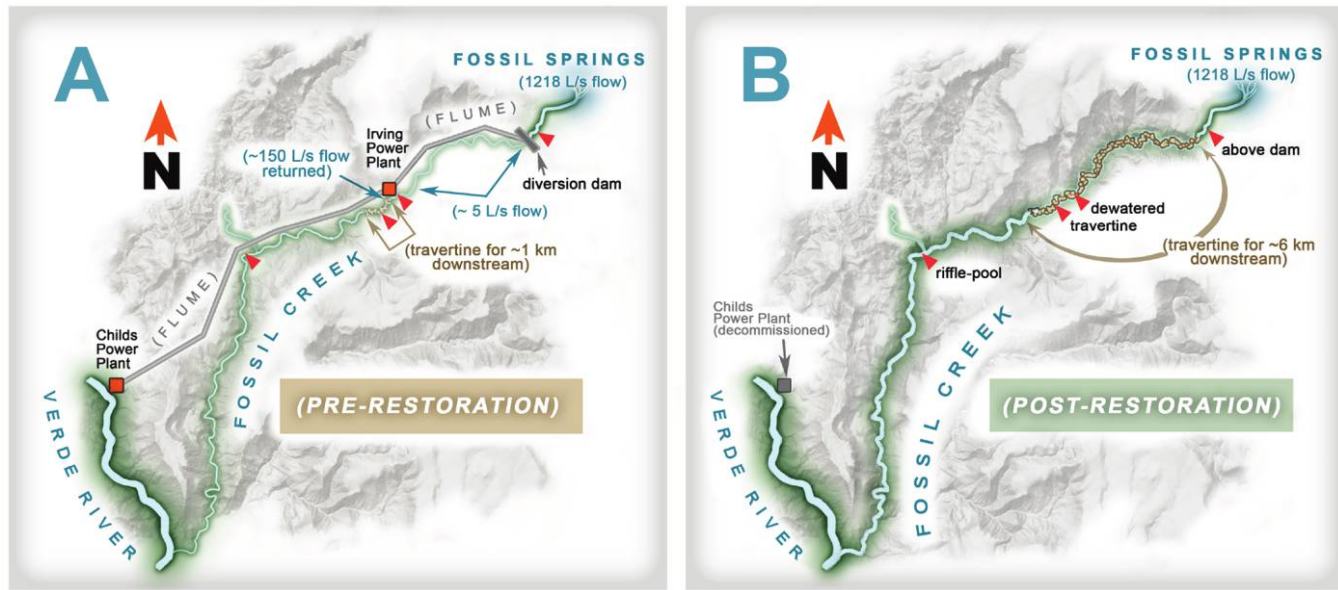
Figure 2. Site map of Fossil Creek, Arizona (UTM Zone 12: 3809309 N, 447275 E). Red triangles indicate sampling sites. Channel sections with active, channel-spanning travertine terraces and pools are indicated before (A) and after (B) restoration of stream flow.

stream hydropower facilities: Irving (5 km below the dam; Fig. 1E) and Childs (27 km below the dam), which was on the Verde River (Fig. 2A). From 1909–2005, the Irving facility returned ~65 to 198 L/s to the creek and supported an ~1-km downstream reach with active travertine deposition, forming travertine dams that spanned the river channel (Fig. 1D; Malusa et al. 2003, Dinger and Marks 2007). Approximately 3 km downstream of Irving, travertine deposition was absent, and the river switched to a riffle–pool geomorphology (Fig. 2B). This was a run-of-the-river dam so the entire river below the dam experienced flood flows over the duration of the power plant operation. Our study was designed to measure how restoring base flow affected ecosystem processes because flood flows did not change before and after restoration.

Restoration of Fossil Creek occurred in stages. The 1st stage was to treat the river with antimycin A to remove exotic fish. In October–November 2004, native fish were salvaged, held in tanks, and reintroduced into the river 3 wk after treatment with antimycin A. In June 2005, the dam was decommissioned, and full flows were returned to the river. In 2009, the dam was lowered, and the small (<0.5 ha) reservoir upstream of the dam was drained (see Marks et al. 2010 and Dinger and Marks 2007 for a description of native fish and macroinvertebrate recovery). Travertine deposition increased dramatically following restoration. Travertine terrace formation increased an average of 2 cm/y and was associated with trapped organic matter and algal growth (Fuller et al. 2011).

We measured rates of Ca^{2+} removal, ecosystem metabolism, and NO_3^- uptake before and after restoration at 4 sites (Fig. 2A, B): 1) downstream of the spring heads and upstream of the small reservoir created by the dam (reference reach); 2) immediately upstream of the Irving power plant, which had the highest level of water diversion prior to restoration; 3) ~1 km downstream of Irving in the reach supporting travertine formation; and 4) in a riffle–pool section of the stream ~3 km downstream of Irving where travertine deposits were absent/minimal (Fig. 2B). All sampled reaches were 100 to 200 m long. Sampling was conducted 22 July 2004, 11 October 2004, 16 June 2005, 11 May 2008, and 21 September 2011. After dam removal, the reference reach was transformed from a single channel to a complex network of small channels, so this reference site could not be sampled in 2011.

