

THESIS

BUILT FOR DISTURBANCE: LIMITED VEGETATION RESPONSES TO LOW-TECH
PROCESS-BASED RESTORATION IN NORTHERN COLORADO FLOODPLAINS

Submitted by

Kailyn E. Atkinson

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Master's Committee:

Advisor: Camille Stevens-Rumann

Co-Advisor: Jeremy Sueltenfuss

Allie Rhea

Ellen Wohl

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ABSTRACT

BUILT FOR DISTURBANCE: LIMITED VEGETATION RESPONSES TO LOW-TECH PROCESS-BASED RESTORATION IN NORTHERN COLORADO FLOODPLAINS

Channel incision is a major driving factor of change in floodplain vegetation communities and is a common outcome in burned watersheds. Low-Tech Process-Based Restoration (LTPBR) methods aim to reconnect channels with their floodplains to restore channel-floodplain connectivity and ecosystem functions such as periodic overbank flooding. However, short-term floodplain vegetation responses to LTPBR remain poorly understood despite the growing popularity of these treatments. We evaluated whether LTPBR increased floodplain inundation, and whether increased flooding led to increased productivity and promoted wetland plant communities. We monitored peak-season flooding extent, sediment deposition, plant community composition and productivity across treated and untreated reaches of variable burn severity. LTPBR increased early-season overbank flooding but did not retain surface water into late-summer. Vegetation composition and productivity remained largely unchanged, although sediment deposits created microsites colonized by clonal graminoids and early successional species. These results suggest that short-term hydrologic changes were insufficient to trigger broad vegetation shifts, likely because disturbance thresholds necessary for community reassembly were not met and community change occurs over longer timescales. Restoration outcomes following LTPBR may depend on sustained, periodic hydrologic disturbance over multiple years to drive floodplain vegetation change.

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TABLE OF CONTENTS

ABSTRACT	ii
ACKNOWLEDGEMENTS	iii
INTRODUCTION	1
METHODS	5
Site description and study design	5
Channel-floodplain connectivity	9
Aboveground biomass	9
Plant community composition	10
Vegetation on fluvial deposits	11
Fire and floodplains	12
RESULTS	13
Channel-floodplain connectivity	14
Aboveground biomass	16
Plant community composition	18
Vegetation on fluvial deposits	22
Fire and floodplains	23
DISCUSSION	28
Channel-floodplain connectivity	28
Aboveground biomass	29
Plant community composition	30
Vegetation on fluvial deposits	32
Fire and Floodplains	34
Limitations & future directions	36
Conclusions	37
REFERENCES	39
APPENDICES	45
Appendix A: Supplemental Figures	45

INTRODUCTION

Incision disconnects rivers from floodplains, altering flooding patterns, water tables, and moisture availability in adjacent riparian areas (Wolf et al., 2007), shifting floodplain plant communities and ecosystem function (Loheide & Booth, 2011). To combat the loss of channel-floodplain connectivity, land managers are increasingly using Low-Tech Process-Based Restoration (LTPBR) methods, including Beaver Dam Analogs (BDAs), and Post-Assisted-Log-Structures (PALs). These methods aim to reconnect channels to their floodplains and promote natural hydrologic and geomorphic processes such as overbank flooding and sediment deposition by reintroducing wood structures into the stream (Beechie et al., 2010). However, the short-term response of vegetation to LTPBR remains unclear, particularly in post-fire landscapes, where vegetation, hydrology and sediment yields are in a state of change (Huffman et al., 2001; Benavides-Solorio & MacDonald, 2001). Because riparian vegetation influences sediment capture in the floodplain, and LTPBR aims to restore hydrologic connectivity through floodplain inundation to capture excess sediment in the floodplain, understanding how connectivity shapes floodplain vegetation and sediment dynamics is essential.

Floodplain vegetation is governed by hydrology, especially the extent of floodplain inundation that determines flooding, sediment deposition, and nutrient delivery. Floodplain vegetation can buffer post-fire sediment fluxes by stabilizing banks (Polvi et al., 2014), and providing roughness to capture sediment in the floodplain during flooding events (Kretz et al., 2021). However, incision decreases floodplain sediment storage because the magnitude of floods needs to reach a higher threshold before overbank flow occurs (Wohl, 2021).

Flooding shapes when and where water and nutrients are available within floodplains (McClain et al., 2003), which in turn influences ecosystem productivity and community composition (Junk et al., 1989). Spatial gradients in particulate nutrient deposition and productivity are reflected in vegetation community patterns: highly productive species dominate in flood-influenced zones, while farther from the river, biomass declines where sediment, water, and particulate nutrient inputs are lower (Keizer et al., 2018). In addition, the frequency and duration of inundation shape community composition by filtering for species traits that are capable of flood tolerance (Casanova & Brock, 2000). Incision-driven reductions in flooding and sediment delivery shift floodplain plant communities toward drier, less productive and less fluvially adapted vegetation (Loheide & Booth, 2011; Wohl, 2025).

Floodplain plants are adapted to disturbance, and fire and floods create a heterogeneous pattern of community composition and recovery trajectories (Kleindl et al., 2015; Bendix & Cowell, 2010). While fire can reshape floodplain vegetation mosaics, the timing and duration of inundation in floodplain communities can have longer-term impacts on vegetation compared to fire (Mackay et al., 2024). The saturated soils of floodplains enhance the resilience of a landscape to severe fires by providing fire breaks, refugia, and seed sources along riparian margins, thereby reducing fire severity and supporting upland recovery following wildfire (Fairfax & Whittle, 2020; Fairfax et al., 2024). Floodplain species are disturbance-adapted with traits such as deep root systems, adventitious resprouting ability, or rapid root extension, and are better adapted to survive fluvial disturbances and wildfire (Merritt et al., 2010), reflecting the resilience of floodplain plant communities. In this study, resilience refers to the capacity of a system to experience disturbance, reorganize, and still maintain ecosystem function and structure (Holling, 1973). Due to observations that long-term floodplain vegetation dynamics are governed

primarily by hydrology rather than fire alone, restoring channel-floodplain connectivity is essential for supporting recovery, resilience, and floodplain function in post-fire river corridors. One approach to protect and restore hydrologic processes in floodplains across the western U.S. is LTPBR.

LTPBR structures aim to mimic the geomorphic and hydrologic effects of beaver (*Castor canadensis*) and large instream wood by reconnecting channels with their floodplains, promoting sediment and nutrient deposition, water-flow dynamics, habitat complexity, and wetland plant communities (Beechie et al., 2010). Beaver ponds and dams are effective at capturing post-fire sediment flux (Dunn et al., 2024), especially within less incised stream reaches (Rees et al., 2024), and beaver meadows have significant impacts on fire severity and vegetation communities (Fairfax & Whittle, 2020; Larsen et al., 2021). The removal of large wood from river corridors has had lasting impacts (Wohl, 2019). In forested river corridors, large wood increases channel complexity by deflecting flow, promoting sediment deposition (Rengers et al., 2023; Wohl & Scott, 2017), and producing heterogenous patches of habitat that support vegetation and other river biota (Gurnell et al., 2005). Evidence from other systems suggests that ecosystems do not always fully recover following disturbance (Jones et al., 2018), and river corridors in the absence of beaver and large wood may persist in altered or alternative stable states (Wohl, 2019; Wolf et al., 2007).

The widespread extirpation of beaver and large wood removal has contributed to incised reaches, lower water tables, and drier floodplain plant communities (Wohl, 2021), which has led to human intervention with LTPBR to restore floodplain function. LTPBR structures can facilitate short-term sediment capture in-stream (Scamardo & Wohl, 2020), but some research has shown that these structures fall short of replicating the long-term geomorphic and ecological

functions provided by natural beaver dams such as channel-floodplain connectivity, sediment storage, and promoting wetland plant communities (Wohl, 2021; Dunn et al., 2024). Although LTPBR structures are effective in slowing water flow, they have shorter water retention times and hold less water volume than natural beaver dams (Nagle, 2024; Wohl & Inamdar, 2025). Wetland vegetation cover and willow recruitment remain lower at LTPBR sites than at beaver-occupied streams (Killooy, 2023; Ritter & Hill 2023), suggesting that additional interventions may be necessary to promote floodplain vegetation.

Although LTPBR is increasingly used to restore riparian function, little is known about short-term vegetation responses after LTPBR installation in post-fire floodplains, especially regarding vegetation community composition and productivity associated with restored flooding disturbance regimes. Thus, this study examined vegetation responses to LTPBR following the Cameron Peak Fire in northern Colorado, to determine whether these treatments increase productivity and wetland plant community composition. In this study, resilience was quantified as the variation in plant community composition and productivity following disturbance. We compared reference versus LTPBR reaches, focusing on four sites within the burn scar, that received LTPBR treatments in varying years, in the summers of 2024 and 2025. These sites are predominantly snowmelt-driven streams, where seasonal high flows are a primary mechanism for reconnecting channels to their floodplains. Specifically, this research asked:

1. Does LTPBR increase floodplain inundation?
2. Does LTPBR increase aboveground biomass and alter plant community composition?
3. What plants colonize fluvial sediment deposits?
4. How has fire influenced aboveground biomass and plant community composition in floodplains, and what do these patterns reveal about community resilience?

