# Unlocking the biogeochemical role of beaver in state-transition of landscapes in Yellowstone's northern range: Tantalizing insights, initial results, and evolving research design

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**Abstract** Extirpation of wolves from the Greater Yellowstone Ecosystem in the 1920s hypothetically triggered a trophic cascade in which herbivores over-browsed riparian zones once released from the fear of wolf (*Canis lupus*) predation. Eventually, vast meadow-wetland complexes transitioned to grass-lodgepole systems. By 1954, beaver (*Castor canadensis*) virtually abandoned the Greater Yellowstone Ecosystem. In 2000, Colorado State University established experimental dams with browsing exclosures for Long Term Environmental Research in Biology (LTREB) on three streams in Lamar Valley to compare hydrologic effects of pseudo-beaver dams and browsing on willow (*Salix* spp.) productivity and state transitions. In 2015, beaver began recolonizing the region. I investigate how the biogeochemical role of beaver versus their hydrologic influence affects the underlying mechanisms of state transition: nutrient cycling, productivity, and stream respiration. Analyses of the 2017 field samples showed that beaver streams trend toward higher nutrient levels and higher variances than the LTREB sites. These trends continued in 2018 and 2019. The data tentatively support the role of beaver as keystone species in state transitions. Interannual modeling of nutrient dynamics, comparisons of stream metabolism, and genetic identification of microbial communities are underway. Similarly, analyses of the repeated measures collected across the month of July 2019 are underway.

## Introduction

Based on increased growth of riparian vegetation following the 1995 reintroduction of the wolf (*Canis lupus*), researchers hypothesized that wolf extirpation in the 1920s released elk (*Cervus elaphus*) and other ungulates from fear of predation in riparian zones (Ripple and Beschta, 2004, 2012; Painter et al., 2015). Subsequent overbrowsing led to degraded riparian vegetation and a state transition from productive meadow-wetland complexes to dry grasslands (Figure 1). A lively scientific debate continues about the relative influences on wetland recovery from the wolf-elk trophic cascade, overall declines in elk populations, effects of other browsers, and periodic drought events (Creel and Christianson, 2009; Kauffman et al., 2010; Beschta and Ripple, 2013; Kauffman et al., 2013). The evidence for both sides of the debate has largely depended on mensurative field studies. Such observational and sampling studies carry tremendous ecological relevance but, because they are fundamentally observational, they face challenges from lack of replication, reproducibility, and strictly controlled reference sites.

Nineteen years ago, David Cooper and Tom Hobbs from Colorado State University established an experimental site for Long Term Environmental Research in Biology (LTREB) in the Lamar Valley, *Understanding controls on state-transition on Yellowstone's northern*