NO_3^- uptake and Ca^{2+} removal rates

At each site on each date, we measured NO_3^- uptake using short-term NO_3^- additions (Webster and Valett 2006). Before each NO_3^- addition, we collected 5 water samples at evenly spaced intervals along each reach. We added $NaNO_3$ and $NaBr$ (as a conservative tracer) with a pump (2004–2008: Watson–Marlowe peristaltic pump, 2011: model RHB; Fluid Metering, Syosset, New York). Solute drip rate and concentration were designed to achieve an enrichment of 25 μg N/L above ambient concentrations for NO_3-N. Time to plateau averaged 90 min across all sites and dates and ranged from 50 to 140 min. We monitored Br^- concentration with a Br^- specific probe (Orion Bromide Electrode Model 94-35; Thermo Scientific, Beverly, Massachusetts) at the bottom of the reach and collected water samples in triplicate every 30 m after $[Br^-]$ reached a plateau. We filtered water samples through glass-fiber filters

Spatial Extent: drainage basin
Temporal Extent: years
Source Data: Field
Study Type: maniupulation
Study Design: before vs. after (no control)
Number of Independent Sampling Units: 4

(Whatman GF/F; Whatman, Maidstone, UK) in the field into acid-washed bottles. We conducted separate solute additions in each reach, typically sampling 1 reach/d over a 4- to 5-d period. No storms or other major hydrologic disturbances occurred during those sampling periods.

We kept water samples on ice until they could be frozen in the laboratory. We analyzed NO_3^- by ion chromatography (2004: Dionex DX-600, 2011: Dionex 2100; Sunnyvale, California) or a flow-injection analyzer (2005–2008: Quik-Chem 8000 Series FIA+; Lachat Instruments, Loveland, Colorado). We analyzed Br^- by ion chromatography (2004: Dionex DX-600, 2005–2008: Dionex 100, 2011: Dionex 2100; Dionex). We used the Br^- addition rate and concentration to calculate discharge (Webster and Valett 2006). Nutrient uptake length (S_w; m), the average distance traveled by a nutrient molecule before being taken up into a particulate form, was calculated as the inverse slope of the line describing the exponential decline in NO_3^- concentration relative to Br^- over downstream distance:

$$\ln N_x = \ln N_0 - kx, \qquad \text{(Eq. 1)}$$

where N_x is the background-corrected NO3-N concentration divided by the Br^- concentration at the sampling site, N_0 is the background-corrected NO3-N concentration divided by the Br^- concentration at the top of the reach, k is the 1/m uptake rate constant, and x is the distance from the top of the reach (Webster and Valett 2006). We calculated nutrient uptake velocity (V_f; mm/min) with standard methods (Webster and Valett 2006).

We measured net removal of Ca^{2+} from the water column as a proxy for travertine deposition at the reach scale. We calculated Ca^{2+} uptake rate based on mass balance (Von Schiller et al. 2008), using the equation described above and substituting Ca^{2+} concentration for background corrected NO3-N concentration. We calculated areal deposition rate (mg Ca^{2+} m^{-2} h^{-1}) using S_w and mean water-column [Ca^{2+}] according to standard methods (Payn et al. 2005, Webster and Valett 2006).

Metabolism

We used a single-station, open-water approach to measure metabolism for 24 h. We measured temperature and dissolved O_2 at 5-min intervals with a temperature and dissolved O_2 probe (2004–2005: Hydrolab DataSonde 4a, Hydrolab–Hach Corporation, Loveland, Colorado; 2008–2011: YSI 600 OMS with optical DO probe, Yellow Springs Instruments, Yellow Springs, Ohio). We field-calibrated probes to air-saturated stream water at ambient temperature prior to each deployment. We estimated reaeration based on sulfur hexafluoride (SF_6) constant-rate injection after Br^- returned to pre-NO_3^- addition levels (Hall and Hotchkiss 2017).

We collected 3 replicate samples in 5-mL Vacutainers® every 20- to 30-m downstream of the injection site. Headspace SF_6 was measured on a gas chromatograph with a flame ionization detector (Agilent 7890A; Agilent Technologies, Santa Clara, California) and reaeration was calculated with the equations:

$$\ln C_x = \ln C_0 - k_{SF6}x, \qquad \text{(Eq. 2)}$$
$$K_{SF6} = k_{SF6}v, \qquad \text{(Eq. 3)}$$

where C_x and C_0 are the dilution-corrected SF_6 concentrations throughout and at the top of the reach, k_{SF6} is the per-meter decline of SF_6, x is the distance downstream, K_{SF6} is the per-time decline in SF_6, and v is average stream velocity. We estimated stream velocity by measuring the time for 50% of the Br^- tracer used in the NO_3^- addition to pass the downstream station and dividing the reach length by this travel time (Hall et al. 2016). We converted the rate of SF_6 reaeration to that of O_2 by multiplying by the Schmidt number (1.4), corrected for temperature (Hall et al. 2015). O_2 data were fit to a metabolism model (Van de Bogert et al. 2007, Genzoli and Hall 2016):

$$mO_{2(t)} = mO_{2(t-1)} + \left(\frac{GPP_{Total}}{\bar{z}} \times \frac{PPFD_t}{\sum PPFD_{24}} \right)$$
$$+ \left(\frac{R_{Total}}{\bar{z}} \times \Delta t \right) + K_{(t)}\left(O_{2sat(t)} - mO_{2(t-1)} \right) \Delta t, \qquad \text{(Eq. 4)}$$