METHODS

Site description and study design

This study was conducted in Roosevelt National Forest, Colorado, USA, in watersheds burned by the 2020 Cameron Peak Fire. The Cameron Peak Fire burned from high elevation spruce-fir (*Picea engelmannii*–*Abies lasiocarpa*) forests to low elevation Ponderosa pine (*Pinus scopulorum*) dominated forests across federal, state and private land (Colorado Division of Fire Prevention & Control, 2024). The 30-year average of annual precipitation is 49.46 cm, and average temperature of 5.5°C with an average maximum of 16.35°C and a low of -7.82°C from the years 1991-2020 (PRISM Group, 2014). Total precipitation for water year 2024 and water year 2025 was 32.8 cm and 25.2 cm, respectively (Colorado Climate Center). Streamflow in these watersheds is driven primarily by snowmelt with peak flows during spring snowmelt, followed by a summer spike due to convective storms, and baseflow is sustained by groundwater in the fall and winter months. Data taken from a nearby long-term gauge site (USGS #402114105350101) with no flow regulation showed that the timing and amount of peak flow discharge varied between years with a larger and later peak in 2024, and a smaller, earlier peak compared to historical averages in 2025 (Figure 1).

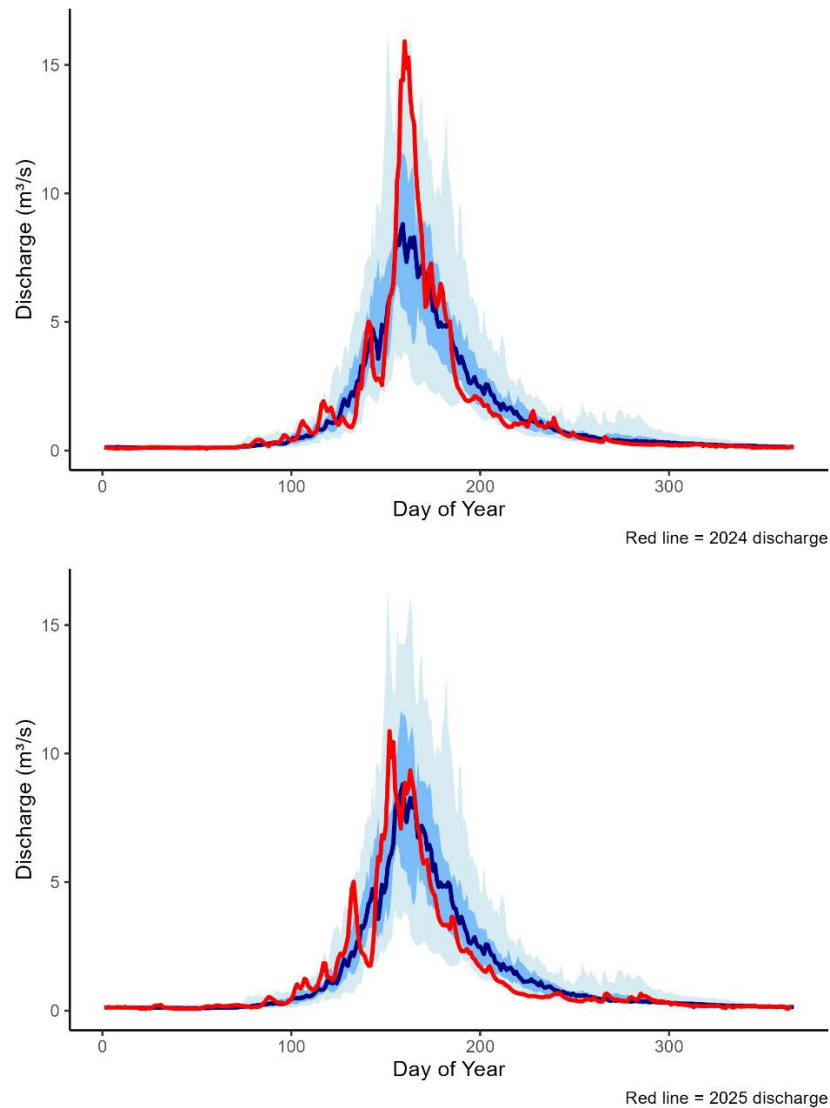


Figure 1. Hydrographs for 2024 (top) and 2025 (bottom) shown as the red line relative to historical daily discharge percentiles, including the median (dark blue line), interquartile range (25–75%; blue ribbon), and 5–95% percentile range (light blue ribbon).

Study sites included streams and floodplains impacted by the Cameron Peak Fire where restoration activities had been implemented in the years 2021, 2022, and 2024 to improve water quality by directing flow onto the floodplains and promote sediment and nutrient deposition (Table 1). Study reaches spanned a gradient of channel sizes and slopes. Annual mean streamflow and channel slope were approximately 1 cubic meter per second (cms) and

1.06% at South Fork, 0.2 cms and 2.88% at Little Beaver Creek, 0.03 cms and 3.66% at Elkhorn Creek, and <0.03 cms and 4.53% at Jack's Gulch (Moore et al., 2019). The NatureServe Terrestrial Ecological System classifies floodplains in this area as Rocky Mountain Subalpine-Montane Riparian Shrublands, typically dominated by *Salix* spp., *Alnus incana*, *Betula glandulosa*, *Betula occidentalis*, *Carex* spp., as well as other mesic graminoids and forbs (NatureServe, 2025).

Using a paired design, we evaluated four low-gradient, unconfined floodplains with LTPBR in the montane zone (2,400-2,620 m) that varied in burn extent and severity (Table 1; Figure 2). Floodplain sites were separated into reference and treatment reaches with 9 plots total in each, apart from the South Fork LTPBR reach which had 11 plots to account for the larger area. Reference reaches were located immediately upstream of the LTPBR reach at each site to best represent pre-installation hydrological conditions and plant communities. We selected a small reach farther upstream of the Jack's Gulch LTPBR reach as the reference site because of an absence of suitable reference habitat immediately upstream. At the South Fork Site, limited floodplain extent upstream constrained reference reach placement, and the selected reach represented the most comparable untreated floodplain available, despite its proximity to a downstream LTPBR structure. LTPBR design differed between sites, with structures installed prior to 2024 (i.e. Jack's Gulch and Elkhorn) being more porous. All sites had a history of livestock grazing and were actively grazed during the study period.

Each river reach included 9 vegetation plots (100 m²), stratified by elevation above streambed (0.05-1 m, 1-2 m, and 2-3 m) using pre-existing digital elevation models (Sanborn Map Company, Inc. 2020; Sanborn Map Company, Inc. 2020), with 3 vegetation plots in each elevation category. Vegetation surveys were conducted in 2024 and 2025, with only a

portion of total plots sampled in both years at South Fork, Little Beaver, and Elkhorn.

Additional plots were added in 2025 to increase sample size and capture variability. Biomass was only sampled in 2025.

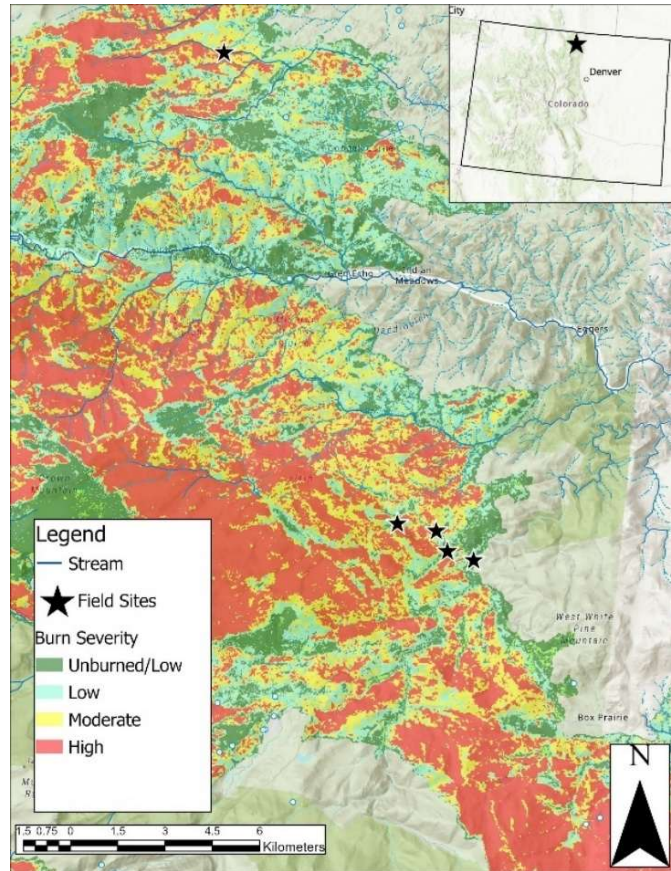


Figure 2. Site map indicating field sites and surrounding burn severity.

