Ecosystem responses to restored flow in a travertine river

Catherine A. Gibson1,3,4, Benjamin J. Koch1,2,5, Zacchaeus G. Compson2,6, Bruce A. Hungate1,2,7, and Jane C. Marks1,2,8

1Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona 86011 USA
2Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, Arizona 86011 USA
3The Nature Conservancy, Albany, New York 12205 USA

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 CaCO3 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

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 recovery 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 CaCO3 as CO2 degasses causing CaCO3 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, Milija 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-
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 riffl–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 riffl–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 \(\mu\)g 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.
(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\textsubscript{3}\textsuperscript{−} 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\textsuperscript{−} by ion chromatography (2004: Dionex DX-600, 2005–2008: Dionex 100, 2011: Dionex 2100; Dionex). We used the Br\textsuperscript{−} addition rate and concentration to calculate discharge (Webster and Valett 2006). Nutrient uptake length (S\textsubscript{n}z 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\textsubscript{3}\textsuperscript{−} concentration relative to Br\textsuperscript{−} over downstream distance:

\[
\ln N_x = \ln N_0 - k_x \text{, (Eq. 1)}
\]

where \(N_x\) is the background-corrected NO\textsubscript{3}\textsuperscript{−}-N concentration divided by the Br\textsuperscript{−} concentration at the sampling site, \(N_0\) is the background-corrected NO\textsubscript{3}\textsuperscript{−}-N concentration divided by the Br\textsuperscript{−} 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\textsuperscript{2+} from the water column as a proxy for travertine deposition at the reach scale. We calculated Ca\textsuperscript{2+} uptake rate based on mass balance (Von Schiller et al. 2008), using the equation described above and substituting Ca\textsuperscript{2+} concentration for background corrected NO\textsubscript{3}\textsuperscript{−}-N concentration. We calculated areal deposition rate (mg Ca\textsuperscript{2+} m\textsuperscript{-2} h\textsuperscript{-1}) using \(S_n\) and mean water-column [Ca\textsuperscript{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\textsubscript{2} at 5-min intervals with a temperature and dissolved O\textsubscript{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\textsubscript{6}) constant-rate injection after Br\textsuperscript{−} returned to pre-NO\textsubscript{3}\textsuperscript{−} addition levels (Hall and Hotchkiss 2017).

We collected 3 replicate samples in 5-mL Vacutainers\textsuperscript{®} every 20- to 30-m downstream of the injection site. Headspace SF\textsubscript{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:

\[
\ln C_x = \ln C_0 - k_{SF6x}, \quad \text{(Eq. 2)}
\]

\[
k_{SF6} = k_{SF6y}, \quad \text{(Eq. 3)}
\]

where \(C_x\) and \(C_0\) are the dilution-corrected SF\textsubscript{6} concentrations throughout and at the top of the reach, \(k_{SF6}\) is the per-meter decline of SF\textsubscript{6}, \(x\) is the distance downstream, \(K_{SF6}\) is the per-time decline in SF\textsubscript{6}, and \(v\) is average stream velocity. We estimated stream velocity by measuring the time for 50% of the Br\textsuperscript{−} tracer used in the NO\textsubscript{3}\textsuperscript{−} 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\textsubscript{6} reaeration to that of O\textsubscript{2} by multiplying by the Schmidt number (1.4), corrected for temperature (Hall et al. 2015). O\textsubscript{2} data were fit to a metabolism model (Van de Bogert et al. 2007, Genzoli and Hall 2016):

\[
mO_{2(t)} = mO_{2(t-1)} + \left(\frac{GPP_{Total}}{Z} \times \frac{PPFD_t}{\sum PPFD_{24}}\right) + \left(\frac{RT_{Total}}{Z} \times \Delta t\right) + K_{o2}(O_{2sat(t)} - mO_{2(t-1)})\Delta t,
\]