where mO_2 is modeled O_2 (mg/L) at time t, GPP_{Total} is GPP (g O_2 m^{-2} d^{-1}), $\bar{z}$ (m) is mean reach depth, PPFD is solar insolation (μmol photons m^{-2} s^{-1}) at time, t, $\sum PPFD_{24}$ is daily solar insolation (Yard et al. 2005), R_{Total} is ER (g O_2 m^{-2} d^{-1}), Δt is the time between O_2 measurements (5 min), and $K_{(t)}$ is K_{SF6} corrected for temperature and each time-step. We fit the equation to the observed O_2 data by selecting the parameter values that minimized the negative log-likelihood function of a normal distribution using function *nlm* in R (version 3.2.3; R Project for Statistical Computing, Vienna, Austria) to solve for GPP_{Total} and R_{Total} (Hall et al. 2015, Genzoli and Hall 2016). Metabolism was not measured in the dewatered site in July 2004 and June 2005.

Data analysis

To test whether ecosystem processes recovered in response to flow restoration, we examined differences in average values before and after restoration across all sites downstream of the dam. One sampling date occurred coincidentally with the restoration of flows (June 2005), so we did not include these data from the downstream sites in the before vs after comparisons. We used permutation tests with 1000 iterations to test whether differences in pre- and post-restoration V_{fNO3}, stream metabolism fluxes, and Ca^{2+} deposition rates deviated from 0. We calculated 95% confidence intervals (CIs) for all variables using bootstrapping. Permutation and bootstrapping were performed in R.

For each variable, we provided context for observed differences by comparing responses below the dam to tempo-

ral variability at the reference (above-dam) site. We measured variables at the single reference site on only 1 to 2 dates during the pre- and post-restoration periods, so pre- to post-restoration differences at this site could not be tested with permutation tests.

To quantify the relationships among travertine deposition, stream metabolism, and NO_3^- uptake, we used ordinary least squares regression and included data across all sites and sampling dates. We tested for 3 relationships: 1) GPP and Ca^{2+} deposition, predicting that increased Ca^{2+} deposition would lead to increased primary productivity, 2) V_{fNO3} and GPP, predicting that increased GPP would increase N uptake, and 3) ER and GPP, predicting that sites with high GPP also would have higher ER. Residuals were normally distributed for all regressions.

RESULTS

As predicted, restoration of natural flows in Fossil Creek increased travertine deposition $>20\times$ (difference in means $= +8.95$ mg Ca m^{-2} h^{-1}, $n_{before} = 6$, $n_{after} = 6$, $p = 0.003$; Fig. 3A), GPP by $1.5\times$ (difference in means $= +1.98$ g O_2 m^{-2} d^{-1}, $n_{before} = 5$, $n_{after} = 6$, $p = 0.023$, Fig. 3B), and V_{fNO3} by $12\times$ (difference in means $= +19.0$ mm/min, $n_{before} = 6$, $n_{after} = 6$, $p = 0.002$; Fig. 3E). Contrary to our predictions, ER did not change after the return of natural flows (difference in means $= -0.86$ g O_2 m^{-2} d^{-1}, $n_{before} = 5$, $n_{after} = 6$, $p = 0.273$; Fig. 3C). With greater GPP and no change in ER, the P : R ratio increased in reaches downstream of the dam (difference in means $= +0.407$, $n_{before} = 5$, $n_{after} = 6$, $p = 0.035$; Fig. 3D).

Travertine deposition

High rates of travertine deposition were associated with high rates of in-stream GPP. The highest rates of Ca^{2+} removal occurred after flow restoration in the formerly dewatered reach where water-column Ca^{2+}, velocity, and discharge were highest (Table S1, Fig. 4A), whereas travertine formation above the dam was not evident (Fig. 4A). Where geochemical conditions allowed Ca^{2+} deposition, GPP increased with Ca^{2+} deposition rate (GPP $= 1.74 + 0.136$(Ca flux), $n = 13$, $R^2 = 0.403$, $F_{1,11} = 7.43$, $p = 0.020$; Fig. 4A), supporting our hypothesis that elevated travertine deposition would stimulate autochthonous production.

