

THESIS

FROM FIRES TO FLOODPLAINS: INTERACTING EFFECTS OF UNCONFINED CHANNEL
SEGMENTS AND SEASONAL DYNAMICS ON ALGAL NUTRIENT LIMITATION FOLLOWING
WILDFIRE

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ABSTRACT

FROM FIRES TO FLOODPLAINS: INTERACTING EFFECTS OF UNCONFINED CHANNEL SEGMENTS AND SEASONAL DYNAMICS ON ALGAL NUTRIENT LIMITATION FOLLOWING WILDFIRE

Severe wildfire has the potential to alter ecosystem processes including nutrient cycling and primary production in streams. Nutrients such as nitrogen (N) can remain elevated in streams for decades following wildfire and can impact downstream water quality, aquatic habitat, and food webs. In this study, nutrient diffusing substrates were deployed in three burned watersheds within the Cameron Peak Fire scar in Colorado, USA during peak and base flows to examine seasonal nutrient limitation of benthic algae upstream and downstream of unconfined channel segments, which are generally zones of nutrient uptake and retention. We also quantified environmental factors expected to mediate the strength of nutrient limitation, including macroinvertebrate grazers, canopy cover, water temperature, depth, ambient nutrients, dissolved oxygen, and velocity. We hypothesized that unconfined segments would act as nutrient sinks during base flows resulting in stronger N limitation downstream. Our results showed that effects of geomorphic position on N limitation and algal responses varied across seasons, with reduced N limitation during high N concentration peak flows, and stronger N limitation downstream of unconfined channel segments during base flows. Of the seven environmental variables, macroinvertebrate grazer density was the strongest mediator of algal N responses. These results highlight the importance of geomorphic context, seasonality, and biological factors in mediating N limitation and are relevant to informing stream restoration efforts that aim to restore and enhance unconfined channel reaches following wildfire.

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DEDICATION

To Dad

To Pete

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FROM FIRES TO FLOODPLAINS: INTERACTING EFFECTS OF UNCONFINED CHANNEL SEGMENTS AND SEASONAL DYNAMICS ON ALGAL NUTRIENT LIMITATION FOLLOWING WILDFIRE

Introduction

Wildfire is increasing in frequency and severity throughout the western United States (Dennison et al. 2014, Abatzoglou and Williams 2016), resulting in widespread impacts on aquatic ecosystem structure and function (Betts and Jones Jr. 2009, Klose et al. 2015, Rhea et al. 2021). Wildfire effects on stream ecosystems are highly complex and can impact stream communities through multiple mechanisms (Bixby et al. 2015). Wildfire has the potential to elevate stream nutrient concentrations (Rhoades et al. 2011, 2019, Rust et al. 2018), reduce riparian canopy cover (Coble et al. 2023), increase sediment transport (Ryan et al. 2024), and change community structure of macroinvertebrates and fishes (Verkaik et al. 2015, Whitney et al. 2016), thereby altering aquatic food webs (Spencer et al. 2003, Mihuc and Minshall 2005, Malison and Baxter 2010, Preston et al. 2023). Changes in physical and biological factors can pose complex management challenges, particularly in headwater streams where effects of wildfire can cascade downstream (MacDonald and Coe 2007). As a result, there is a growing need to understand both catchment-scale and local factors that may enhance resistance and resilience to ecological changes following wildfire.

Freshwater ecosystems are typically limited by the availability of nitrogen (N) and/or phosphorous (P) (Elser et al. 1990), but wildfire can alter nutrient limitation. In burned catchments, nutrient inputs to streams, especially of N, often increase after wildfire. Fire increases terrestrial to aquatic N transfer by killing vegetation and reducing terrestrial N uptake and demand, as well as by increasing soil N mineralization, allowing for increased leaching of excess mobile nitrate (NO₃-N) into streams (Wan et al. 2001, Certini 2005, Turner et al. 2007, Smithwick et al. 2009). Increased stream nutrient concentrations following wildfire are a common short-term (<5 years) response throughout streams in the

western United States (Rust et al. 2018), although long-term studies have shown that nutrient levels can remain elevated compared to pre-fire conditions in burned catchments for longer than ten years (Rhoades et al. 2019). Increases in nutrient availability can affect primary producers via bottom-up effects, potentially influencing the aquatic food web (Silins et al. 2014).

Benthic algae, the autotrophic component of periphyton, are key primary producers in streams (Minshall 1978) and are important drivers of in-stream nutrient dynamics through the uptake, assimilation, and transformation of N and P (Borchardt 1996). Wildfire-driven nutrient inputs, especially N, can alleviate algal nutrient limitation and increase primary production and algal biomass in burned streams relative to unburned streams (Betts and Jones Jr. 2009, Klose et al. 2015, Rhea et al. 2021). Under elevated stream nutrients, algal communities may shift from being primarily N-limited to N and P co-limited (Rhea et al. 2021). Shifts in limitation can impact both algal abundance and nutrient content with impacts on secondary consumers and higher trophic levels (Atkinson et al. 2017). While post-fire increases in nutrients have been shown to increase algal responses in fire-affected streams, a variety of physical and ecological factors can mediate the ways in which wildfire affects stream nutrients and periphyton.

Montane watersheds generally vary in geomorphic characteristics from steep, confined, and narrow channels to wider, unconfined floodplain areas, and this variation in the geomorphic template of watersheds can regulate aspects of aquatic ecosystem structure and function (Bellmore and Baxter 2014, Wegener et al. 2018, Venarsky et al. 2018), and can control both nutrient and periphyton dynamics (Doyle and Stanley 2006). This continuous network of transitions between wide and narrow valley bottoms throughout catchments has been described as “beads on a string” (Stanford et al. 1996). River “beads”, the low gradient, wide valley bottom channel segments, may play an important role in N cycling and assimilation at the reach scale through controls on physical and biological conditions that enhance the potential for retention of sediment, water, and organic matter (Wohl et al. 2018). The geomorphic complexity and storage capacity of river beads typically results in increased surface water area, decreased velocity, and increased residence time of water and nutrients relative to more confined reaches (Hall and

Tank 1999, Ye et al. 2012). Longer residence times can lead to enhanced biogeochemical activity and biotic uptake by periphyton communities, increasing in-stream nutrient processing and retention (Doyle and Stanley 2006, Bellmore and Baxter 2014). Additionally, laterally unconfined beads can result in zones of flow heterogeneity and sediment deposition, both of which are necessary for nutrient retention (Robert Hall and Tank 1999, Ye et al. 2012). As a result, the geomorphic template of streams not only mediates nutrient dynamics but also plays a role in structuring dynamics of benthic algal communities, although these interactions are not well understood in fire-affected streams. Given that common post-fire stream restoration techniques aim to create or enhance floodplain connectivity in unconfined river beads (Wheaton 2021), understanding their ability to alter stream nutrient concentrations and influence algal communities after fire can inform restoration and recovery of aquatic ecosystems in post-fire montane watersheds.