**Figure 1.** Comparison of historic photos of Elk Creek in the Lamar Valley. In 1923, the beaver dam was more than 100 m long with a robust willow stand (Warren, 1926). The dam had drained and the willows were gone by 1954 (Jonas, 1955). By 2002, a grass and lodgepole pine community entirely replaced the willow-meadow complex. The black line marks the old dam location with the deeply incised stream in the foreground. (From Wolf et al., 2007, Figure 8).
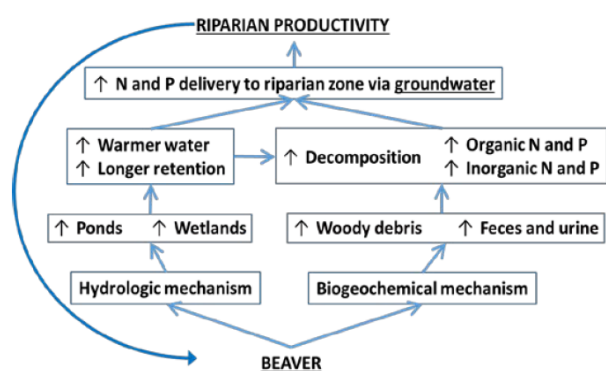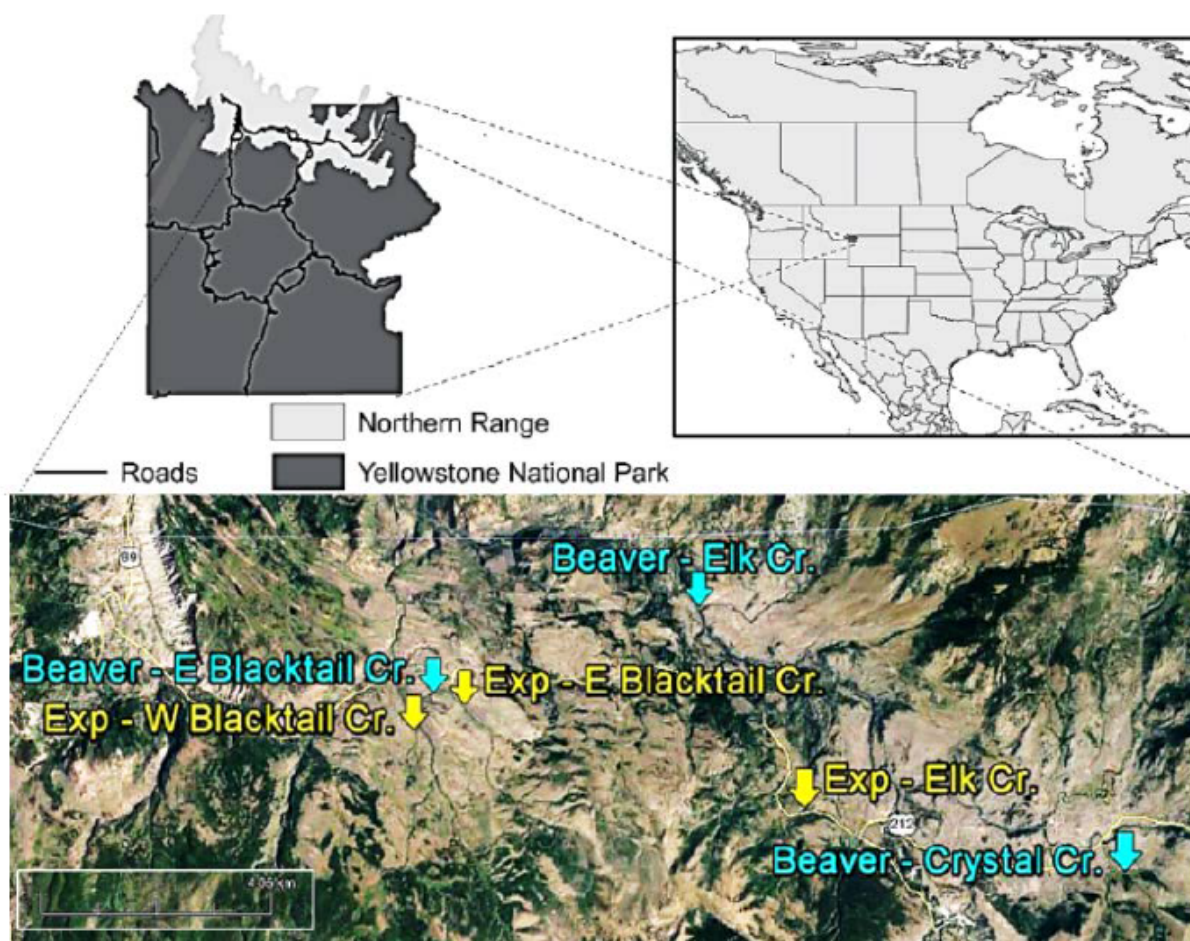


**Figure 2.** Conceptual model of beaver as keystone species in the state-transition of streams to wetland meadow complexes.