Table 1. Site descriptions with LTPRB installation dates and amount of early season flooding

<i>Site</i>	<i>Reach</i>	<i>Area (ha)</i>	<i>Flood Extent (ha)</i>	<i>Coverage (%)</i>	<i>LTPBR Installation</i>	<i>Elevation (m)</i>	<i>Average Floodplain Burn Severity</i>
South Fork	Reference	2.79	0.06	2	NA	2,402	Unburned
	LTPBR	11.24	3.77	34	09/2024 – 11/2024		
Little Beaver	Reference	2.34	0.01	0.4	NA	2,433	Low
	LTPBR	1.76	0.99	56	09/2024 – 11/2024		
Elkhorn	Reference	0.96	0.01	1	NA	2,711	Low
	LTPBR	1.79	0.06	3	09/24/2022 – 10/09/2022		

Jack's	Reference	1.2	0.01	0.8	NA	2,559	
Gulch	LTPBR	2.3	0	0	10/16/2021 – 10/27/2021	2,612	Unburned

Note: Average floodplain burn severity is averaged at site-scale using MTBS data. All sites had portions burned at unburned to high severity.

Channel-floodplain connectivity

To test whether LTPBR increased channel-floodplain connectivity, repeated qualitative assessments of overbank flooding were conducted during peak-flow (05/27/2025–06/18/2025) when flooding was most likely to occur, and in August (08/01/2025–08/09/2025, 08/19/2025–08/29/2025) during baseflow when flooding was likely to have receded. Flood extent was mapped using meandering surveys, recording points whenever floodwater or indicators of flooding such as scour marks, sediment deposits, or flattened vegetation were observed. In August, surveys were repeated to document locations of sediment deposition across the floodplain, capturing the spatial extent of deposition for subsequent assessment of plant community composition on fluvial deposits.

Aboveground biomass

To test whether LTPBR increased aboveground biomass, destructive biomass sampling was conducted from late-June to early-August of 2025 in both reference and LTPBR treatment reaches at each study site. These surveys were done after plant community surveys. Two 0.25 m² quadrats were placed within each 100 m² plot at the northeast and southwest corners, and all live aboveground vegetation within the quadrat, including all herbaceous

vegetation and shrubs up to 1.5 cm diameter, were harvested. Harvested material was weighed in the field, transported to the laboratory, dried at 60°C for ≥ 72 hours, and reweighed to determine biomass (g/m^2).

All data analyses were conducted in R (version 4.4.3; R Core Team, 2025). All data manipulation and visualization were performed using *tidyverse* packages (Wickham et al., 2019). We modeled log-transformed total dry biomass (g/m^2), averaged per plot across the two 0.25 m^2 quadrats, using a linear mixed-effects model fit with the *lme4* package and evaluated with the *lmerTest* package (Bates et al., 2015; Kuznetsova et al., 2017). Fixed effects included treatment (LTPBR vs. Reference), flooding (yes/no), and their interaction. Reference plots without flooding were specified as the baseline to represent pre-LTPBR biomass conditions. Burn severity and plant community type were included as covariates to account for variation in fire effects and vegetation composition. To explicitly test for site-level differences in aboveground biomass, an additional model including site as a fixed effect was fit, and the significance of site was assessed using Type III analysis of variance.

Plant community composition

To assess whether LTPBR alters vegetation communities, we conducted plant surveys from early-May to late-August in each 100 m^2 plot. Two nested quadrats (10 m^2 and 1 m^2) were placed in the northeast and southwest corners of each plot. All vascular plant species were identified and recorded in the smallest quadrat in which they occurred, and additional species present within the full 100 m^2 plot were recorded. Species-specific plant cover was ocularly estimated at the 100 m^2 plot scale to characterize dominant vegetation.

We used a two-stage PERMANOVA on Bray-Curtis dissimilarities of Hellinger-transformed plant community composition using the *vegan* package to evaluate variation in vegetation composition across different parameters (Oksanen et al., 2025). The initial model tested treatment (LTPBR vs. reference), flooding occurrence (yes/no), and their interaction, with permutations stratified by site. Because these effects were not significant, we conducted hierarchical clustering of the community matrix and identified two plant community types. We then fit an expanded PERMANOVA including elevation above streambed, burn severity, and plant community type, with permutations stratified by site.

To analyze differences in plant community types, we performed an indicator species analysis using the *indicspecies* package to identify species strongly associated with each community type (De Cáceres et al., 2009). To summarize plot-level hydrologic affinity within each community, we calculated the community-weighted mean Wetland Indicator Status score ("OBL" = 1, "FACW" = 2, "FAC" = 3, "FACU" = 4, "UPL" = 5), weighing species by calculated relative cover. We analyzed differences in community-weighted mean Wetland Indicator Status among community types using a linear mixed-effects model with the *lme4* and *lmerTest* packages (Bates et al., 2015; Kuznetsova et al., 2017).

Vegetation on fluvial deposits

If a sediment deposit was present at a site, a 1 m² vegetation survey was conducted to assess colonization on fluvial deposits. Plots were placed along a gradient from the deposit edge to the center to capture both encroachment by adjacent perennial grasses and recruitment of colonizing species. All vascular species within each 1 m² plot were recorded on a presence-absence basis.

We used a PERMANOVA on Jaccard dissimilarities to test whether plant community composition differed between 1 m² plots on recently deposited sediment and 1 m² quadrats within established 100 m² vegetation plots. Jaccard dissimilarity was chosen over Bray-Curtis because it supports presence/absence data. Permutations were stratified by site, and an indicator species analysis was used to identify species associated with sediment and quadrat communities. Quadrat plant communities were filtered to sites with sediment deposition (i.e., Little Beaver, Elkhorn, and South Fork) to better represent differentiation between plant communities on fluvial deposits and their quadrats. These data were visualized with a principal coordinates analysis to assess species significantly correlated with each community type. In addition, we used the *betapart* package to assess whether differentiation between plant communities was a result of nestedness (i.e. a subset of the larger plant community) or turnover (Baselga et al., 2025). Differences in nestedness between sediment and quadrat communities were tested using a PERMANOVA with site included as a blocking factor.

Fire and floodplains

To evaluate how fire influenced aboveground biomass and plant community composition in floodplains, we assessed fire severity using Monitoring Trends in Burn Severity (MTBS) data supplemented by field measurements of woody species rooted within established 100 m² vegetation plots. Field measurements were used exclusively to replace plots where MTBS indicated increased greenness, ensuring burned plots were not misclassified as unburned. In-field fire severity was assessed following methods adapted from the USDI *Fire Monitoring Handbook* to accommodate wetland plant species (USDI, 2003). Shrubs rooted within established 100 m² vegetation plots showing signs of scorching at the base were classified as

burned: shrubs fully top-killed by fire were classified as high severity, those retaining most of the main stem were moderate severity, and those retaining the main stem plus smaller lateral stems were low severity. Shrubs without basal scorching were considered unburned.

We examined differences in biomass across burn severity classes using the linear mixed effects model described in Section 0. Estimated marginal means and pairwise comparisons were calculated using the *emmeans* package to identify specific differences between burn severity classes (Lenth & Piaskowski, 2025). To assess the influence of burn severity on plant community composition, we calculated marginal effects from the PERMANOVA model described in the plant community subsection. These approaches allowed us to evaluate the specific contribution of burn severity while accounting for flooding, plant community, and elevation above streambed.

Analyses of temporal changes in plant community composition were restricted to a subset of plots sampled in both 2024 and 2025 (54 plots, 3 sites). Percent cover was averaged by species within each plot, Hellinger-transformed, and ordinated using principal components analysis (PCA). PCA scores were used to calculate directional changes in community composition between years for the subset of plots with repeat measurements in 2024 and 2025. Burn severity and functional group were fitted as environmental vectors using *envfit* in the *vegan* package (Oksanen et al., 2025). PCA points were colored to represent whether the plot flooded in 2025 as a result of LTPBR.

RESULTS

Channel-floodplain connectivity

Early-season overbank flooding varied substantially among sites and between reference and LTPBR reaches (Table 1; Figure 3). Reference reaches consistently exhibited minimal flooding ($\leq 2.15\%$ coverage), whereas LTPBR reaches showed a wider range of responses, from no detectable overbank flooding to $>50\%$ floodplain coverage. At South Fork, Little Beaver, and Elkhorn, LTPBR reaches accounted for the largest absolute and proportional flooded areas (Table 1).

At South Fork, moderate overbank flooding was observed in the LTPBR reach relative to the reference. Flooding in the reference reach originated from a PAL located just beyond the northeast boundary of the reference reach within the LTPBR reach. Flood pathways primarily followed historic meanders, with additional flooding along channel margins (Figure 3). The LTPBR reach exhibited 3.77 ha of flooded area (34% of the reach), compared to 0.06 ha (2%) in the reference reach (Table 1). Recent beaver activity was also observed within the LTPBR reach, reinforcing existing PALs and directing flow and sediment onto the floodplain.

The Little Beaver LTPBR reach exhibited the highest proportional flooding among all sites, with 0.99 ha inundated (56% of the reach; Table 1). Flooding followed historical side channels and included localized flow around BDAs, forming a complex, multi-thread flow pattern (Figure 3). In contrast, the reference reach exhibited limited flooding (0.01 ha; 0.4%), confined to a historical meander adjacent to the active channel. The historic meander was sparsely vegetated and composed primarily of sandy gravel. Little Beaver LTPBR reach also had the highest amount of sediment deposits and reflects most of our plant data on fluvial deposits.

Elkhorn exhibited limited overbank flooding in both reaches. The LTPBR reach had 0.06 ha flooded (3% of the reach), while the reference reach exhibited 0.01 ha of flooding (1%; Table 1). Overbank flooding was minimal during early-season surveys, coinciding with operation of an upstream diversion weir, which was diverting water during peak flow. Following late-season weir adjustments, convective storm events in August generated short-duration overbank flooding, with flow paths observed going around LTPBR structures (Figure 3).