Seasonal changes in the stream environment may interact with geomorphology to influence stream nutrient dynamics and algal responses. Periphyton is regulated by both bottom-up and top-down factors that vary spatially and temporally (Hillebrand 2002, 2009). For instance, bottom-up effects of nutrient availability can be site-specific and dependent on environmental factors such as light, temperature, velocity, and macroinvertebrates grazing pressure; all of which vary across seasonal and spatial gradients (Beck et al. 2017). In the southern Rocky Mountains, N concentrations of streams in burned catchments fluctuate seasonally, peaking during snowmelt runoff and decreasing as flow returns to baseflow conditions in late summer and fall (Rhoades et al. 2019). While fire can significantly alter stream nutrient dynamics and shift seasonal nutrient availability, light or temperature can affect algal responses to nutrients and in some cases, can be more limiting to periphyton than nutrients (Francoeur et al. 1999, Lange et al. 2011, Beck et al. 2017). Current velocity, which also varies seasonally and spatially, can both increase nutrient availability (Hiatt et al. 2019) and decrease growth rates (Biggs 1998). Macroinvertebrate communities are known to shift seasonally, resulting in functional feeding group assemblages that may change based on temperature and flow regimes (Bogan and Lytle 2007). Grazing macroinvertebrates are an important top-down control on periphyton through consumption as well as

physical disruption (Eichenberger and Schlatter 1978, Hillebrand 2009), and can change periphyton community composition through selective grazing (Rosemond et al. 1993). These seasonally and spatially varying factors can also be impacted by fire. For example, fire can destroy riparian vegetation, reducing canopy cover and increasing light availability to the benthos (Coble et al. 2023), increase stream temperatures (Rhoades et al. 2011) and stream flow (Soulis et al. 2021), and change macroinvertebrate community structure (Verkaik et al. 2015). However, relatively little is known about how these environmental factors interact in combination with stream geomorphology and altered nutrient dynamics to influence algal responses in fire-affected streams.

Nutrient diffusing substrates (NDS) are a standard method used to assess nutrient limitation of benthic periphyton in streams and rivers (Fairchild et al. 1985). NDS have been used to evaluate algal responses to nutrient amendments under a variety of conditions with varying bottom-up and top-down factors, including variations in light (Taulbee et al. 2005, Warren et al. 2017), velocity (Hoch 2008), temperature (Myrstener et al. 2018), macroinvertebrate grazers (Rosemond et al. 1993, Wellnitz and Leroy Poff 2006, Beck et al. 2019), and nutrients (Rhea et al. 2021, Beck et al. 2021); however little is known about how these environmental factors interact in combination with stream geomorphology and altered nutrient dynamics to influence algal responses in fire-affected streams.

Our objective was to evaluate the role of river beads in mediating stream biogeochemistry and nutrient limitation of benthic algae across seasons after severe wildfire in Colorado, USA. We deployed nutrient diffusing substrate (NDS) experiments at the upstream and downstream ends of unconfined channel segments in three fire-affected streams within the Cameron Peak Fire scar during peak flow, high $\text{NO}_3\text{-N}$ conditions and base flow, low $\text{NO}_3\text{-N}$ conditions. We hypothesized that algal N limitation would be stronger downstream of beads than upstream due to downstream reductions in $\text{NO}_3\text{-N}$, especially during late summer base flow conditions when $\text{NO}_3\text{-N}$ concentrations are lower. During peak flows, we predicted that higher $\text{NO}_3\text{-N}$ concentrations may exceed limitation thresholds, alleviating limitation regardless of position relative to beads and weakening spatial differences in N limitation. To help interpret NDS results, we collected data on a suite of environmental variables expected to influence the strength of

algal responses to nutrient amendments to test whether other biological and physical environmental variables could also help explain spatial and temporal variation in N limitation under post-fire conditions.

Methods

Study area – We conducted the field experiment in the South Fork Cache la Poudre catchment, a mountainous drainage in the southern Rocky Mountains located northwest of Fort Collins, Colorado, USA (Fig. 1). The South Fork Cache la Poudre is a major tributary of the Cache la Poudre River, the main source of drinking water for a large portion of the Colorado Front Range and the only river designated under the Colorado Wild and Scenic Rivers Act. The South Fork Cache la Poudre drainage lies between 1199 and 4079 m elevation and is characterized by mixed conifer forest, with underlying geology consisting of biotitic gneiss, schist, and migmatite (Tweto 1979). The hydrograph is dominated by spring snowmelt which typically peaks in June and subsides to baseflow conditions by late summer. A significant portion of the catchment was burned in 2020 during the Cameron Peak Fire, which burned a total of 84,544 hectares at mixed severity from alpine to lower montane forest, making it Colorado's largest wildfire in recorded history. Long-term post-fire water quality data collected by the US Forest Service Rocky Mountain Research Station (RMRS, unpublished data) from streams draining burned South Fork catchments in the Cameron Peak Fire show that $\text{NO}_3\text{-N}$ concentrations peak during snowmelt runoff and decrease as flow returns to baseflow conditions in late summer and fall (RMRS, unpublished data), which is consistent with prior studies (Rhoades et al. 2019).

Experimental design – We selected three stream reaches within the fire perimeter that were unconfined river bead sites (see Table 1 for drainage area, upstream area burned, and elevation). These sites included the main stem South Fork Cache la Poudre, Little Beaver Creek, and Jack's Gulch (Fig. 1). Nutrient diffusing substrates were deployed as near to the upstream and downstream ends of the beads as possible, while considering tributary confluences and land ownership boundaries (see aerial imagery in Fig. S1 for exact locations within each study reach). Sites were selected in an effort to minimize

differences in canopy cover, current velocity, and depth. NDS deployment required moderate flow and substrate types amenable to anchoring NDS arrays, so these characteristics also influenced the exact locations where the arrays were installed on the stream bed.

The nutrient diffusing substrate treatments included an unamended control (C), nitrogen amendment (N), phosphorus amendment (P), and a nitrogen and phosphorus amendment (NP). All treatments were replicated five times at each upstream and downstream bead location. We constructed NDS by filling 1 oz polyethylene containers with unamended 2% laboratory grade agar for controls, agar with 0.5 M sodium nitrate (NaNO_3) for N treatments, and agar with 0.5 M potassium phosphate dibasic (K_2HPO_4) + 0.5 M potassium phosphate monobasic (KH_2PO_4) for P treatments. Treatments containing P utilized both dibasic and monobasic forms of phosphorous to mitigate potential negative effects on periphyton colonization (Beck and Hall 2018). Containers were topped with fritted glass discs (5.7 cm^2 , EA Consumables) and lids were perforated to allow direct contact of the substrates with stream water and promote diffusion and colonization. We attached five randomly placed replicates of each treatment to steel racks and anchored them to the stream bed using rebar at each site. In 2023, NDS were incubated at the South Fork site for 20 days in baseflow conditions from September 5th to September 25th. In 2024, NDS were incubated for 20 days at Little Beaver Creek and Jack's Gulch during high flow, high stream nutrient conditions from June 20th to July 10th and again at baseflow, low nutrient conditions from August 30th to September 19th. NDS were not deployed at the South Fork in spring because this site had much higher discharge than the others, which would potentially destroy the experimental array. After the incubation periods, we collected fritted glass discs from containers in the field, placed them in plastic bags covered with tin foil to protect from chlorophyll-*a* (Chl *a*) degradation by sunlight during transportation, and stored them in a dark freezer (-18° C) until further processing.