precipitously throughout the Greater Yellowstone Ecosystem and virtually disappeared from the Lamar Valley (Persico and Meyer, 2013). Beaver apparently abandoned because of a combination of overbrowsing and drought events in the 1930s. Without beaver maintenance, spring runoff eventually breached their dams, which dramatically changed wetland-meadow hydrology (Wolf et al., 2007; Persico and Meyer, 2013). Beyond their hydrologic influences, beaver biologically facilitate ecosystem productivity by adding nutrients as feces and transferring woody debris into streams (Figure 2). Their activity enhances primary production, while promoting higher decompositional rates and nutrient regeneration (Johnston and Naiman, 1987, 1990; Naiman et al., 1994; Klotz, 1998). For example, Naiman and Melillo (1984) found that nitrogen fixation in a stream riffle contributed 4.2% of the nitrogen, but in a similar reach dammed by beaver, fixation contributed 68% of the annual nitrogen budget (Naiman and Melillo, 1984). Although such benefits are well described, dynamic thresholds, chronology of changing system productivity, the magnitude of their influence, and separation of hydrologic from biologic mechanisms are not (arrows between compartments in Figure 2).

In the past, detection and investigation of the separate hydrologic and biologic processes provided by beaver were impossible because there were no beaver dams to compare to the experimental dams. Starting in 2015, however, beaver conveniently be-

*range.* To evaluate the effects of increased hydrologic delivery of groundwater and elk browsing, they installed a series of experimental dams at three stream sites with adjacent exclosures that prohibit browsing. The experimental dams mimic the influence of beaver (*Castor canadensis*). They and their students show that hydrologic changes, water availability, and drought regimes determine willow growth (Schook and Cooper, 2014) to a greater extent than elk grazing (Wolf et al., 2007; Marshall et al., 2013, 2014). In addition to hydrologic influences, the next logical step is to investigate the biological mechanisms by which beaver alter nutrient cycling, stream metabolism, or system productivity.

By the mid-1950s, beaver populations had declined

**Figure 3.** Locations of LTREB experimental dams (West Blacktail Creek, East Blacktail Creek, Elk Creek) and beaver dams (Crystal Creek, Elk Creek, East Blacktail Creek) (after Marshall et al., 2014).

gan colonizing streams, below or near the LTREB sites (Figure 3). LTREB research had not previously included nutrient assessments.

Beaver immigration presents an unprecedented opportunity in ecology to investigate several important questions about the interplay between the hydrologic and biologic mechanisms. Will the recovery of systems be adequate to sustain viable beaver populations? Will productivity approach historical levels of productivity that can sustain beaver and many wetland-dependent species and fishes (Collen and Gibson, 2001; Hossack et al., 2015; Law et al., 2016)? What timeframe is required for their sustainability? The aims of this research are consistent with Research Needs for the Greater Yellowstone Ecosystem for recovery following wolf reintroduction.