Stream metabolism and NO_3^- dynamics

GPP varied $10\times$ across all sampling sites and dates (Table S1, Fig. 4B). GPP was <2 g O_2 m^{-2} d^{-1} below the dam before the restoration of flow, but doubled after flows were returned (Fig. 3B). The increase in GPP was associated with higher rates of NO_3^- uptake ($V_{fNO3} = -11.0 + 10.5$GPP, $n = 16$, $R^2 = 0.644$, $F_{1,14} = 25.4$, $p = 0.0002$; Fig. 4B), supporting our prediction that increased autoch-
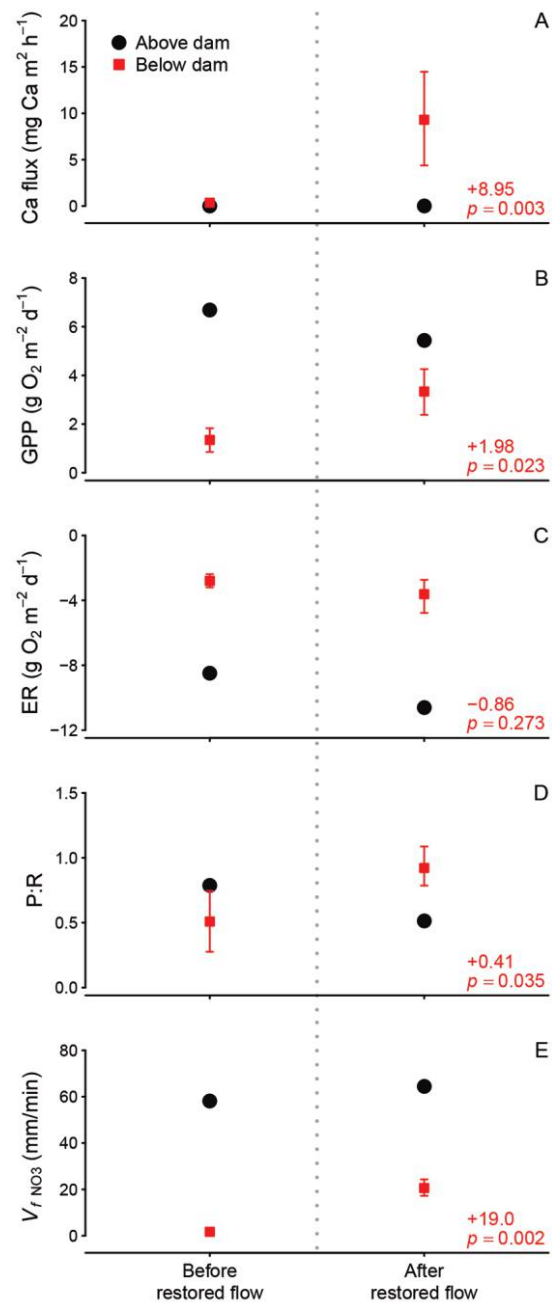
Figure 3. The restoration of natural flows in Fossil Creek altered multiple ecosystem processes including Ca^{2+} deposition rate (Ca flux) (A), gross primary production (GPP) (B), production to respiration ratio (P : R) (D), and NO_3^- uptake velocity (V_{fNO3}) (E). In-stream ecosystem respiration (ER) (C) did not change. Square symbols and error bars indicate medians and 95% confidence intervals of bootstrapped distributions for 6 site–date measurements throughout an 11-km study reach below the dam. The difference in means (*after − before*) and estimated *p*-value from a permutation test with 1000 iterations is shown for each variable. Circular symbols indicate the mean of 2 measurements (before flow restoration) or a single measurement (after flow restoration) from a 180-m reference reach immediately upstream of the dam.
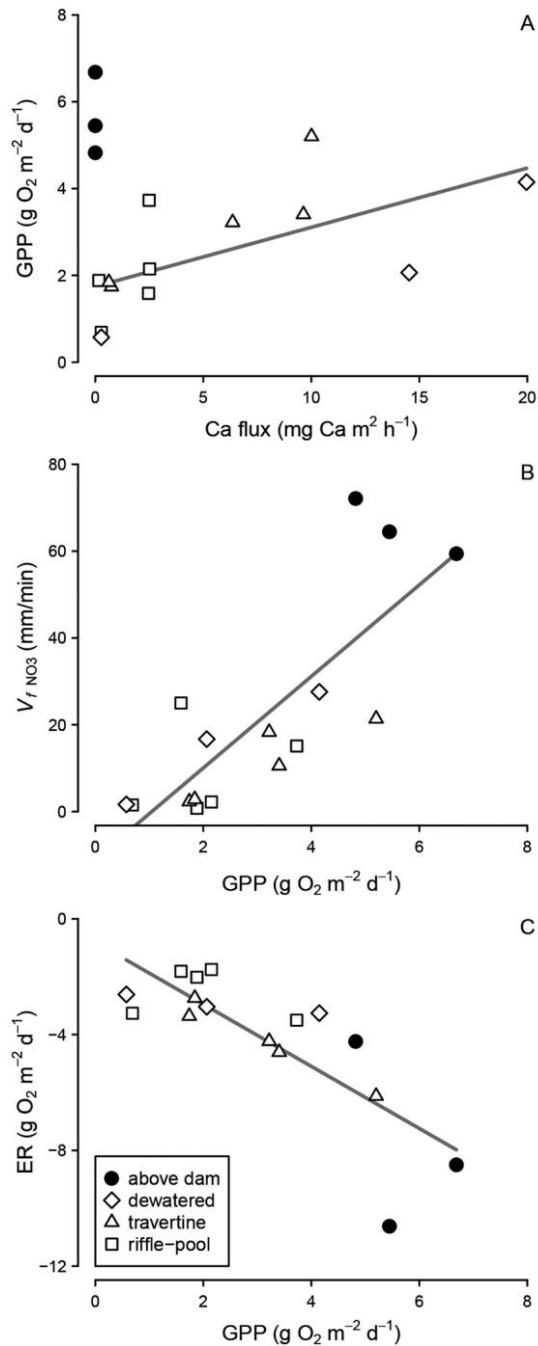
Figure 4. A.—Gross primary production (GPP) was positively related to Ca^{2+} deposition rate (Ca flux) for all sampling dates and reaches below the dam in Fossil Creek (GPP = 1.74 + 0.136 Ca flux, $n = 13$, $R^2 = 0.403$, $F_{1,11} = 7.43$, $p = 0.020$). No relationship was found when measurements from the reach above the dam were included (GPP = 2.88 + 0.044 Ca flux, $n = 16$, $R^2 = 0.022$, $F_{1,14} = 0.316$, $p = 0.583$, regression line not shown). B.—NO_3^- uptake velocity (V_{fNO3}) was positively related to GPP across all sampling dates and sites ($V_{fNO3} = -11.0 + 10.5$GPP, $n = 16$, $R^2 = 0.644$, $F_{1,14} = 25.4$, $p = 0.0002$). C.—Ecosystem respiration (ER) was related to GPP across all dates and sites (ER = $-0.805 - 1.07$GPP, $n = 16$, $R^2 = 0.633$, $F_{1,14} = 24.1$, $p = 0.0002$).