Environmental factors – We characterized physical and biological variables at each study site to evaluate their influence on algal responses to nutrients. Stream temperature (°C) and dissolved oxygen (mg/L) were recorded in 15-minute intervals throughout the experiments at each site using miniDOT loggers (Precision Measurement Engineering, Vista, CA). We collected two water grab samples in acid-

washed, stream-rinsed 1L and 250 ml high-density polyethylene bottles once-weekly during NDS deployment in 2024 and once each during installation and takedown in 2023 to measure stream nitrate (NO₃-N), ammonium (NH₄-N), phosphate (PO₄-P), and total dissolved N (TDN). Samples were analyzed for TDN using a total organic C/N analyzer (Shimadzu Corporation, Columbia, MD) and for anions and cations using ion chromatography (Thermo Fisher, Waltham, MA). Samples were analyzed for alkalinity, pH, and specific conductivity (SC) using an inMotion Pro autosampler (Mettler Toledo). We collected three replicate Surber samples (0.09 m² in area, 600 μm mesh) to quantify potential differences in grazing macroinvertebrates once during each NDS incubation period at each site. Samples were collected from riffle habitats located near the NDS experiments, preserved in 80% ethanol, and transported to the laboratory. Macroinvertebrate samples were subsampled to 200 individuals using a gridded tray with 150 μm mesh and then identified to family to assign functional feeding groups including predators, collectors, shredders, and grazers (Merritt et al. 2019). We also measured the percentage of riparian canopy cover approximately above each NDS site as a proxy for light availability using a densiometer, and current velocity and depth were measured at each experimental location using a velocity meter and top-setting wading rod.

Laboratory sample processing – Fluorometric analysis of Chl *a* was used to quantify autotrophic algae on fritted glass discs following Environmental Protection Agency (EPA) method 445.0 (Arar and Collins 1997). Each fritted glass disc was placed in a 0.5 oz polypropylene jar with 10 ml of acetone and extracted for 24 hours in a dark refrigerator. Extracts were run on a fluorometer to quantify Chl *a* (raw fluorescence unit, RFU) using a non-acidification module (Turner Designs) to account for the presence of chlorophyll *b* and pheophytin *a* in the samples. Chl *a* concentration (μg/cm²) was calculated by multiplying the difference between the fluorometer reading of the sample (*R_b*) and the average blank sample reading (blank) by the response factor (=0.1724 μg/L * RFU⁻¹) and the sample extract volume (*V*) divided by the area of the fritted glass disc (*a*) using the following equation (Arar and Collins 1997):

$$\text{Chl}_a = \frac{(R_b - \text{blank}) \times F_s \times V}{a}$$

We calculated the response ratios of each treatment type to measure treatment effect sizes (i.e., $\ln[\text{mean treatment Chl } a \text{ concentration}/\text{mean control Chl } a \text{ concentration}]$). Positive response ratios indicate algal growth was enhanced in the amended treatments relative to controls whereas negative ratios indicate that the amendments suppressed growth. We inferred primary limitation if just the N or P treatment significantly enhanced growth, co-limitation if the N and P or N+P treatments significantly enhanced growth, and secondary limitation if N or P alone plus the N+P treatment significantly enhanced growth (Tank and Dodds 2003).

Statistical analyses – We analyzed changes in stream nutrient concentrations ($\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$ or TDN) using linear mixed effects models (LME) with geomorphic position (upstream or downstream of beads) and season (peak flow, base flow) as fixed effects, stream identity as a random effect, and log-transformed $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$ or TDN as the response variable. We analyzed results from the NDS experiments using a LME that included interactions between treatment type (C, N, P, NP), geomorphic position, and season as the predictor variables, stream as a random effect, and log-transformed Chl *a* concentration as the response variable. Following this LME, we used post-hoc Dunnett’s tests to assess whether Chl *a* treatment concentrations were significantly different from control treatments at each position and season to identify nutrient limitation status during experiments. To test our hypothesis about whether algal N limitation was stronger downstream of beads seasonally, we used a LME with geomorphic position, season, and their interaction as fixed effects, stream identity as a random effect, and effect sizes (i.e., response ratios) of N-containing treatments (N, NP) as the response variable. To help interpret NDS results and evaluate how environmental factors influenced algal N limitation, we used a LME with $\text{NO}_3\text{-N}$, $\text{NH}_4\text{-N}$, temperature, DO, canopy cover, current velocity, depth, and macroinvertebrate grazer density as predictor variables, a random effect of stream, and N-containing amendment response ratios (N, NP) as the response variable. All statistical analyses were completed in R statistical software (v4.4.2; R Core Team 2024).

Results

Water chemistry – In-stream $\text{NO}_3\text{-N}$ and TDN concentrations decreased significantly from peak flows to base flows (LME, season, $\text{NO}_3\text{-N}$: $p = 0.002$; TDN: $p = 0.01$). The magnitude of the seasonal decrease was on average 63% for $\text{NO}_3\text{-N}$ and 50% for TDN (Figs. 2a, 2b). $\text{NO}_3\text{-N}$ and TDN slightly decreased from upstream to downstream of beads (Fig. 2a, 2b). Depending on the season, these decreases ranged from ~10% to 25% from upstream to downstream, but the differences were not statistically significant (LME, location, $\text{NO}_3\text{-N}$: $p = 0.69$; TDN: $p = 0.94$). We also did not observe a significant bead position-by-season interaction for $\text{NO}_3\text{-N}$ or TDN (Table S1). $\text{NH}_4\text{-N}$ concentrations did not differ significantly by season, position, or their interaction (Fig. 2c, Table S1), although concentrations were approximately 75% higher during base flows. Stream $\text{PO}_4\text{-P}$ concentrations were below the analytical detection limit (< 0.01 mg/L) in all samples.

Algal responses and nutrient limitation patterns – The effects of nutrient treatments on algal growth (i.e., Chl *a*) depended on both season and geomorphic position, resulting in a significant three-way interaction (LME, treatment*season*position, F value = 2.8, $p = 0.04$). During peak flows, N-containing amendments significantly increased algal growth by 140% for N (LME, Dunnett's test, $p = 0.008$) and 275% for NP amendments ($p < 0.0001$, Fig. 3c) at the upstream sites. The P amendment also significantly enhanced algal growth relative to controls by ~111% upstream of beads at peak flows ($p = 0.01$, Fig. 3c). Downstream of beads at peak flows, the N and NP amendments enhanced algal growth relative to controls by 97% and 116%, respectively (N, $p = 0.2$; NP, $p = 0.02$). Significant, positive responses of Chl *a* to both N and P-containing amendments (i.e., positive response ratios) during peak flows indicated that N and P were co-limiting regardless of location (Figs. 3a, 3c). During base flows, N-containing amendments significantly enhanced algal growth relative to controls by approximately 145% for N ($p = 0.001$) and 190% for NP ($p = < 0.0001$, Fig. 3d) at the downstream location only, indicating primary N and secondary P limitation downstream of beads and no evidence for nutrient limitation upstream of beads at this time of year.

Effect sizes for treatments containing N were dependent on both season and geomorphic position, resulting in a significant two-way interaction (LME, season*location, F value = 12.56, $p = 0.003$, Fig. 4;

see Table S1 for all LME test statistics). During peak flows, N-containing amendment effect sizes were larger upstream of beads than downstream by approximately 30% for N and 75% for NP (Fig. 3a). This pattern was opposite to what was observed during base flows, where N-containing amendment effect sizes were larger downstream of beads than upstream (Fig. 3b, d). Downstream effect sizes of the N and NP amendments were 120% and 250% higher, respectively, than upstream at base flows (Fig. 3b).