### Rationale and significance

As in areas fertilized by salmon and river otters (Helfield and Naiman, 2001; Roe et al., 2010; Kominoski et al., 2015), I posit that biological feedback of nutrients mediated by beaver is critical to full system recovery. Unlike otters, beavers seldom defecate onshore. However, their biologic influence on nutrient levels within streams can reach riparian vegetation via surface flooding or lateral seepage of groundwater to the hyporheic zone. My preliminary data collected in 2015 and 2016 from newly established beaver ponds indicate higher N and P concentrations in groundwater beneath riparian zones adjacent to beaver dams than in experimentally dammed streams (Figure 4). If this pattern holds in further studies, it would represent **a newly discovered**
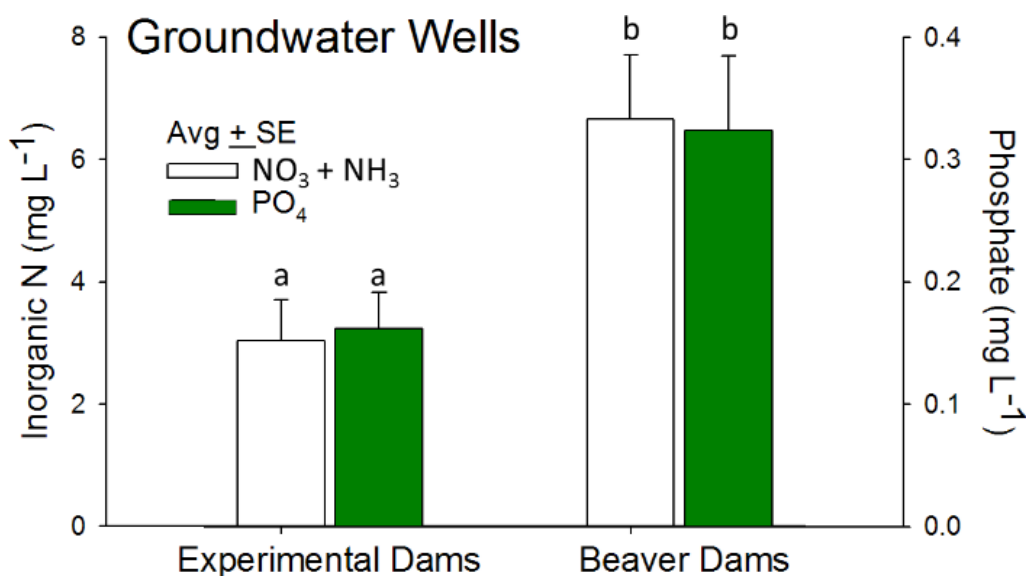
**Figure 4.** Comparison of total inorganic nitrogen and phosphate collected in 2016 from groundwater wells adjacent to LTREB experimental dams and beaver dams shown in Figure 3 (Brooks, unpublished data).

**mechanism** by which alteration of nutrient dynamics within streams by beaver accelerates the transition from elk meadows lacking willows to beaver meadows with vigorous willow growth. This nutrient-driven process, which occurs in tandem with greater surface flooding around dams and accompanying lateral seepage of groundwater, adds a novel parallel dimension to better-recognized hydrologic effects of beaver (Figure 2).

### Research questions and new hypotheses

1. How do nutrient levels and cycling depend on the biological influence of beaver (i.e. active nutrient input) compared to analogous hydrologic alterations at the LTREB sites?
2. What effect does beaver presence have on ecosystem respiration and net primary production of streams compared to LTREB sites that lack beaver?
3. Do beaver contribute significantly to riparian willow and aspen productivity (e.g. shift in stable isotopic signatures)?
4. *Beaver legacy hypothesis.* Having observed conditions as beaver intermittently colonize, abandon, and reoccupy streams, I hypothesize that beaver leave a legacy of higher nutrient levels, but also a persistent alteration of the structure and function of microbial communities.
5. *Microbes as bioengineers hypothesis.* I further hypothesize that the differential influence of beaver on microbial communities promotes nutrient release to a greater extent than other factors such as bison fecal input and groundwater hydrology.

Coupling the LTREB monitoring with my biogeochemical sampling will allow greater understanding of these questions about ecosystem function and the trajectory of system productivity over time as beavers recolonize the Greater Yellowstone Ecosystem. The steps in the process of characterizing and testing beaver influence include sampling: (1) levels of nutrients and rates of nutrient regeneration and cycling in the streams (Hall Jr et al., 2013; Kominoski et al., 2015; Hall et al., 2016), (2) nutrient levels in groundwater wells within the riparian zone, and (3) growth rates and nutrient levels in leaves of riparian vegetation (Ben-David et al., 1998; Hubbard Jr et al., 2010; Roe et al., 2010).

The system does not readily give up its secrets, which leads to exciting new directions and hypotheses required to understand nutrient cycling, whole system metabolism, links to net primary production,

| Sample types (n per site) | Analytes or parameters |
|---|---|
| Stream waters (n = 2 to 4) Well waters (n = 7 to 12) | temperature, pH, conductivity, dissolved $O_2$, $NO_3$, $NH_3$, $PO_4$, total N, particulate & dissolved organic carbon DNA extracted from waters |
| Willows (n = 6) Stream metabolism (n = 1) Sediments (n =2) | total P, total N, $\delta^{13}C$, $\delta^{15}N$, C:N, % C, % N Whole stream respiration and organic carbon spiraling DNA extracted from sediments |

**Table 1.** Samples and data collection at each field site in 2019.

and overall ecosystem productivity.