thonous production would stimulate NO_3^- demand with full stream flow.

ER did not respond to flow restoration (Fig. 3C). ER was negatively related to GPP (ER = $-0.805 - 1.07$GPP, $n = 16$, $R^2 = 0.633$, $F_{1,14} = 24.1$, $p = 0.0002$; Fig. 4C), indicating that photosynthetic algae responded more strongly than heterotrophic microbes to flow restoration. Autochthonous production amounted to ½ of total respiration prior to restoration, but roughly equaled the in-stream respiration flux after the return of flows (P : R ratio, Fig. 3D). V_{fNO3} increased with the absolute value of ER ($V_{fNO3} = -7.20 + 6.97|$ER$|$, $n = 16$, $R^2 = 0.512$, $F_{1,14} = 14.7$, $p = 0.002$), but the relationship was weaker than that for GPP.

DISCUSSION

Restoring flow altered multiple ecosystem processes in Fossil Creek. Despite 100 y of nearly complete water withdrawal, V_{fNO3} and whole-stream GPP rebounded <3 y after flow restoration, approaching values typical of reference conditions. These data demonstrate that function-based restoration that addresses a root cause of ecosystem degradation can succeed in restoring rates of physical and biological processes (Beechie et al. 2010).

Functional metrics, such as N uptake and metabolism, may be more appropriate for evaluating stream restoration than structural metrics because they describe energy flow and nutrient cycling, critical processes for higher trophic levels and ecosystem dynamics (Palmer and Febria 2012). Flow restoration restored autotrophy in Fossil Creek and increased P : R of the previously dewatered reaches from 0.51 to 0.97, closely matching values for minimally disturbed western streams, which tend to have P : R values just above 1 (Fisher 2006). V_{fNO3} increased with GPP because of the strong link between C fixation and N demand (Hall and Tank 2003). Furthermore, elevated GPP shifted the base of the food web in Fossil Creek and led to a greater reliance of the native fish assemblage on algae (O'Neill 2013). In short, reinstating the natural flow regime resulted in dramatic shifts in biogeochemical fluxes that propagated through the ecosystem. These results stand in contrast with many structure-based restoration projects in which reengineering channel geomorphology and riparian vegetation has rarely improved in-stream metabolism and nutrient retention (Hoellein et al. 2012).

Geomorphic response to restoration: travertine deposition

Restored reaches in Fossil Creek experienced a 10 to 100× increase in travertine deposition (Fuller et al. 2011). Travertine dams provide rich habitat and enhance primary productivity (Malusa et al. 2003, Carter and Marks 2007), consistent with the positive correlation between Ca^{2+} deposition and GPP we observed (Fig. 4A). During our summer

measurements, Ca^{2+} deposition was not correlated with reach-scale ER, and the tight correlation of ER with GPP (Fig. 4C) indicated dominance of respiration by autotrophs (Roberts et al. 2007). The effect of travertine deposition on litter decomposition and invertebrate abundance is not consistent across ecosystems. For example, in a Mediterranean stream in Spain, travertine deposition was associated with slower decomposition rates and lower invertebrate abundances (Casas and Gessner 1999). Similarly, in streams along the California coast (Big Sur, USA), invertebrate densities were inversely correlated with travertine deposition rates (Rundio 2009). In contrast, in the Plitvice Lakes in Croatia, like Fossil Creek, travertine deposition was associated with increased decomposition and invertebrate abundance (Belančić et al. 2009, Miliša et al. 2010). One possible explanation for this discrepancy is that the Plitvice Lakes and Fossil Creek have relatively high flow rates and steep gradients, such that travertine deposition forms large terraces and deep pools. In contrast, in other travertine ecosystems deposition may cement the substrate, thereby interfering with decomposition (Casas and Gessner 1999). We did not measure reach-scale ER after litterfall but we would expect different patterns in autumn because travertine dams in Fossil Creek retain leaf litter (Compson et al. 2009), and leaves decompose more rapidly in channels with travertine dams than in riffle–pool reaches (Carter and Marks 2007). Reaeration rates were 30 to 45% higher after flow restoration, and Ca^{2+} mass fluxes were 2 to 3 orders of magnitude higher. It is likely that the increase in Ca^{2+} deposition is the result of more available Ca^{2+}, higher CO_2 efflux from higher reaeration creating favorable chemical conditions for deposition and, potentially, the positive feedback loop of initial travertine formation creating higher roughness, which leads to greater travertine deposition (Fuller et al. 2011, Florsheim et al. 2013).