Environmental influences – Several of the environmental variables were significantly correlated with N-containing amendment effect sizes (response ratios). Grazer density had the strongest effect, negatively impacting N-containing amendment effect sizes (LME, partial $R^2 = 0.25$, $\beta = -0.0003$, $p < 0.001$, Fig. 5a). Canopy cover (partial $R^2 = 0.097$, $\beta = -0.07$, $p = 0.001$, Fig. 5b), temperature (partial $R^2 = 0.025$, $\beta = -4.18$, $p = 0.02$, Fig. 5c) and stream depth (partial $R^2 = 0.00005$, $\beta = -0.3$, $p = 0.03$, Fig. 5d) were also negatively associated with N-containing amendment effect sizes, although these variables explained relatively little variation in the model. Stream nutrients were not as influential: stream $\text{NO}_3\text{-N}$ and $\text{NH}_4\text{-N}$ explained 8-10% of the model variation and $\text{NH}_4\text{-N}$ was marginally significant ($\text{NO}_3\text{-N}$, partial $R^2 = 0.1$, $\beta = 14.05$, $p = 0.3$; $\text{NH}_4\text{-N}$, partial $R^2 = 0.08$, $\beta = -75.3$, $p = 0.08$, Figs. 5e, 5f). Dissolved oxygen (DO, partial $R^2 = 0.04$, $\beta = 0.2$, $p = 0.6$) and velocity (partial $R^2 = 0.07$, $\beta = 13$, $p = 0.2$) were not significant predictors of N-containing amendment effect sizes (Fig. 5g, 5h).

Discussion

We used nutrient diffusing substrates to experimentally evaluate how algal N limitation varied spatially and temporally in relation to stream geomorphology in fire-affected, high elevation streams. Our results showed that N limitation patterns shifted with both season and geomorphic position, and that algal responses to nutrient amendments were influenced by this interaction. Consistent with our hypothesis, algal responses to N were stronger downstream of beads than upstream in lower stream $\text{NO}_3\text{-N}$ conditions during base flows. At this time of year, algae downstream of beads were primarily limited by N, while we found no evidence of nutrient limitation upstream of beads. We observed the opposite pattern during high flow, high stream $\text{NO}_3\text{-N}$ conditions, where algal responses to N were stronger upstream than

downstream, and N and P co-limitation at both geomorphic positions suggested reduced primary N limitation under high NO₃-N conditions. Our findings also showed that some seasonally shifting environmental variables, especially macroinvertebrate grazer density, may have played a role in influencing algal responses to N in fire-affected streams. These results highlight that under altered post-fire N conditions, biological and physical processes may be interacting with stream geomorphology to collectively shape spatial and temporal patterns of N limitation across streams.

To better understand the mechanisms driving spatial and temporal variation in N limitation, we evaluated seasonal patterns in stream chemistry across geomorphic positions and seasons. In-stream NO₃-N and TDN concentrations changed significantly by season but not by geomorphic position, though we did generally observe downstream nutrient reductions. Significant seasonal declines in stream NO₃-N and TDN concentrations aligned with our expectations that snowmelt-driven peak flows mobilize and transport terrestrial NO₃-N to the aquatic environment, increasing in-stream concentrations during spring and early summer and decreasing during base flows in late summer and fall. While spatial differences in NO₃-N and TDN were not significant, downstream reductions were most pronounced during base flows. In contrast, NO₃-N concentrations decreased relatively little from above to below beads during peak flows, suggesting that the capacity for beads to act as nitrate sinks may be greater during base flow conditions. This finding contrasts with a previous study in an unburned catchment in the Colorado Rockies that found that an unconfined valley segment in a stream acted as a NO₃-N sink during peak flows and a NO₃-N source during low flows (Wegener et al. 2018). Notably, NO₃-N concentrations in our study streams were more than double the reported NO₃-N concentrations in the previous study (Wegener et al.), demonstrating that differences in seasonal retention capacity of river beads may be altered by post-fire hydrologic, biogeochemical, and ecological processes that can disrupt typical patterns of nutrient retention in streams. It is possible that higher in-stream NO₃-N reduction during base flows in our study may be due to higher biological uptake under limiting NO₃-N concentrations as opposed to elevated NO₃-N conditions (Marti et al. 2004). During base flows, lower stream velocities and longer water residence times can further enhance biological processing and nutrient removal (Kaushal et al. 2008, Klockner et al.

2009, Cunha et al. 2018), particularly when nitrate is more limiting. In contrast, during peak flows, higher $\text{NO}_3\text{-N}$ concentrations and shorter residence times may exceed biological demand and lead to less efficient uptake and reduced retention across stream segments. Stream $\text{NH}_4\text{-N}$ concentrations were higher during base flows compared to peak flows – a pattern likely due to $\text{NH}_4\text{-N}$ -rich groundwater contributions during base flows. Interestingly, downstream reductions in $\text{NH}_4\text{-N}$ were more pronounced during peak flows than base flows. Previous research has shown biological preference for $\text{NH}_4\text{-N}$ over $\text{NO}_3\text{-N}$ in Colorado streams (Day and Hall 2017), which may help explain higher downstream reductions during peak flows through increased biotic demand and uptake when $\text{NH}_4\text{-N}$ is less available despite high stream $\text{NO}_3\text{-N}$ concentrations. While $\text{PO}_4\text{-P}$ was below the detection limit (<0.01 mg/L) regardless of geomorphic position or season, it is worth noting that other organic and inorganic forms of P that were not measured in this study are known to impact post-fire water quality (Rust et al. 2018).

Our study demonstrated that nutrient limitation patterns were strongly influenced by season. The significant, positive response of algae to the N amendment and the NP amendment indicated a primary N limitation with secondary P limitation downstream of beads during base flows under low stream $\text{NO}_3\text{-N}$ conditions (Tank and Dodds 2003). In contrast, the significant, positive response of algae to the N, P, and NP amendments upstream of beads as well as to the NP amendments downstream of beads during peak flows indicated co-limitation of N and P (Tank and Dodds 2003) across geomorphic positions under high stream $\text{NO}_3\text{-N}$ conditions. Our findings during peak flows were consistent with a previous study in the Colorado Front Range that found that undisturbed streams were primarily N-limited, whereas streams draining burned catchments were N and P co-limited, likely due to elevated post-fire $\text{NO}_3\text{-N}$ concentrations (Rhea et al. 2021). This seasonal shift from primary N limitation during base flows to N and P co-limitation during peak flows aligns with our hypothesis that N limitation would be stronger during late summer base flows when $\text{NO}_3\text{-N}$ concentrations are lower, and that higher $\text{NO}_3\text{-N}$ concentrations may alleviate N limitation regardless of geomorphic position. Indeed, previous studies have shown that under high N conditions, nutrient limitation may shift toward P (Xu et al. 2010, Mamun et al. 2018, Rhea et al. 2021). The reduced response to N alone during peak flows suggests that elevated

NO₃-N concentrations seasonally alleviated primary N limitation, contributing to N and P co-limitation. Collectively, these findings suggest that wildfire-driven seasonal changes in nutrient availability can shape the temporal context of nutrient limitation in fire-affected streams. However, nutrient concentrations alone did not fully explain our observed spatial patterning of N limitation.