At Jack's Gulch, little to no overbank flooding was observed in either reach. The LTPBR reach exhibited saturated soils and lateral inputs from springs but no evident overbank flow from the main channel. In the reference reach, limited flooding and deposition were confined to areas immediately adjacent to the channel within a willow-dominated corridor (Figure 3).

Across sites, LTPBR reaches exhibited greater peak-season channel-floodplain connectivity than reference reaches, although floodplain inundation was not sustained throughout the growing season. Repeat surveys conducted in August showed no evidence of persistent flooding, indicating that overbank inundation was limited to early season near peak-flow. LTPBR reaches installed earlier (Jack's Gulch, 2021; Elkhorn, 2022) appeared more structurally porous at the time of surveys, whereas more recently installed reaches (South Fork and Little Beaver, 2024) retained water more effectively and exhibited greater flooding extent (Figure 3). Site-specific hydrology further influenced flooding outcomes, with larger streams (e.g., South Fork) exhibiting greater inundation, while smaller systems (e.g., Jack's Gulch and Elkhorn) exhibited limited overbank flooding.



Figure 3. Overbank flooding extent from 05/27/25 - 06/18/2025 at each site shown in pale blue shading. Study area boundaries are outlined in white.

Aboveground biomass

Aboveground biomass varied across plots but showed no response to LTPBR treatment, overbank flooding occurrence, or elevation above the streambed (Figure 4). There was no statistical evidence that log-transformed aboveground biomass increased within LTPBR reaches relative to reference reaches ($\beta = 0.09$, 95% CI [-0.15, 0.34], $t = 0.74$, $p = 0.46$),

flooding occurrence ($\beta = -0.02$, 95% CI [-0.47, 0.42], $t = -0.11$, $p = 0.92$), or the interaction between treatment and flooding ($\beta = 0.24$, 95% CI [-0.27, 0.74], $t = 0.90$, $p = 0.38$). Biomass also did not vary with elevation above streambed (1.0-2.0 m: $\beta = 0.018$, 95% CI [-0.09, 0.44], $t = 1.28$, $p = 0.20$; 2.0-3.0 m: $\beta = 0.05$, 95% CI [-0.21, 0.31], $t = 0.39$, $p = 0.70$), although elevation was retained in the final model as a proxy for channel-floodplain connectivity assumptions.

Variation in biomass was primarily explained by plant community type and burn severity. Biomass differed significantly among plant community types (Type III ANOVA: $p = 0.022$), with Plant Community 2 exhibiting lower biomass than Community 1 ($\beta = -0.37$, 95% CI [-0.68, -0.07], $t = -2.33$, $p = 0.02$). Biomass also declined linearly across burn severity levels (linear contrast: $\beta = -0.35$, 95% CI [-0.62, -0.07], $t = -2.42$, $p = 0.02$) (Figure 5).

Aboveground biomass did not differ among sites ($F = 1.19$, $p = 0.32$) (Figure 6).

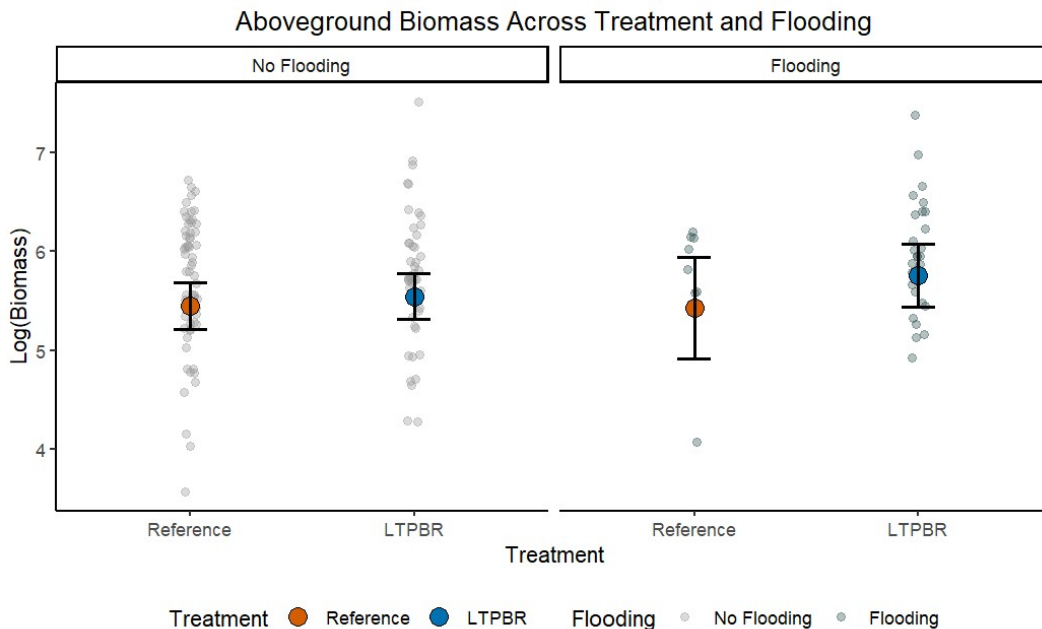


Figure 4. Aboveground biomass across treatment and flooding conditions. Model-adjusted means \pm 95% CI shown in blue and orange with observed plot-level values shown in gray.

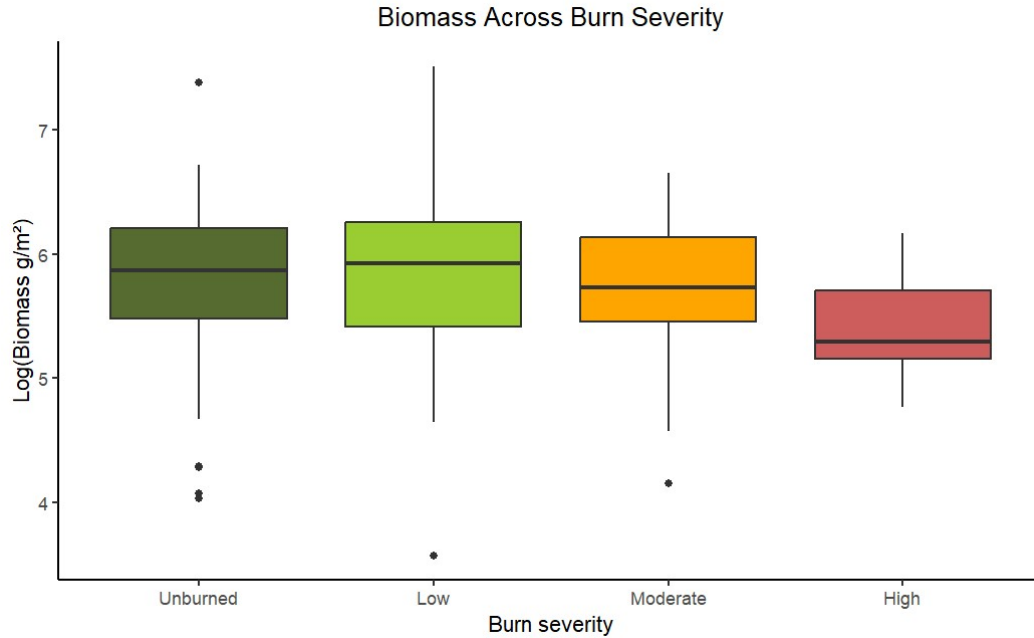


Figure 5. Biomass across burn severity classes from the 2020 Cameron Peak Fire. Biomass declined linearly with increasing fire severity.

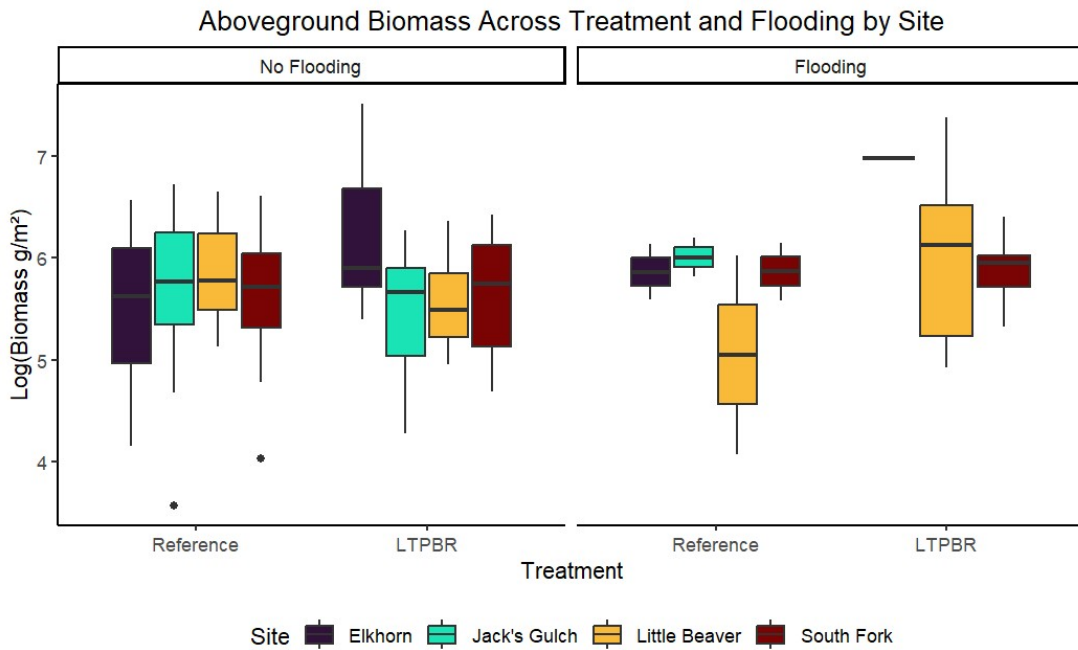


Figure 6. Aboveground biomass across treatment and flooding conditions by site. There were no significant differences in biomass across sites despite site-differences in flooding extent.