Biological response to restoration: metabolism

GPP nearly doubled after flow restoration and approached values (1.5–5.2 g O_2 m^{-2} d^{-1}) similar to other southwestern streams in undeveloped watersheds (Bernot et al. 2010). In contrast, ER did not change after flow restoration, and values (1.8–6.1 g O_2 m^{-2} d^{-1}) were slightly lower than those measured for similar southwestern streams (Bernot et al. 2010). Increased stream flow may have increased GPP because higher water velocities (Table S1) can promote algal growth by increasing nutrient delivery (King et al. 2014). In addition, the increase in travertine deposition created more shallow pools below the travertine terraces that had visible large blooms of filamentous green algae. Because GPP increased at all sites where flow was restored but was higher in sites with higher travertine deposition, we think it likely that the increase in flow interacted with the changes in geomorphology to create better conditions for algal growth. Multiple mechanisms could explain

why ER did not increase with increased GPP. We think that the 2 most likely mechanisms are: 1) Leaf litter inputs did not change because the dam was run of the river, and the riparian forest was not significantly altered despite the increase in base flow; and 2) Retention of coarse particulate organic matter decreased with increased flow (Compson et al. 2009). In summary, any increases in respiration driven by increases in algal productivity were offset by decreases in respiration caused by lower retention of leaf litter.

Biological response to restoration: N dynamics

The increase in GPP in response to flow restoration fueled greater demand for N, as indicated by a 6× increase in V_{fNO3}. Post-restoration values of V_{fNO3} (15.1–27.6 mm/min) were at the high end of values for headwater streams (Hall et al. 2009). N can limit GPP in southwestern streams (Grimm and Fisher 1986), and these high V_f values probably reflect strong N-limitation in Fossil Creek. Similar patterns of strong autotrophic control of NO_3^- uptake are typical of well-lit, western streams (Hall and Tank 2003, Arango et al. 2015).

The springs above the decommissioned dam supplied much of the N to downstream reaches. NO_3^- concentration was highest above the dam and did not vary from before to after restoration (~125 μg N/L). After the restoration of flow, NO_3^- concentrations declined to 2.7 μg/L at the furthest downstream site, a consequence of the high biotic demand for N in the restored reaches that removed most dissolved NO_3^- from the water column.

Nutrient enrichment studies in Fossil Creek before restoration indicated that algae in this stream were limited by N and P in the summer and were limited by N in autumn (Carter and Marks 2007). Travertine deposition can reduce P concentrations in the water column because of coprecipitation with $CaCO_3$ (Corman et al. 2015, 2016) and may consequently be associated with decreased periphyton biomass due to P limitation (Corman et al. 2016). In Fossil Creek, however, we observed increased primary productivity associated with $CaCO_3$ deposition suggesting that P may not be as limiting to autotrophs in this stream. Future studies along the travertine gradient in Fossil Creek focusing on P dynamics could test for interactions among travertine, P, and GPP in this ecosystem.

We interpret the postrestoration increase in N uptake primarily as a consequence of increased GPP. The increase also could be caused, in part, by increased denitrification, which we did not measure. Denitrification can represent a large proportion of N retention, but median values of denitrification across stream ecosystems are ~16% (Mulholland et al. 2008). Denitrification rates tend to be higher in streams with significantly higher NO_3^- concentrations than Fossil Creek, under anaerobic conditions, and where respiration rates are high (Mulholland et al. 2008, Graham et al. 2010). The high discharge, high dissolved O_2, low ambient

N levels, and high rates of GPP lead us to conclude that the most parsimonious explanation for the increase in N uptake is the increase in GPP. Hot spots of denitrification could exist in Fossil Creek, and future research focusing on denitrification could elucidate unexplored relationships between travertine deposition and denitrification.

Implications for river restoration

Disruption of flow is the most common driver of river degradation worldwide (Nilsson et al. 2005). Nevertheless, most stream restoration projects in the USA do not target flow, but rather undertake costly geomorphic modifications despite little evidence of their effects on in-stream ecosystem processes (Palmer et al. 2014). Streams are defined by flowing water, and restoring flow may go a long way toward achieving functional recovery in degraded rivers.

Our findings inform river restoration following dam removal, which have increased 10× in the USA over the last 30 y (O'Connor et al. 2015). Geomorphic and biogeochemical fluxes responded quickly to restored flow in Fossil Creek, and those changes were sustained for at least 6 y. Future studies of dam removals across a range of rivers will help reveal the conditions under which restoring natural flow leads to nearly complete recovery and when it does not. Nevertheless, our work demonstrates the resiliency of streams and the primacy of the natural flow regime.

LITERATURE CITED

Arango, C. P., P. W. James, and K. B. Hatch. 2015. Rapid ecosystem response to restoration in an urban stream. Hydrobiologia 749: 197–211.