Algal responses to nutrient treatments were also dependent on geomorphic position. Effect sizes of N-containing amendments were greater upstream of beads during peak flows in high N conditions, and downstream of beads during base flow, low N conditions. While the finding that N limitation was more prevalent downstream of beads during baseflow conditions was consistent with our hypothesis, stream nutrient concentrations alone did not entirely explain this spatial response. In-stream NO₃-N and TDN concentrations changed significantly by season but not in relation to geomorphic position, though we did generally observe downstream nutrient reductions depending on the season. N-containing amendment effect sizes were larger upstream of beads than downstream during peak flows, despite fairly stable NO₃-N and TDN concentrations across geomorphic positions. In contrast, the largest downstream reductions in biologically preferable NH₄-N were observed during this period. During base flows, N-containing amendment effect sizes were higher than upstream effect sizes, coinciding with downstream reductions in TDN and NO₃-N across beads. Stream NH₄-N concentrations were higher during this time of year with minimal downstream reductions. Although we expected geomorphic position to influence algal responses by modulating nutrient availability, our results indicate that nutrient concentrations alone were weak predictors. Instead, geomorphology may have shaped nutrient limitation patterns more indirectly, potentially through its effects on other environmental variables rather than strong controls on nutrient retention.

Our findings also suggest that seasonally shifting environmental factors including canopy cover, stream depth, and temperature in combination with nutrient concentrations can influence the strength of N limitation in fire-affected streams with elevated N. Contrary to our expectations, both NO₃-N and NH₄-N were positively associated with N-containing amendment effect sizes instead of reducing limitation as indicated by a negative association. Indeed, other studies utilizing NDS under high N conditions have

found that N amendments can still promote algal growth due to differences between stream concentrations and bioavailability, saturation under high N conditions, and other colimiting factors such as P (Earl et al. 2006, O'Brien et al. 2007). This unexpected relationship may reflect other factors that more strongly influenced algal responses to nutrient amendments. Several of the environmental factors we evaluated were shown to be predictors of N-containing amendment effect sizes, demonstrating that both biological and physical stream conditions can influence nutrient limitation, even under high N conditions. Average canopy cover, stream depth, and mean temperature were significantly negatively associated with N-containing amendment effect sizes. These factors are known to individually influence algal responses to nutrients both spatially and temporally. For example, stream periphyton can be nutrient limited under low canopy cover, high light conditions and light limited under high canopy, low light conditions along a stream reach (Warren et al. 2017). Conversely, other work has shown that nutrients were more limiting during seasons with higher light availability (Rosemond et al. 2000). In our study, canopy cover was nearly 1.5 times higher during late summer base flows, suggesting that seasonal as well as locational differences in canopy cover can modulate the strength of N limitation. Similarly, stream depth is associated with light attenuation, as deeper water may inhibit light availability to the benthos. Previous research has demonstrated negative relationships between Chl *a* and stream depth (Morgan et al. 2006), likely due to light limitation in deeper water. Stream depth was similar across geomorphic positions in our study but varied slightly between study streams and seasons, with higher depths during peak flows. It is possible that stream depth during our experiments remained below thresholds where light limitation can become a strong influence on algal response to nutrients. Mean temperature was also a significant predictor of N effect sizes, and other studies have found that temperature is an important factor in algal response to nutrients, increasing growth and uptake rates (Cross et al. 2015) as well as biomass (Francoeur et al. 1999, Myrstener et al. 2018). Given that temperature primarily varied seasonally in our study with warmer temperatures during peak flows, this weak effect likely reflects temporal rather than spatial trends. Surprisingly, current velocity was not a strong predictor of N-containing amendment effect sizes, though it has been shown to both increase algal nutrient availability (Hiatt et al. 2019) and decrease

algal growth rates (Biggs 1998). Current velocities in our study were nearly twice as high in peak flows than base flows, suggesting that despite strong seasonal differences, other factors more strongly influenced algal responses to N. Dissolved oxygen (DO) was also a weak predictor of N-containing effect sizes. While DO is associated with ecosystem productivity and stream metabolism (Odum 1956, Hall and Hotchkiss 2017), the latter of which can control N uptake (Hall and Tank 2003), it may not directly influence algal nutrient uptake at the scale of our experiment.

Although light, depth, and temperature have demonstrated effects on algal growth, it appears these effects were less pronounced than influences of macroinvertebrate grazer density. Grazers exert strong top-down controls on periphyton by consuming algal biomass and altering community structure (Rosemond et al. 1993, Feminella and Hawkins 1995), especially under high grazer densities (Hillebrand 2009, Beck et al. 2019). Additionally, a meta-analysis of 85 experiments found that negative effects on periphyton biomass by macroinvertebrate grazers were stronger than the positive effects of nutrient additions (Hillebrand 2002). In our study, we found the highest grazer densities composed primarily of mayflies (families *Baetidae* and *Heptageniidae*) at upstream bead locations during late summer base flows, coinciding with the absence of nutrient limitation at this site. Similarly, Beck et al. (2019) found that grazing effects on periphyton in the South Fork Cache la Poudre upstream of our study sites were strongest in late summer when grazer densities, particularly of heptageniid mayflies, were highest. While upstream and downstream experimental sites within streams were selected for similar canopy cover, velocity, and depth, the elevated grazer densities observed at upstream sites may reflect favorable microhabitat conditions associated with the transition from steeper, high-velocity confined reaches into broader, low-gradient unconfined segments. The hydraulic transition from confined to unconfined stream reaches typically results in decreased velocities, reduced shear stress, and enhanced depositional environments, all of which can create favorable habitats for macroinvertebrates. These transitional areas can accumulate organic matter and sediment from the upstream transport reach, supporting algal growth and providing food resources (Rice et al. 2001). This finding suggests that heavy grazing pressure may have suppressed algal responses to nutrient amendments, potentially masking indications of nutrient

limitation. Strong top-down control by grazers may explain the observed support for our hypothesis; however, this finding contrasts with our original reasoning, as the mechanism appears to be less driven by N reduction across river beads and more by spatial variation in grazer densities. While multiple studies have assessed the influences of these environmental factors on algal nutrient responses alone, fewer studies have examined these factors in combination. Together, these findings demonstrate that while nutrient concentrations primarily shaped the seasonal context of nutrient limitation, spatial patterns were more strongly influenced by local stream conditions. Future work on spatial variation in macroinvertebrate communities in relation to geomorphic context would be useful to test the generality of this finding.

The influence of the beads in our study on nutrient dynamics should be considered within the historical context of stream ecosystem changes in the study area. A majority of the river beads had indications of degradation such as channel incision and straightening, generally lacking the full complexity and hydrologic connectivity typically associated with unconfined stream-floodplain environments. Historically, the study beads may have supported greater nutrient, sediment, and water retention (Wohl et al. 2018) facilitated by beaver dams and large wood. Long-term effects of historic logging and beaver removal have reduced the biotic drivers of stream complexity in the study area (Polvi and Wohl 2013), potentially dampening the capacity of beads to function as zones of nutrient retention. This loss of complexity may partially explain why observed downstream reductions in N were lower than expected. Additionally, increasing N deposition has been observed on the Colorado Front Range for decades (Lewis and Grant 1980), potentially limiting biological uptake of N as streams become saturated and fulfill nutrient demands (Wegener et al. 2018). Together, fire-driven increases in nutrient inputs, degraded stream structure, and chronic N deposition may interact to reduce the sink potential of stream reaches that might otherwise serve as key biogeochemical hotspots in the stream network (McClain et al. 2003).