Plant community composition

Stage 1 PERMANOVA indicated that plant community composition did not vary significantly among plots as a function of treatment or flooding ($R^2 = 0.06$, $F = 1.57$, $p = 0.07$). Because this model explained only a small portion of variation, we performed a hierarchical cluster analysis, which identified two plant community types (Figure 8b). A linear mixed effects model showed that plant community type indicated a significant difference in hydrological adaptations of species within each plant community. The baseline cluster (Community 1) had a mean community weighted mean Wetland Indicator Stats of 2.34 ± 0.09 (SE), whereas plots in Community 2 had higher values by 1.53 ± 0.22 compared to Community 1 ($t = 6.85$, $p < 0.001$) (Appendix A: Figure 1; Appendix A: Table 1). Plant Community 1 consisted of an average of Facultative Wet and Facultative species, whereas Community 2 consisted of an average of Facultative Upland and Upland species.

Functional group cover across sites is shown for LTPBR and reference reaches (Figure 7). Most sites were dominated by graminoids, while forbs, shrubs, and trees varied in cover across sites. Proportionally, Community 1 had higher cover of Obligate and Facultative Wet species, whereas Community 2 that had greater representation of Upland species (Appendix A: Figure 2). Random effects indicated that variation among sites was small ($\sigma^2 = 0.006$, $\sigma = 0.08$) relative to residual variation among plots ($\sigma^2 = 0.42$, $\sigma = 0.65$). Overall, these results indicated that plant community type is associated with differences in hydrologically adapted plant species.

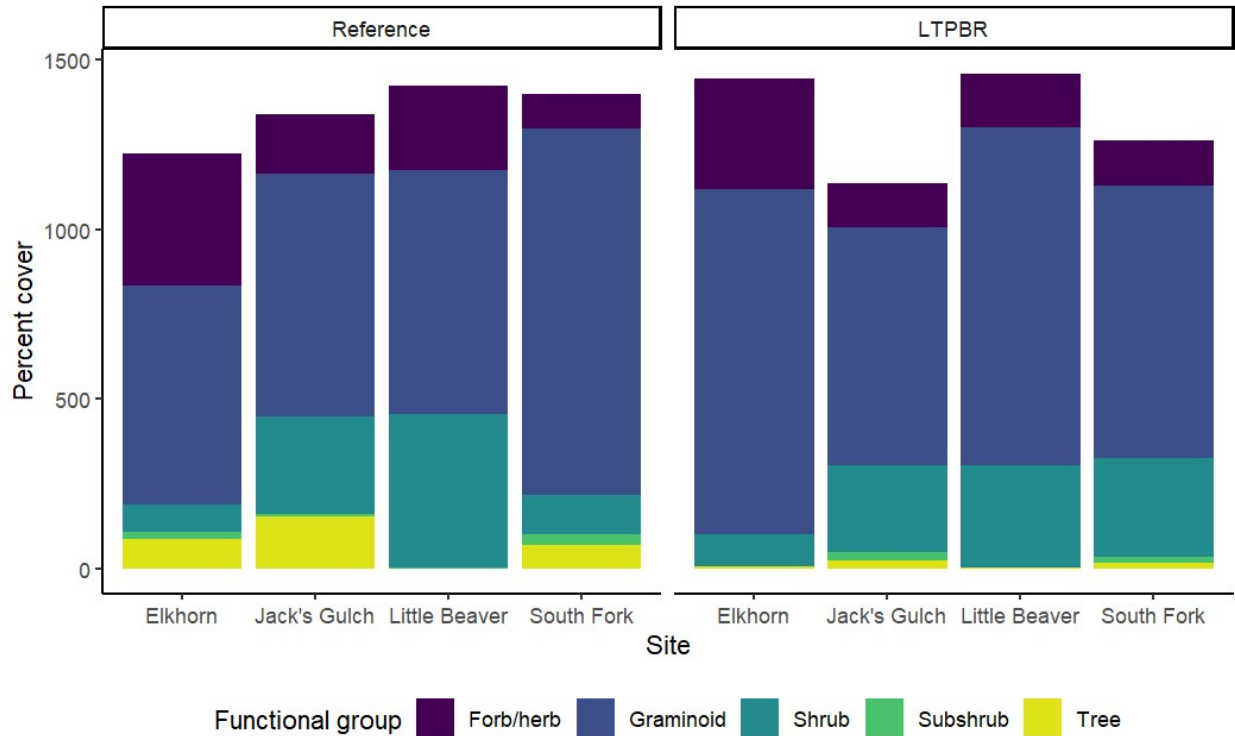


Figure 7. Functional group cover across sites faceted by LTPBR or reference reach.

Stage 2 PERMANOVA showed that plant community composition varied significantly among plots as a function of treatment and flood conditions, elevation above streambed, burn severity, and plant community type ($R^2 = 0.30$, $F = 3.04$, $p = 0.001$). Marginal tests indicated significant effects of burn severity ($R^2 = 0.10$, $F = 3.00$, $p = 0.001$) and plant community type ($R^2 = 0.11$, $F = 10.08$, $p = 0.001$) (Figure 8). In contrast, treatment and flooding explained little variation ($R^2 = 0.02$, $F = 1.50$, $p = 0.35$), and elevation above streambed remained a non-significant predictor ($R^2 = 0.02$, $F = 0.77$, $p = 0.65$).

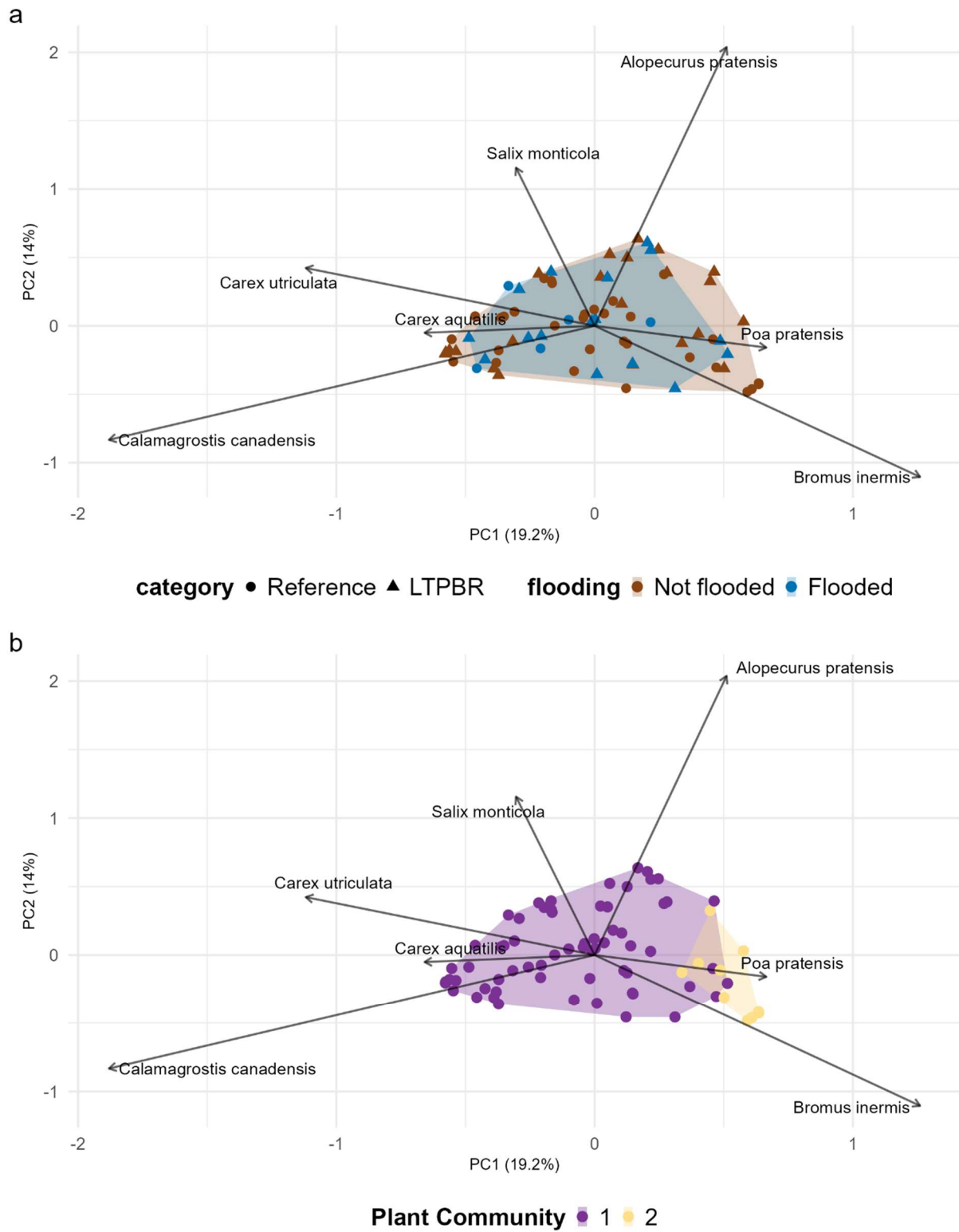


Figure 8. Principal component analyses of vegetation composition across (a) flooding and treatment conditions, and (b) plant communities.