where \(mO_2\) is modeled O\textsubscript{2} (mg/L) at time \(t\), GPP\textsubscript{Total} is GPP (g O\textsubscript{2} m\textsuperscript{-2} d\textsuperscript{-1}), \(z\) (m) is mean reach depth, PPFD is solar insolation (\(\mu\)mol photons m\textsuperscript{-2} s\textsuperscript{-1}) at time \(t\), \(\sum PPFD_{24}\) is daily solar insolation (Yard et al. 2005), R\textsubscript{Total} is ER (g O\textsubscript{2} m\textsuperscript{-2} d\textsuperscript{-1}), \(\Delta t\) is the time between O\textsubscript{2} measurements (5 min), and \(K_{o2}\) is \(K_{SF6}\) corrected for temperature and each time-step. We fit the equation to the observed O\textsubscript{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\textsubscript{Total} and R\textsubscript{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 \(V_{NO3}\) stream metabolism fluxes, and Ca\textsuperscript{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-
r al 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) $V_{/NO3}$ 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× (difference in means = +8.95 mg Ca m$^{-2}$ h$^{-1}$, $n_{\text{before}} = 6$, $n_{\text{after}} = 6$, $p = 0.003$; Fig. 3A), GPP by 1.5× (difference in means = +1.98 g O$_2$ m$^{-2}$ d$^{-1}$, $n_{\text{before}} = 5$, $n_{\text{after}} = 6$, $p = 0.023$, Fig. 3B), and $V_{/NO3}$ by 12× (difference in means = +19.0 mm/min, $n_{\text{before}} = 6$, $n_{\text{after}} = 6$, $p = 0.002$; 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$^{-1}$, $n_{\text{before}} = 5$, $n_{\text{after}} = 6$, $p = 0.273$; Fig. 3C). With greater GPP and no change in ER, the R : P ratio increased in reaches downstream of the dam (difference in means = +0.407, $n_{\text{before}} = 5$, $n_{\text{after}} = 6$, $p = 0.035$; 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× 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 ($V_{/NO3} = -11.0 + 10.5$GPP, $n = 16$, $R^2 = 0.644$, $F_{1,14} = 25.4$, $p = 0.0002$; Fig. 4B), supporting our prediction that increased autoch-
GPP was positively related to \( \text{Ca}^{2+} \) 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.—\( \text{NO}_3^- \) uptake velocity \( (V_{\text{NO}_3^-}) \) was positively related to GPP across all sampling dates and sites \( (V_{\text{NO}_3^-} = -11.0 + 10.5 \text{GPP}, n = 16, R^2 = 0.644, F_{1.14} = 25.4, p = 0.0002) \). C.—Ecosystem respiration (ER) was related to GPP across all dates and sites \( (ER = -0.805 - 1.07 \text{GPP}, n = 16, R^2 = 0.633, F_{1.14} = 24.1, p = 0.0002) \).

ER did not respond to flow restoration (Fig. 3C). ER was negatively related to GPP \( (ER = -0.805 - 1.07 \text{GPP}, n = 16, R^2 = 0.633, F_{1.14} = 24.1, p = 0.0002; \text{Fig. 4C}) \), 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 \( (P : R \text{ ratio, Fig. 3D}) \). \( V_{\text{NO}_3^-} \) increased with the absolute value of ER \( (V_{\text{NO}_3^-} = -7.20 + 6.97 |ER|, n = 16, R^2 = 0.512, F_{1.14} = 14.7, p = 0.002) \), 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, \( V_{\text{NO}_3^-} \) 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). \( V_{\text{NO}_3^-} \) 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 \( \text{Ca}^{2+} \) 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 greater 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 \(V_{\text{fNO}_3}\). Post-restoration values of \(V_{\text{fNO}_3}\) (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 \(V_{\text{f}}\) 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.

**ACKNOWLEDGEMENTS**

Author contributions: CAG, JCM, and BAH designed the study; CAG and ZGC performed experiments; CAG and BJF analyzed data; CAG wrote first draft of the manuscript; all authors contributed substantially to revisions. We thank K. Adams, A. Pastor, G. A. Haden, and M. James for help with fieldwork and B. Moan and J. Hogan for help with water-chemistry analysis. Funding was provided by the National Science Foundation (SGER and DEB 0543612 and DBI 0959476). We thank Victor Leshyk for creating Fig. 2 and Associate Editor Bob Hall for help with calculating GPP and ER.

**LITERATURE CITED**