Barnes, I. 1965. Geochemistry of Birch Creek, Inyo County, California a travertine depositing creek in an arid climate. Geochimica et Cosmochimica Acta 29:85–112.

Beechie, T. J., D. A. Sear, J. D. Olden, G. R. Pess, J. M. Buffington, H. Moir, P. Roni, and M. M. Pollock. 2010. Process-based principles for restoring river ecosystems. BioScience 60:209–222.

Belančić, A., R. M. Kepčija, M. Miliša, A. P. Moraj, and I. Habdija. 2009. Flow velocity effect on leaf litter breakdown in tufa depositing system (Plitvice Lakes, Croatia). International Review of Hydrobiology 94:391–398.

Bernot, M. J., D. J. Sobota, R. O. Hall, P. J. Mulholland, W. K. Dodds, J. R. Webster, J. L. Tank, L. R. Ashkenas, L. W. Cooper, C. N. Dahm, S. V. Gregory, N. B. Grimm, S. K. Hamilton, S. L. Johnson, W. H. McDowell, J. L. Meyer, B. Peterson, G. C. Poole, H. M. Valett, C. Arango, J. J. Beaulieu, A. J. Burgin, C. Crenshaw, A. M. Helton, L. Johnson, J. Merriam, B. R. Niederlehner, J. M. O'Brien, J. D. Potter, R. W. Sheibley, S. M. Thomas, and K. Wilson. 2010. Inter-regional comparison of land-use effects on stream metabolism. Freshwater Biology 55:1874–1890.

Casas, J. J., and M. O. Gessner 1999. Leaf litter breakdown in a Mediterranean stream characterized by travertine precipitation. Freshwater Biology 41:781–793.

Carter, C. D., and J. C. Marks. 2007. Influences of travertine dam formation on leaf litter decomposition and algal accrual. Hydrobiologia 575:329–341.

Chamberlain, F. M. 1904. Notes on work in Arizona – 1904. Unpublished report on file with the Smithsonian Institution Archives, Washington, DC.

Compson, Z. G., M. Z. Mier, and J. C. Marks. 2009. Effects of travertine and flow on leaf retention in Fossil Creek, Arizona. Hydrobiologia 630:187–197.

Corman, J. R., E. K. Moody, and J. J. Elser. 2015. Stoichiometric impact of calcium carbonate deposition on nitrogen and phosphorus supplies in three montane streams. Biogeochemistry 126:285–300.

Corman, J. R., E. K. Moody, and J. J. Elser. 2016. Calcium carbonate deposition drives nutrient cycling in a calcareous headwater stream. Ecological Monographs 86:448–461.

Dinger, E. C., and J. C. Marks. 2007. Effects of high levels of antimycin A on aquatic invertebrates in a warm water Arizona stream. North American Journal of Fisheries Management 27: 1243–1256.

Fisher, S. G. 2006. Stream ecosystems of the western United States. Pages 61–88 in C. E. Cushing, K. W. Cummins, and G. W. Minshall (editors). River and stream ecosystems of the world. University of California Press, Berkeley, California.

Florsheim, J. L., S. L. Ustin, Y. Tang, B. Di, C. Huang, X. Qiao, H. Peng, M. Zhang, Y. Cai. 2013. Basin-scale and travertine dam-scale controls on fluvial travertine, Jiuzhaigou, southwestern China. Geomorphology 180/181:267–280.

Fuller, B. M., L. S. Sklar, Z. G. Compson, K. J. Adams, J. C. Marks, and A. C. Wilcox. 2011. Ecogeomorphic feedbacks in regrowth of travertine step-pool morphology after dam decommissioning, Fossil Creek, Arizona. Geomorphology 126:314–332.

Genzoli, L., and R. O. Hall. 2016. Shifts in Klamath River metabolism following a reservoir cyanobacterial bloom. Freshwater Science 35:795–809.

Graham, D. W., C. Trippett, W. K. Dodds, J. M. O'Brien, E. B. Banner, I. M. Head, M. S. Smith, R. K. Yang, and C. W. Knapp. 2010. Correlations between in situ denitrification activity and nir-gene abundances in pristine and impacted prairie streams. Environmental Pollution 158:3225–3229.

Grimm, N. B., and S. G. Fisher. 1986. Nitrogen limitation in a Sonoran Desert stream. Journal of the North American Benthological Society 5:2–15.

Hall, R. O., and E. R. Hotchkiss. 2017. Stream metabolism. Pages 219–233 in G. A. Lamberti and F. R. Hauer (editors). Methods in stream ecology. Volume 2: Ecosystem function. Academic Press, London, UK.

Hall, R. O., and J. L. Tank. 2003. Ecosystem metabolism controls nitrogen uptake in streams in Grand Teton National Park, Wyoming. Limnology and Oceanography 48:1120–1128.

Hall, R. O., J. L. Tank, M. A. Baker, E. J. Rosi-Marshall, and E. R. Hotchkiss. 2016. Metabolism, gas exchange, and carbon spiraling in rivers. Ecosystems 19:73–86.

Hall, R. O., J. L. Tank, D. J. Sobota, and P. J. Mulholland. 2009. Nitrate removal in stream ecosystems measured by N addition experiments: total uptake. Limnology and Oceanography 54:653–665.