## Methods

### 2019 sampling design

Repeated sampling at six locations was conducted from 5 to 29 July 2019. The West Blacktail beaver site was added in part to test question 4, but also because some beaver activity had been reported in spring 2019. This is particularly interesting because the site was apparently abandoned between spring 2017 to fall 2019.

### Sample collection

Samples were collected approximately 100 and 5 m above the dam furthest upstream and 5 and 100 m below the dam furthest downstream. Samples were transported from the field on ice, and stored frozen at -5 °C until analysis. Following thawing, samples were analyzed or stabilized within 24 hours. Temperature, pH, conductivity, and dissolved oxygen were collected at each stream with appropriate probes (HQ40d, HACH multi-parameter meter). Similarly, field data were collected for gross primary production (GPP), ecosystem respiration rates (ERR), and organic carbon spiraling by two-station oxygen logging with modeled gas exchange and organic carbon spiraling. Aside from stable isotopic analyses, which are sent to the UWYO Stable Isotope Facil-

ity at the University of Wyoming, all other analyses are conducted in my laboratory at Southern Illinois University. Organic carbon spiraling is determined from particulate organic carbon (total dry mass minus ash-free dry mass of fraction > 0.45 $\mu$m) relative to dissolved organic carbon (fraction < 0.45 $\mu$m; catalytic combustion; Shimadzu TOC-VCSN). Nitrate and phosphate are analyzed by ion chromatography (Dionex ICS 2000, method 300.0), total nitrogen by chemoluminescence (Shimadzu TOC-VCSN), and ammonia, nitrate, and total phosphorus by colorometric analyses (Hach 5000 spectrometer) using EPA standard methods (P method 365.2, $NH_3$ method 350.2). Quality assurance and quality checks follow standard QA/QC protocols of duplicates, spikes, and external quality checks and external reference materials (APHA et al., 2005). For Next Generation Sequencing (NGS) of the microbial communities (Table 4), waters were pumped through Sterivex filter units. Sediment samples were collected directly into sterile falcon tubes. All samples were frozen immediately at -4 °C and stored at -80 °C within ten days of collection. Sediments were processed using equal parts of sediment, and a 0.8 M solution of dibasic sodium phosphate at pH 7.2. The samples were mixed and then allowed to incubate for 30 minutes at room temperature. After this incubation, no further modification was made. DNA was extracted from both the Sterivex filters and sediments according to the standard manufacturer's procedure using a DNA Soil Isolation Kit

| | | Dissolved Oxygen (mg/L) | $NO_3$ (mg/L) | $NH_3$ (mg/L) | $PO_4$ (mg/L) | DOC (mg/L) | Total N (mg/L) |
|---|---|---|---|---|---|---|---|
| 2019 | Beaver sites | 7.83 ±0.45 | 0.37 ±0.63 | 0.00 ±0.10 | 0.58 ±0.60 | 12.12 ±5.06 | 1.05 ±0.52 |
| | LTREB sites | 8.35 ±0.29 | 0.04 ±0.4 | 0.00 ±0.06 | 0.52 ±0.42 | 9.98 ±3.52 | 0.95 ±0.59 |
| 2018 | Beaver sites | 8.75 ±1.09 | 0.31 ±0.30 | 0.11 ±0.12 | 0.65 ±0.19 | 11.85 ±2.30 | 0.69 ±0.54 |
| | LTREB sites | 9.46 ±0.51 | 0.48 ±0.18 | 0.14 ±0.05 | 0.82 ±0.53 | 8.98 ±3.27 | 0.47 ±0.35 |