Our results emphasize the need to interpret NDS experiments in the broader context of physical and biological environmental variation. While NDS are widely used to assess benthic periphyton nutrient

limitation, they may not fully isolate nutrient effects when bottom-up (i.e., light availability regulated by canopy cover) and top-down (i.e., macroinvertebrate grazers) factors exert strong controls. Future experiments would benefit from incorporating controls on these factors such as shading and electrical grazer exclusions to isolate effects and disentangle environmental interactions. Further, our findings demonstrate important implications for stream restoration in post-fire catchments. Our study included two stream reaches prior to restoration using low-tech-process-based restoration (LTPBR) to mitigate post-fire impacts, presenting an opportunity to repeat and refine post-restoration studies that evaluate how LTPBR affects nutrient retention and algal dynamics in burned catchments. Restoring geomorphic complexity may improve the capacity of unconfined channel segments to retain nutrients (Bukaveckas 2007) and regulate primary production following fire. Increasing stream-floodplain connectivity and enhancing structural heterogeneity may support more resilient nutrient uptake and retention dynamics in streams with elevated N. As both stream restoration efforts and wildfire expand across the western U.S., studies that link geomorphology and ecological processes will be critical for advancing our understanding of stream resilience in the face of growing disturbance.

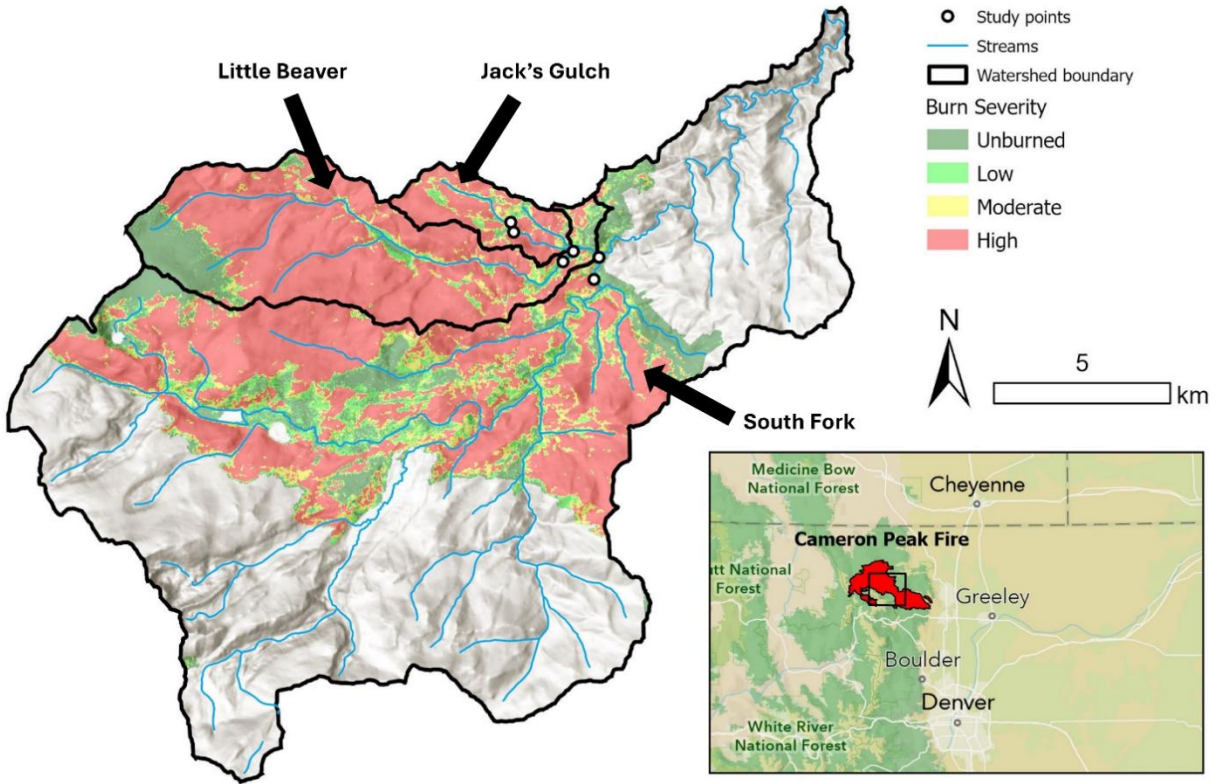


Figure 1. The South Fork Cache la Poudre River basin with Little Beaver Creek and Jack's Gulch watershed boundaries. Cameron Peak Fire burn severity within the catchments is denoted by red (high severity), yellow (moderate severity), and light green (low severity). The bottom right inset shows the general study location within the Cameron Peak Fire perimeter along the Colorado Front Range.

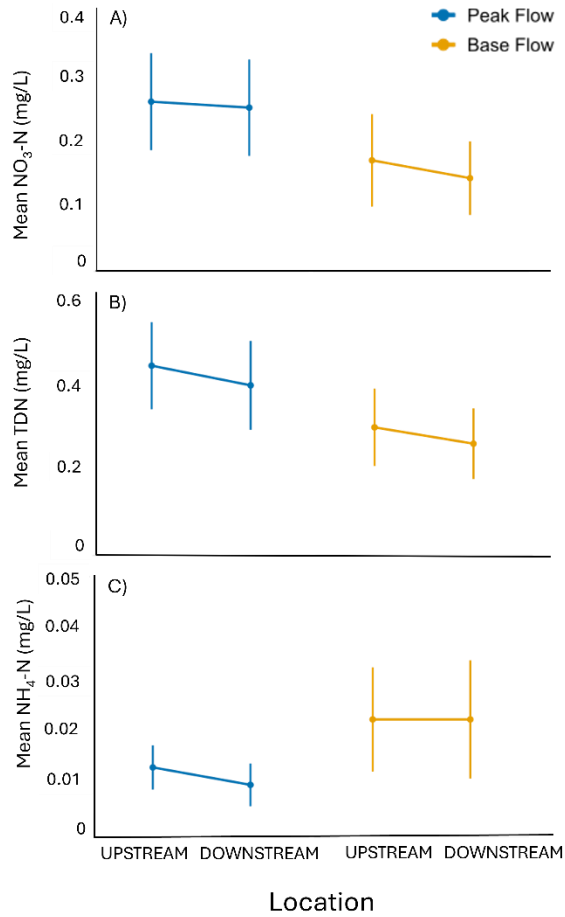


Figure 2. Mean NO₃-N (A), TDN (B), and NH₄-N (C) concentrations upstream and downstream of beads during peak (blue) and base (orange) flows throughout the duration of NDS experiments. Bars represent standard errors of the mean nutrient concentration for each group.