Vegetation on fluvial deposits

Comparisons of plant communities in sediment deposits versus established vegetation plots revealed significant compositional differences ($F = 13.01$, $p = 0.001$), although the plot type explained only a small proportion of variation ($R^2 = 0.09$). Perennial graminoids such as *Calamagrostis canadensis*, *Carex utriculata*, and *Alopecurus pratensis* were strongly associated with sediment deposit communities, whereas species including *Galium boreale*, *Poa pratensis*, *Achillea millefolium*, and *Taraxacum officinale* were associated with established vegetation plots (Figure 9). Indicator species analysis identified only one species (*Gnaphalium exilifolium*) as significantly associated with sediment plots (Appendix A: Table 2), suggesting that while some colonization occurred, very little established consistently on fluvial sediment deposits via seed. Although perennial, rhizomatous grasses were abundant in sediment plots, they were not identified as indicators because they are common across the floodplain. However, they did colonize sediment deposits clonally.

Differences between sediment and quadrat communities were primarily driven by nestedness rather than species turnover. PERMANOVA indicated a significant effect of source (i.e. if the plot was on a sediment deposit or in an established quadrat) after accounting for site-level variation, suggesting that sediment communities represented a subset of quadrat communities ($F = 74.04$, $R^2 = 0.37$, $p = 0.001$).

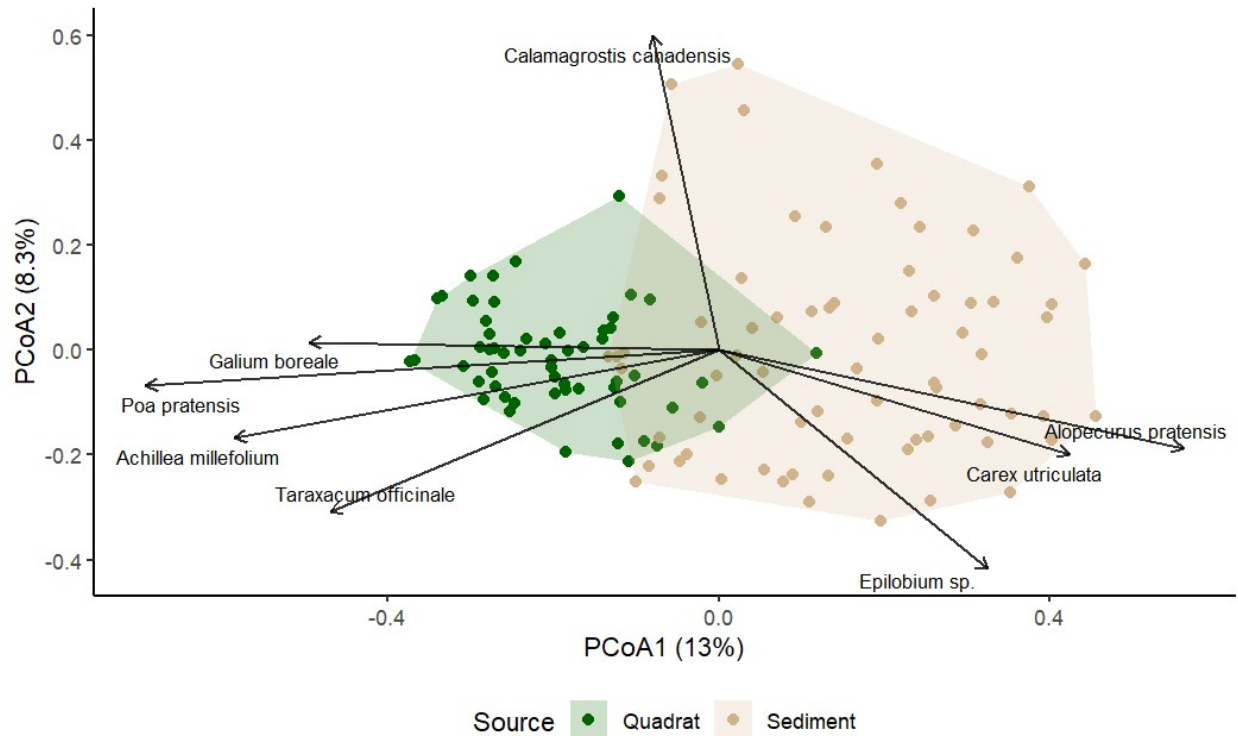


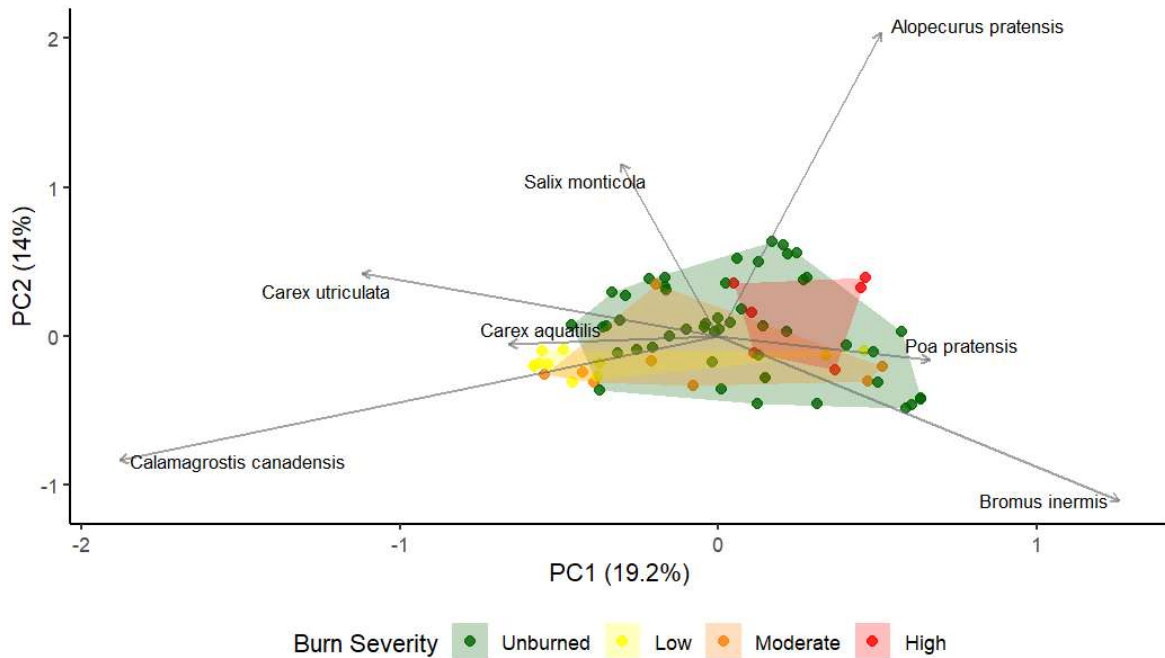
Figure 9. Principal coordinates analysis of sediment plant communities shown in tan, and 1 m² quadrat from established vegetation plots plant communities shown in green.

Fire and floodplains

Combining field observations with MTBS data revealed that 44.8% of the plots classified as Increased Greenness by MTBS were unburned in the field, while 6.9% were low severity, 20.7% were moderate severity, and 27.6% were high severity. These results suggest that MTBS may underestimate burn severity in floodplains

Aboveground biomass declined linearly with increasing burn severity, but model-estimated biomass values were similar across burn severity classes five years post-fire (Figure 5). Estimated marginal means overlapped among unburned (5.66 [95% CI: 5.45–5.87]), low (5.79 [5.44–6.15]), moderate (5.48 [5.13–5.83]), and high-severity plots (5.25 [4.84–5.66]), and pairwise comparisons were not significant after Tukey adjustment (all $p > 0.10$).

Fire severity influenced plant community composition more strongly than aboveground biomass. Plant community composition exhibited modest differentiation across burn severity classes (Figure 10). Unburned plots occupied a broad region of ordination space that encompassed most moderate and high severity plots, whereas a portion of low severity plots were more distinctly separated along the first principal component axis. Consistent with this ordination pattern, marginal PERMANOVA tests from the plant community subsection indicated that burn severity explained a significant but limited proportion of variation in community composition ($R^2 = 0.10$, $p = 0.001$), which is comparable to difference among plant community types ($R^2 = 0.11$, $p = 0.001$). The large overlap in ordination space between differing fire severities suggests that post-fire compositional shifts occurred largely within the range of pre-existing plant community types rather than representing new community states, although there is variation in plots within low and moderate severities compared to high severity plots. High severity plots trended toward plots with species like *Alopecurus pratensis*, *Poa pratensis*, and *Bromus inermis*, and low to moderate severity plots were strongly associated with wetland species like *Salix monticola*, *Carex utriculata*, and *Calamagrostis canadensis* (Figure 10).