Hall, R. O., C. B. Yackulic, T. A. Kennedy, M. D. Yard, E. J. Rosi-Marshall, N. Voichick, and K. E. Behn. 2015. Turbidity, light, temperature, and hydropeaking control primary productivity in the Colorado River, Grand Canyon. Limnology and Oceanography 60:512–526.

Hoellein, T. J., J. L. Tank, S. A. Entrekin, E. J. Rosi-Marshall, M. L. Stephen, and G. A. Lamberti. 2012. Effects of benthic habitat restoration on nutrient uptake and ecosystem metabolism in three headwater streams. River Research and Applications 28:1451–1461.

Hoffer-French, K. J., and J. S. Herman. 1989. Evaluation of hydrological and biological influences on CO_2 fluxes from a karst stream. Journal of Hydrology 108:189–212.

King, S. A., J. B. Heffernan, and M. J. Cohen. 2014. Nutrient flux, uptake, and autotrophic limitation in streams and rivers. Freshwater Science 33:85–98.

Malusa, J., S. T. Overby, and R. A. Parnell. 2003. Potential for travertine formation: Fossil Creek, Arizona. Applied Geochemistry 18:1081–1093.

Marks, J. C., G. A. Haden, M. O'Neill, and C. Pace. 2010. Effects of flow restoration and exotic species removal on recovery of native fish: lessons from a dam decommissioning. Restoration Ecology 18:934–943.

Marks, J. C., R. Parnell, C. Carter, E. C. Dinger, and G. A. Haden. 2006. Interactions between geomorphology and ecosystem processes in travertine streams: implications for decommissioning a dam on Fossil Creek, Arizona. Geomorphology 77:299–307.

Miliša, M., A. Belančić, R. M. Kepčija, M. Sertić-Perić, A. Ostojić, and I. Habdija. 2010. Calcite deposition in karst waters is promoted by leaf litter breakdown and vice versa. Annales de Limnologie – International Journal of Limnology 46:225–232.

Mulholland, P. J., A. M. Helton, G. C. Poole, R. O. Hall, S. K. Hamilton, B. J. Peterson, J. L. Tank, L. R. Ashkenas, L. W. Cooper, C. N. Dahm, and W. K. Dodds. 2008. Stream denitrification across biomes and its response to anthropogenic nitrate loading. Nature 452:202–205.

Nilsson, C., C. A. Reidy, M. Dynesius, and C. Revenga. 2005. Fragmentation and flow regulation of the world's large river systems. Science 308:405–408.

O'Connor, J. E., J. J. Duda, and G. E. Grant. 2015. 1000 dams down and counting. Science 348:496–497.

O'Neill, M. W. 2013. An ecophysiological approach to native fish conservation. PhD Dissertation, Northern Arizona University, Flagstaff, Arizona.

Palmer, M. A., and C. M. Febria. 2012. The heartbeat of ecosystems. Science 336:1393–1394.

Palmer, M. A., K. L. Hondula, and B. J. Koch. 2014. Ecological restoration of streams and rivers: shifting strategies and shifting goals. Annual Review of Ecology, Evolution, and Systematics 45:247–269.

Payn, R. A., J. R. Webster, P. J. Mulholland, H. M. Valett, and W. K. Dodds. 2005. Estimation of stream nutrient uptake from nutrient addition experiments. Limnology and Oceanography: Methods 3:174–182.

Poff, N. L., J. D. Allan, M. B. Bain, J. R. Karr, K. L. Prestegaard, B. D. Richter, R. E. Sparks, and J. C. Stromberg. 1997. The natural flow regime. BioScience 47:769–784.

Roberts, B. J., P. J. Mulholland, and W. R. Hill. 2007. Multiple scales of temporal variability in ecosystem metabolism rates: results from 2 years of continuous monitoring in a forested headwater stream. Ecosystems 10:588–606.

Rundio, D. E. 2009. Community–habitat relationships in coastal streams in Big Sur, California, USA: travertine influences macroinvertebrate abundance and community structure. Hydrobiologia 620:91–108.

Scheffer, M., S. Carpenter, J. A. Foley, C. Folke, and B. Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

Stumm, W., and J. J. Morgan. 1970. Aquatic chemistry: an introduction emphasizing chemical equilibria in natural waters. Wiley–Interscience, New York.

Van de Bogert, M. C., S. R. Carpenter, J. J. Cole, and M. L. Pace. 2007. Assessing pelagic and benthic metabolism using free water measurements. Limnology and Oceanography: Methods 5:145–155.

Von Schiller, D., E. Martí, J. L. Riera, M. Ribot, J. C. Marks, and F. Sabater. 2008. Influence of land use on stream ecosystem function in a Mediterranean catchment. Freshwater Biology 53:2600–2612.

Webster, J. R., and H. M. Valett. 2006. Solute dynamics. Pages 169–185 in F. R. Hauer and G. A. Lamberti (editors). Methods in stream ecology. Academic Press, San Diego, California.

Yard, M. D., G. E. Bennett, S. N. Mietz, L. G. Coggins, L. E. Stevens, S. Hueftle, and D. W. Blinn. 2005. Influence of topographic complexity on solar insolation estimates for the Colorado River, Grand Canyon, Arizona. Ecological Modelling 183:157–172.