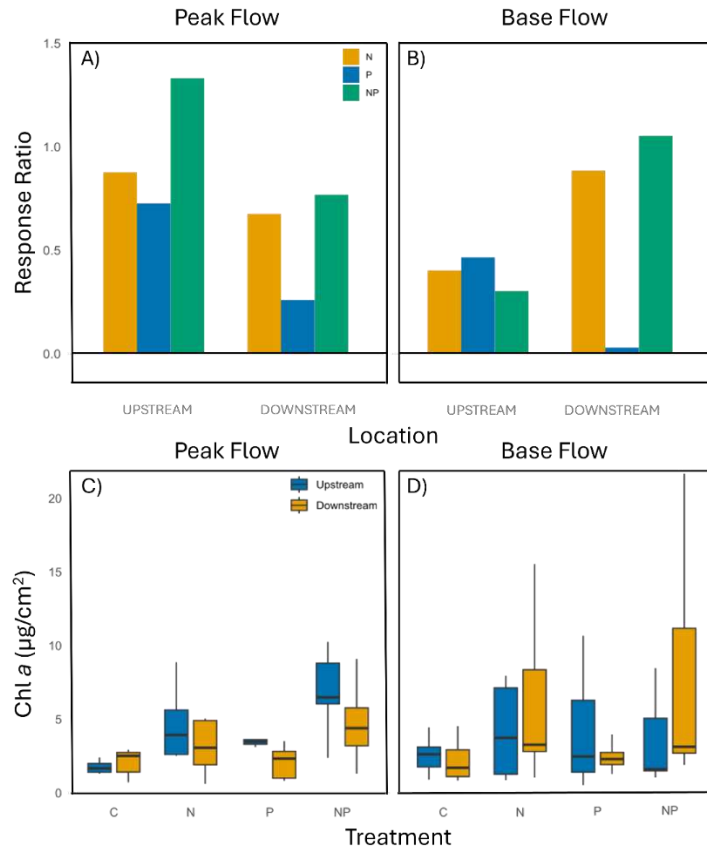


Figure 3. Algal response to NDS nutrient treatments above and below river beads during peak (A, C) and base (B, D) flows. The top panel shows nutrient amendment effect sizes calculated as response ratios ($\ln[\text{mean treatment Chl } a / \text{mean control Chl } a]$) upstream and downstream of beads during peak (A) and base (B) flows (nitrogen, blue; nitrogen + phosphorous, orange; phosphorous, green). The bottom panel shows raw Chl *a* of controls and nutrient treatments upstream (blue) and downstream (orange) of beads during peak (C) and base (D) flows. The bold horizontal lines in each boxplot indicate medians, the height of the box shows the extent of the interquartile range, and the whiskers extend 1.5 times the interquartile range.

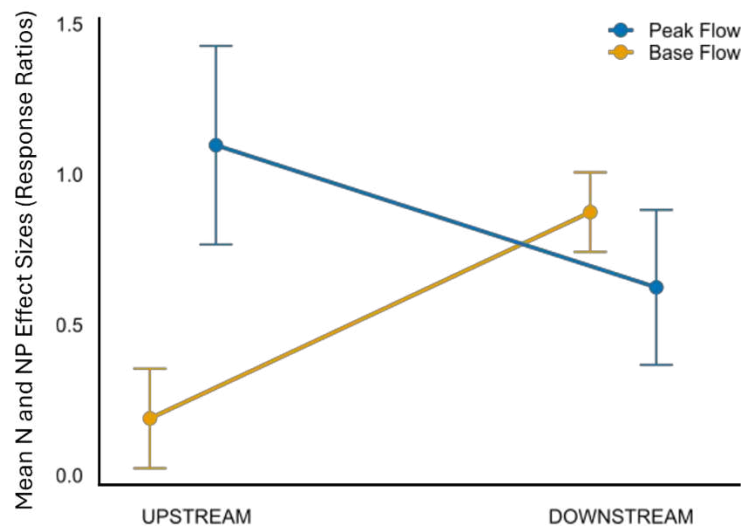


Figure 4. Mean effect sizes (response ratios) of N-containing (N, NP) nutrient treatments upstream and downstream of river beads during peak (blue) and base (orange) flows. Bars represent standard errors of the mean N-containing amendment response ratios.

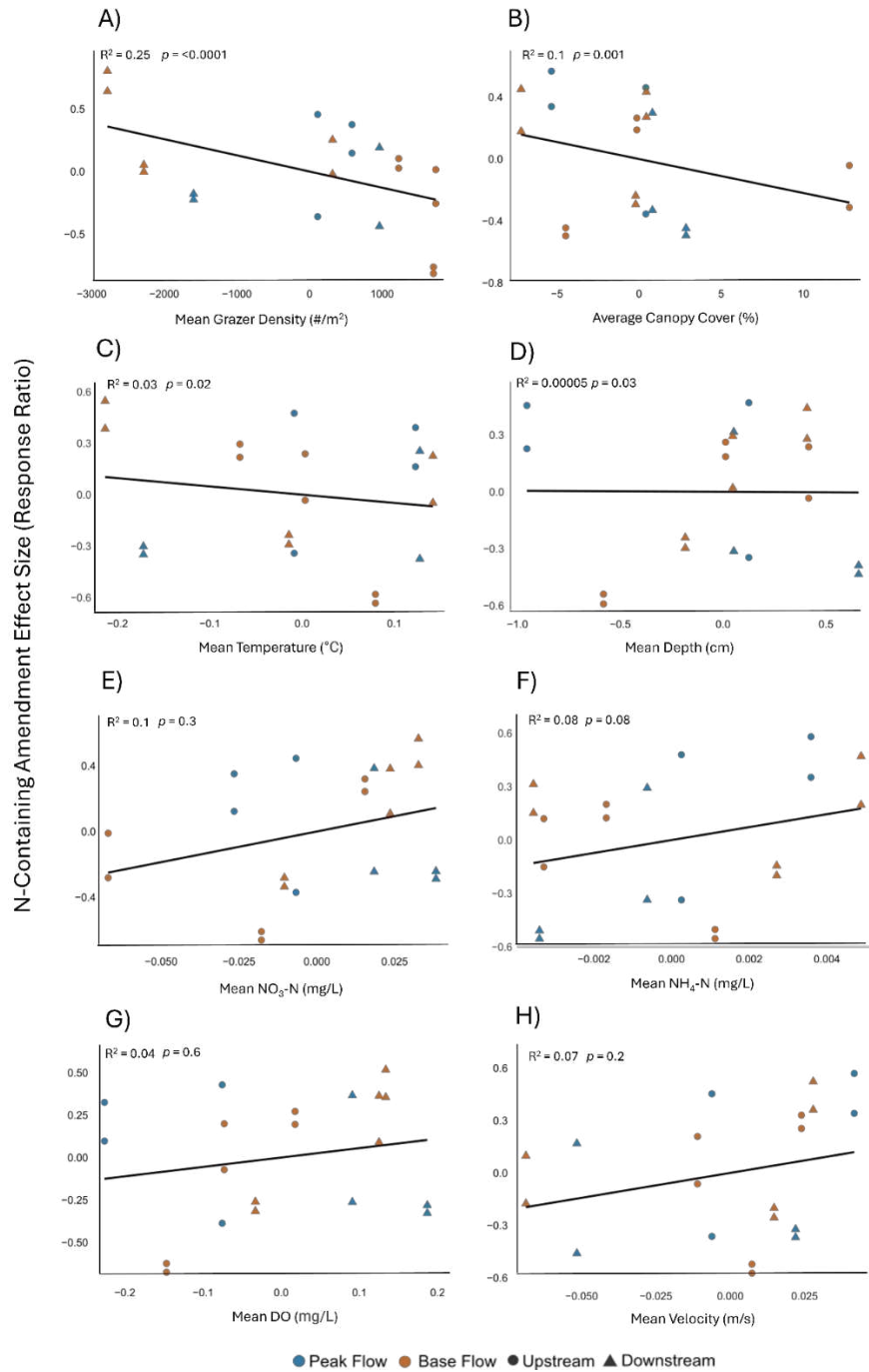


Figure 5. Partial regression plots showing relationships between N-containing amendment effect sizes and mean grazer density (A), average canopy cover (B), mean temperature (C), mean stream depth (D), mean NO₃-N (E), mean NH₄-N (F), mean dissolved oxygen (G), and mean current velocity (H). The x-axis displays residuals of the predictor variable after accounting for all other predictors in the model, and the y-axis shows residuals of the N-containing amendment effect sizes after accounting for the remaining predictors in the model (not including the one on the x-axis). Each point represents an individual sample symbolized by location (upstream, circle; downstream, triangle) and season (peak flow, blue; base flow, orange). The solid black line indicates the linear relationship between the N-containing amendment effect size and the predictor variable.