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Figure 10. Plant community composition across burn severity. Low (yellow), moderate (orange), and high (red) severity plots are overlapped by unburned (green) plots.

Temporal ordinations of resampled plots from 2024 to 2025 showed directional movement in plant community composition at most sites, but no consistent pattern was evident across burn severity, flooding, or treatment categories. Flooded plots did not occupy a distinct region of ordination space but tended to shift right on the first principal component axis, and reference and LTPBR plots exhibited variable directional shifts (Figure 11). While plant communities were dynamic over the one-year period, compositional changes between years were not strongly structured by fire severity, flooding, or treatment, and no clear functional group shifts were observed.

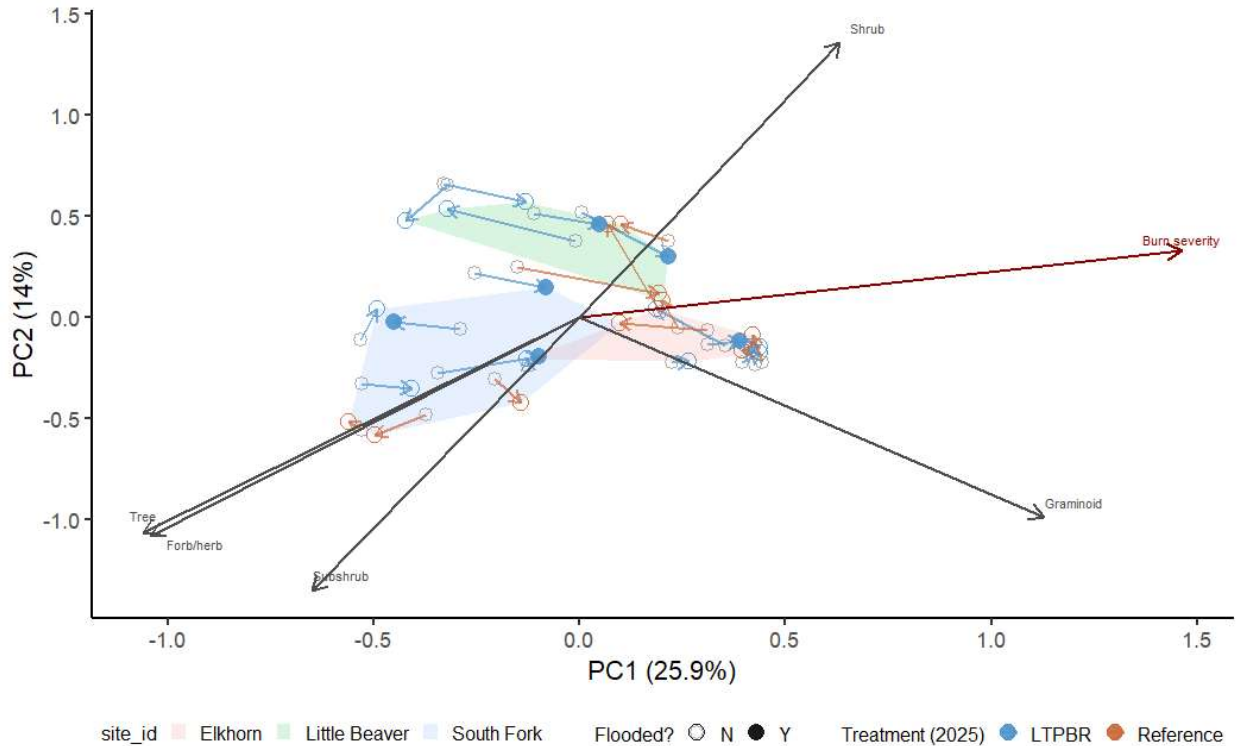


Figure 11. Plot-level PCA trajectories for LTPBR (blue) and reference (brown) reaches from 2024–2025. Filled points indicate flooding occurred; open points indicate no flooding. Small arrows connecting points show directional change between years for each site. Large arrows represent fitted environmental vectors (e.g., burn severity, functional groups).

Species-level responses to fire severity varied across floodplain plant communities

(Figure 12). Some shrub species, including *Alnus incana*, *Betula occidentalis*, and *Lonicera*

involucrata, showed decreased cover with increasing burn severity, whereas *Dasiphora*

fruticosa increased in cover on burned plots. Stress-tolerant species such as *Salix* spp.

maintained relatively consistent cover across burn severities. Among graminoids,

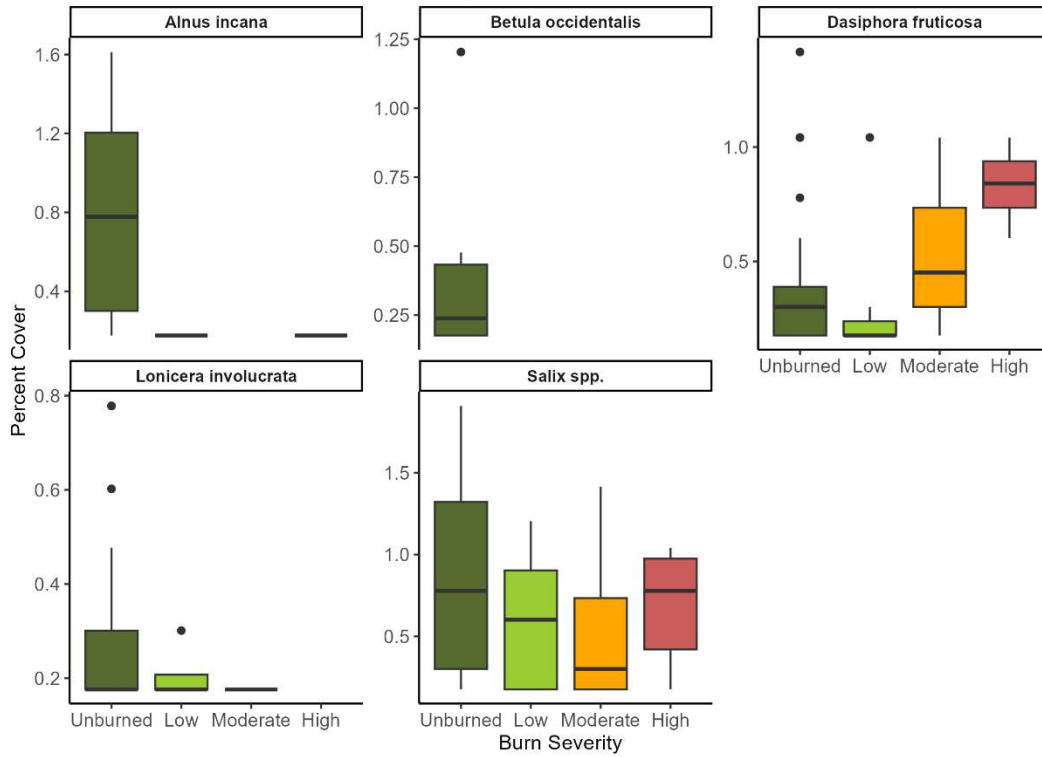
Calamagrostis canadensis, *Alopecurus pratensis*, and *Carex utriculata* showed higher cover

at low to moderate severity burns, whereas *Juncus arcticus* ssp. *balticus* and *Phleum pratense*

were more abundant in high severity plots. *Carex aquatilis*, and *Poa pratensis* exhibited

broad tolerance to fire, with similar cover across all or most burn severities.

Shrub Response Across Burn Severity



Common Graminoids Across Burn Severity

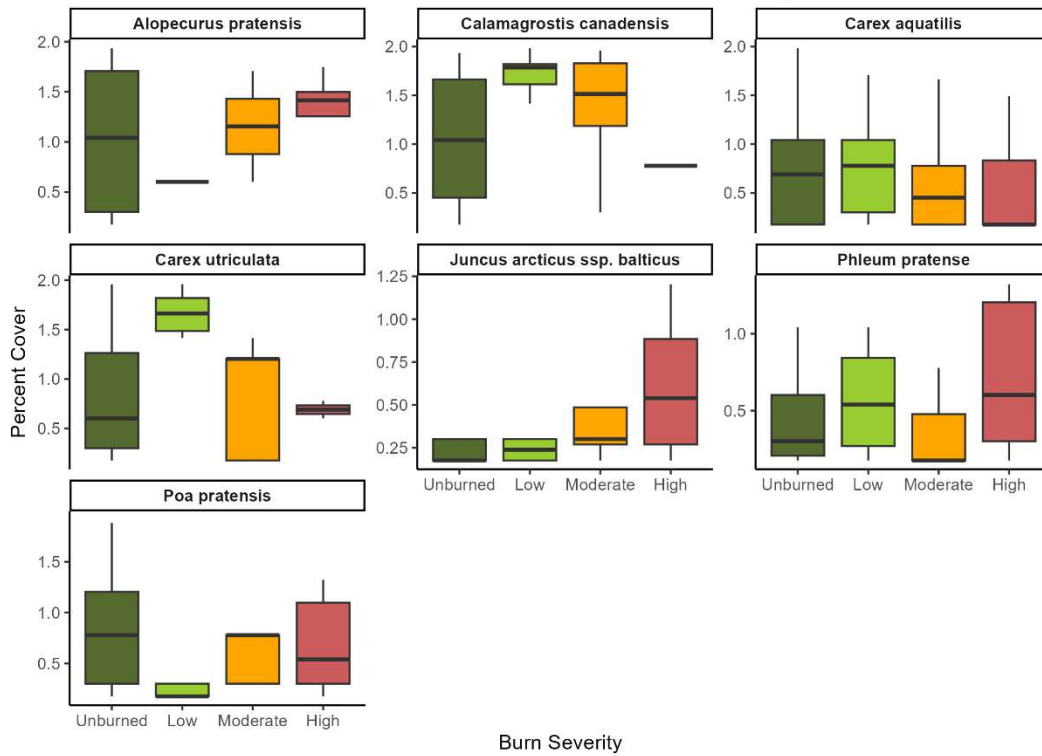


Figure 12. Shrub and common graminoid cover across burn severity.