**Table 2.** Nutrient-related biogeochemistry of beaver-colonized and LTREB streams, collected in 2018 and 2019.

| | | Temperature (ºC) | Conductivity (µS/cm) | pH | Hardness (as mg CaCO3/L) | Alkalinity (as mg $CaCO_3$/L) |
|---|---|---|---|---|---|---|
| 2019 | Beaver sites | 15.01 ±1.58 | 179.56 ±1.28.92 | 7.58 ±0.75 | 65.17 ±64.64 | 86.33 ±62.73 |
| | LTREB sites | 11.53 ±1.22 | 126.28 ±39.45 | 7.87 ±.20 | 36.33 ±17.31 | 61.33 ±19.28 |
| 2018 | Beaver sites | 11.40 ±1.51 | 341.28 ±206.45 | 8.08 ±0.25 | 167.50 ±115.11 | 186.25 ±114.13 |
| | LTREB sites | 10.05 ±1.68 | 175.69 ±52.18 | 7.79 ±0.12 | 81.25 ±16.39 | 93.33 ±25.97 |

**Table 3.** Geochemistry of beaver-colonized and LTREB streams, collected in 2018 and 2019.

(SurePrep # BP2815-50). Extracted DNA was quantified by Nanodrop. In December 2019, NGS will be conducted at the University of Illinois at Chicago Sequencing Core (UICSQC). Turnaround time is approximately three months.

## Statistical analyses

Statistical analyses include Bayesian network models for the strength of relationships in Figure 2 (Ayre and Landis, 2012; Raiho et al., 2015). For hypothesis testing of differences in system productivity between undammed reaches, experimental dams and beaver dams, I use permutational multivariate analysis of variance (PERMANOVA; PRIMER software ver 7.0.11, PERMANOVA, 1.0.5; PRIMER-E) (Anderson, 2001) and non-metric multidimensional scaling with Akaike Information Criteria adjusted for variance in sample size (AICc). For inference, I use permutational distance-based linear modeling (DistLM; multivariate multiple regression) (Anderson et al., 2004; Kraft et al., 2011). Bayesian inverse modeling is used to generate GPP and ER (Hall et al., 2016). For genetic analyses of microbial communities, raw sequences of NGS data are first assembled, filtered, and processed using QIIME2 (version 2018.2.0). Reads are trimmed based on quality scores and extra

bases are removed to compensate for bidirectional 300 base pair (bp) reads (Bolyen et al., 2019). Processed sequences are then aligned to the Silva taxonomic database for 16S rRNA (version 132) for taxonomic classification. Chimeric reads are removed using VSearch (Rognes, 2011) and reads classified as Eukaryotic, mitochondria, chloroplasts or unknown domains are removed. Remaining sequences are clustered into operational taxonomic units (OTU's) at 97% similarity. Subsequent alpha diversity analyses are then carried out using the Mothur software package (v1.41.1) (Schloss et al., 2009). Once the community is sequenced to the genus level, we use permutational multivariate techniques (PRIMER software) to characterize relatedness, and $\alpha$- and $\beta$-diversity.

## Preliminary results

Sample analyses from the 2019 season are partially complete. I present some findings from both the 2018 and 2019 field seasons herein. Biogeochemical values (defined as parameters strongly influenced by nutrient uptake and primary production), are shown in Table 2. Even though alkalinity and pH can vary tremendously depending on photosynthetic and respiration rates, for simplicity I present them with other