Table 1. Site characteristics of the three study catchments. Burn extent is the proportion of the catchment burned during the Cameron Peak Fire as calculated using Rapid Initial Assessment of Vegetation Condition After Wildfire (RAVG, USDA Forest Service) data.

Site	Catchment area (km ²)	Elevation range (m)	Burn extent by severity (%)			
			Total	Low	Moderate	High
Little Beaver Creek	46.75	2403-3546	88.2	5.4	7.8	75.0
Jack's Gulch	7.67	2425-2969	94.5	8.2	13.7	72.6
South Fork Cache la Poudre	268.92	1199-4079	40.7	4.7	5.5	30.5

Table 2. Mean nitrate-nitrogen (NO₃-N), ammonium-nitrogen (NH₄-N), total dissolved nitrogen (TDN), temperature, dissolved oxygen (DO), depth, current velocity, canopy cover, and grazer density at each geomorphic position (upstream or downstream of beads) during peak flows and base flows.

Season	Geomorphic Position	Environmental Factors								
		Mean NO ₃ -N (mg/L)	Mean NH ₄ -N (mg/L)	Mean TDN (mg/L)	Mean Temperature (°C)	Mean DO (mg/L)	Mean Depth (cm)	Mean Velocity (m/s)	Mean Canopy Cover (%)	Mean Grazer Density (#/m ²)
Peak Flow	Upstream	0.26	0.013	0.43	11	6.7	22	0.39	16.5	2742.5
	Downstream	0.25	0.01	0.39	11	7.4	19.7	0.38	30.3	3132.8
Base Flow	Upstream	0.16	0.021	0.28	9.5	7.7	16.3	0.2	36.6	9377.9
	Downstream	0.13	0.02	0.23	9.7	7.8	16.6	0.19	29.1	5116.5

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APPENDIX

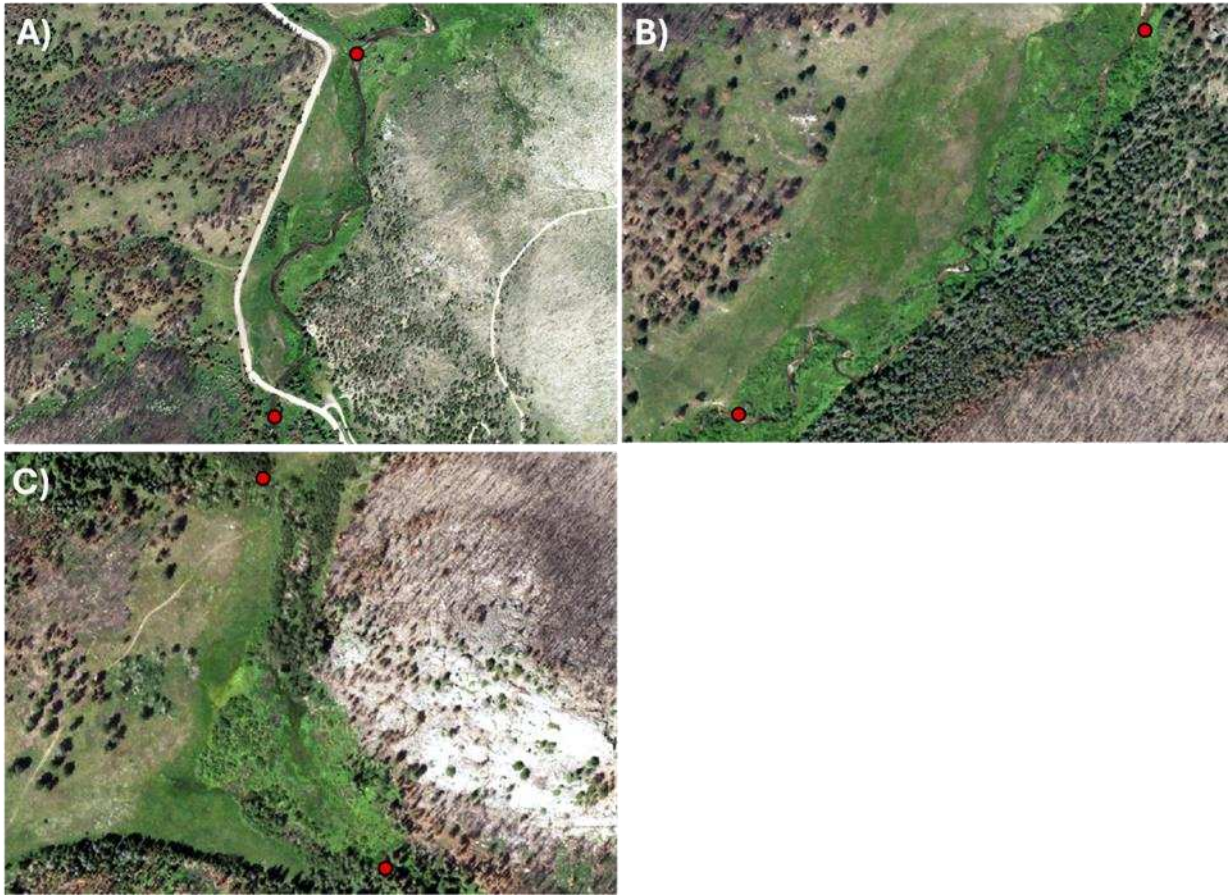


Figure S1. Study site locations upstream and downstream of river beads in South Fork (A), Little Beaver Creek (B), and Jack's Gulch (C). See Table 1 for catchment characteristics of each stream. Study site locations are denoted by red circles.

Table S1. Results of the linear mixed effects models (LME) for each response variable and associated predictor variables.

Response Variable	Predictors	F value	P value
N-containing RR	Season	1.9	0.1
	Location	0.42	0.5
	Season::Location	12.56	0.003
Chl a	Treatment	13.79	<0.0001
	Season	2.96	0.08
	Location	1.07	0.3
	Treatment::Season	1.84	0.14
	Treatment::Location	1.13	0.33
	Season::Location	6.7	0.01
	Treatment::Season::Location	2.8	0.04
NO3-N	Season	11.52	0.006
	Location	0.15	0.49
	Season::Location	2.36	0.64
NH4-N	Season	2.15	0.12
	Location	0.0008	0.84
	Season::Location	0.0008	0.85
TDN	Season	6.83	0.017
	Location	0.004	0.63
	Season::Location	0.288	0.88
N-containing RR	NO3-N	2.9	0.3
	NH4-N	4.04	0.09
	Mean temperature	12.3	0.02
	Mean DO	0.2	0.6
	Mean Depth	6.08	0.03
	Mean Velocity	4.3	0.2
	Mean Canopy Cover	19.3	0.001
	Grazer Density	33.6	0.0001

Table S2. Post-hoc Dunnett's test following the Chl *a* response LME (see Table S1 for LME results) p-values comparing each nutrient treatment with the control within locations during peak flow and base flow experiments.

Treatment	<i>p-value</i>			
	Peak Flow		Base Flow	
	Upstream	Downstream	Upstream	Downstream
N	0.008	0.236	0.804	0.001
P	0.018	0.928	0.994	0.817
NP	<0.0001	0.025	0.989	<0.0001