| Data Source | Sample ID | Sample Type |
|---|---|---|
| Yell-8076 | LB4 U100 | water |
| Yell-8076 | LB4 U100 | sediment |
| Yell-8076 | LB4 D5 | water |
| Yell-8076 | LB4 D5 | sediment |
| Yell-8076 | LB4 Well 650 | water |
| Yell-8076 | LB4 Well 600 | water |
| Yell-8076 | LB4 Well 601 | water |
| Yell-8076 | CRYS U100 | water |
| Yell-8076 | CRYS U100 | sediment |
| Yell-8076 | CRYS D5 | water |
| Yell-8076 | CRYS D5 | sediment |
| Yell-8076 | CRYS Well 311 | water |
| Yell-8076 | CRYS Well 313 | water |
| Yell-8076 | CRYS Well 310 | water |
| Yell-8076 | WB-BV U100 | water |
| Yell-8076 | WB-BV U100 | sediment |
| Yell-8076 | WB-BV D5 | water |
| Yell-8076 | WB-BV D5 | sediment |
| Yell-8076 | WB-BV Well S3 | water |
| Yell-8076 | WB-BV Well 508 | water |
| Yell-8076 | WB-BV Well 505 | water |
| Yell-8076 | ELK Well 3DC | water |
| Yell-8076 | ELK Well 12DX | water |
| Yell-8076 | ELK Well 16CC | water |
| Yell-8076 | ELK Well 19CX | water |
| Yell-8076 | EB U100 | water |
| Yell-8076 | EB U100 | sediment |
| Yell-8076 | EB D5 | water |
| Yell-8076 | EB D5 | sediment |
| Yell-8076 | EB Well 70DX | water |
| Yell-8076 | EB Well 47CX | water |
| Yell-8076 | WB-EX U100 | water |
| Yell-8076 | WB-EX U100 | sediment |
| Yell-8076 | WB-EX D5 | water |
| Yell-8076 | WB-EX D5 | sediment |
| Yell-8076 | WB-EX Well 62DC | water |
| Yell-8076 | WB-EX Well 58DX | water |
| Yell-8076 | WB-EX Well 41CX | water |
| Yell-8076 | Field Blank | water |

**Table 4.** 2019 samples sent for next generation sequencing of the microbial communities.

geochemical aspects of water (Table 3).

The values in Tables 2 and 3 compare the three beaver sites to the LTREB sites during September (2018) and mid-summer base flow conditions. The values are averages of all upstream and downstream samples. The signal to noise ratio for longitudinal patterns from upstream to downstream was high both years. With some exceptions, beaver sites had higher variances in all parameters than the LTREB sites.

Results of isotopic analyses, carbon, and nitrogen content in willow leaves collected in 2017 at the beaver dams at West Blacktail Creek and Crystal Creek have $\delta^{15}$N values that suggest the nitrogen is approximately two trophic levels above those of nitrogen sources for willows collected 50 m upstream of the dams. If, as hypothesized in the 2018 report, the microbial community is significantly different between those reaches, then microbial processing of nitrogen is the logical explanation. Bison are common at Crystal Creek but frequent both up and downstream reaches. Based on my limited observations, and also the minimal number of bison feces, they are less frequent visitors to the Lower Blacktail Creek.

## Conclusions

Relative to my research questions, trends in distinctions between upstream and downstream conditions support the probability that beaver increase the magnitude of nutrients in streams, and thus, that their biologic influence outpaces hydrologic influences of dam building alone (i.e. slowed flow, warmer temperatures). Network modeling is underway, so I cannot yet provide evidence whether or not beaver increase rates of nutrient cycling or increase stream metabolism via feces and import of terrestrial woody debris. Regarding the question, "Do beaver contribute significantly to riparian willow and aspen productivity (e.g. shift in stable isotopic signatures)?" $\delta^{15}$N values downstream of beaver dams at two sites in 2017 indicate that the nitrogen values likely derive from beaver feces. More isotopic analyses of leaves collected in 2019 will provide more insights. My very preliminary modeling and analyses of data collected since 2015 have not shown definitive patterns sup-

porting my hypothesis that beaver leave a legacy of higher nutrient levels. NGS of the microbial communities will likely provide some insights and support for my hypothesis that microbes are the fundamental engineers of stream metabolism and productivity (question 5). It's equally likely the data will generate many new lines of unanswered questions and inquiry!

## Future work

My challenge now is to complete the analyses of the 2019 samples and continue both modeling stream metabolism and statistical assessment of biological influence of beaver on stream systems to better understand state transitions over time as beavers recolonize the Greater Yellowstone Ecosystem.

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