DISCUSSION

Contrary to our hypotheses, we found that LTPBR methods implemented as PALs and BDAs did not substantially alter plant community composition or increase plant productivity. However, LTPBR increased early-season flooding at sites with less porous structures, and sediment deposition within the floodplain created patch-scale habitat heterogeneity. These findings suggest that vegetation community composition would be a poor short-term metric of restoration success. If increased productivity is a management objective, LTPBR design should promote greater spatial extent of floodplain inundation by directing flow farther from the channel and incorporating additional structures and large woody debris in the floodplain to enhance water retention.

Channel-floodplain connectivity

LTPBR treatments increased channel-floodplain connectivity by facilitating overbank flooding during high flow events, but the spatial extent and duration of inundation were site and time specific. The majority of overbank flooding occurred during peak-flow in May, but surface water was not retained within the floodplain throughout the growing season.

Similarly, LTPBR structures in Wyoming elevated surface and groundwater levels and enhanced lateral exchange during high-flow events (Pearce et al., 2021). Reaches with less porous structures, such as South Fork and Little Beaver, had increased early season flooding within LTPBR reaches than those with more porous structures, like Elkhorn and Jack's Gulch. Consistent with this pattern, a study examining how dam dimensions affected

hydraulic residence time found that BDA height and porosity significantly influence pool volume, with LTPBR structures retaining less water overall than natural beaver dams (Nagle, 2024). The porosity observed in structures at Jack's Gulch and Elkhorn may reflect not only differences in structure design, but also structure age, with porosity increasing over time. LTPBR structures can alter hydrologic processes in incised streams by increasing channel-floodplain connectivity, especially in terms of floodplain inundation, by restoring floodplain functions, particularly during high-flow events, thus restoring floodplain disturbance regimes like flooding and sediment deposition.

Aboveground biomass

In contrast to our hypothesis, we did not observe an increase in aboveground biomass in flooded LTPBR reaches, and despite site differences in hydrologic response to LTPBR, there were no significant differences in aboveground biomass between sites. Variation in biomass was dominated by pre-existing differences among plant community types and fire rather than short-term hydrologic treatment effects during the study period. This lack of response likely reflects the short duration of inundation, particularly because surface water did not persist into the peak growing season when water limitation is more common. Plants in LTPBR-influenced areas may allocate more resources belowground, investing in rhizomes and root systems rather than shoot growth (Martinez, 2025). Alternatively, these floodplains may not have been water limited prior to restoration, in which case increased water availability did not translate into increased plant growth. However, if biomass increased without sustained soil moisture later in the growing season, additional fine fuels could accumulate and potentially increase fire risk (Pettit & Naiman, 2007).

Other studies have found similar results to ours, attributing the lack of response to an absence of water limitation or temporal scale limitations (Askam et al., 2022; Bolyard et al., 2026). A further explanation is that vegetation responses to restored hydrology and flooding disturbance regimes may be nonlinear and threshold dependent (Jentsch, 2007; An et al., 2022), suggesting that the frequency, duration, and spatial extent of hydrologic change observed in this study may not have exceeded the threshold to increase plant productivity. Floodplains with a long history of hydrologic alterations, such as the floodplains within this study, may remain in an alternative stable state and require greater or more sustained hydrologic change before vegetation productivity responds (Scheffer et al., 2001). Prior to restoration, these floodplains did not experience overbank flooding during peak flows and have a long history of grazing, both of which likely impose strong legacy effects on vegetation structure and species composition.

Contrary to our findings, Silverman et al. (2019) found an increase in productivity following LTPBR installation in semiarid rangelands using Normalized Difference Vegetation Index (NDVI) using vegetation greenness as a proxy for productivity. Although a synthesis of LTPBR outcomes reported that most studies documented increases in vegetation following LTPBR installation (Winford, 2024), our study does not. This discrepancy likely reflects site-specific differences in climate, time since restoration, and structural design, which mediate how LTPBR alters water storage, sediment retention, and vegetation greenness (Scamardo et al., 2025).

Plant community composition

We found that despite compound disturbances (i.e. incision-driven hydrological changes, wildfire, restoration activities, and flooding), neither aboveground biomass nor plant community composition differed across LTPBR, and reference reaches or flooding conditions. In the short term, plant communities are remaining unchanged in response to recent hydrological disturbance dynamics. Compositional differences were more strongly associated with fire severity and plant community type rather than with recent hydrological disturbance indicating that longer term disturbance legacies play a larger role. One reason we may not have observed a change in vegetation composition is the limited timeframe of this study, which was 4-5 years post-fire but only 1-4 years post-restoration. Plant compositional change may take much longer to respond to restoration actions.

To see variation in plant composition, there may need to be multiple years of overbank flooding at spatially and temporally variable timescales, along with sustained water retention in the floodplain. Short-term studies commonly report hydrologic responses first, such as increased soil moisture and surface water, and reduced bare ground, but weak shifts in plant community composition up to three years after implementation (Bolyard et al., 2026; Winford, 2024), similar to our findings. In contrast, longer-term evaluations of LTPBR show that while hydrologic changes occur soon after implementation, willow growth and establishment were dependent on planting depth and floodplain elevation (Orr et al., 2020; Orr et al., 2024), highlighting the importance of channel-floodplain connectivity in plant establishment. Similarly, other wetland restoration projects have demonstrated that restoring water table levels does not lead to similarity in plant communities in reference and restored sites (Sueltenfuss & Cooper, 2019), indicating that abiotic filters, such as hydrology, are only one component of vegetation composition.

LTPBR may increase hydrologic connectivity without immediately restructuring plant communities because both disturbance filters, such as sediment deposition, flooding (Driscoll et al., 2025), and fire (Mason et al., 2023; Pettit & Naiman, 2007), as well as biotic filters, such as assembly mechanisms (Breton et al., 2023; Grime, 1998), shape community composition. The floodplains within this study were burned in 2020, and plant communities typically stabilize within five years after severe fire (Fornwalt et al., 2014); by the time of this study, plant communities are likely structured more by competitive or facilitative interactions than by initial colonization. By reintroducing historical disturbance regimes, LTPBR creates new opportunities for habitat heterogeneity. Applying a functional trait approach could therefore provide a more informative measure of vegetation change in areas with LTPBR (Driscoll et al., 2025).

Vegetation composition is a weak short-term indicator of restoration success because community shifts depend on sustained, periodic flooding, as well as water retention. LTPBR can influence this trajectory only if it is able to promote overbank flooding throughout the floodplain and retain water in the floodplain throughout the growing season. Additionally, disturbance and biotic filters can further influence vegetation composition trajectories.

Vegetation on fluvial deposits

Overall, LTPBR and overbank flooding had limited short-term influence on established plant communities, but recent hydrological disturbance and sediment deposition caused by LTPBR facilitated small-scale habitat heterogeneity with clonal graminoids stabilizing sediment on which early colonizers could establish. Intermediate disturbances like flooding

and deposition may therefore promote patch-scale heterogeneity not only through the creation of novel sediment deposits, but also by shifting plant allocation strategies that enhance persistence and recolonization on recently deposited sediment through root systems (Martinez, 2025). These newly deposited materials represent open microsites, but colonization is driven by species already present within the surrounding floodplain, so early colonizers exert strong pressures that influence community trajectories (Pattison et al., 2018). Consistent with this, sediment communities in our study represented subsets of adjacent vegetation rather than novel assemblages, indicating rapid colonization by adjacent species rather than species turnover. Perennial grasses clonally expanded into sediment deposits, suggesting that colonization dynamics are governed more by the spread of adjacent species than through new germination.

Notably, we observed an absence of *Salix* spp. seedlings on fluvial deposits within the floodplain. Willow regeneration largely depends on fluvial disturbances that create exposed, moist, fine substrates suitable for seedling establishment (Díaz-Alba, 2023; Wolf et al., 2007; Karrenberg et al., 2002). This pattern may reflect limitations associated with the temporal scope of this study, such as a mismatch between sediment deposition and seed release or germination windows. Alternatively, the lack of *Salix* spp. recruitment may indicate broader constraints on willow regeneration in these systems, such as grazing pressures (Beschta & Ripple, 2016; Kay & Chadde, 1992), or altered flow regimes under a changing climate preventing successful hydrochory (Perry et al., 2020). This can have implications for longer-term riparian recovery trajectories, which LTPBR can influence through floodplain inundation (Orr et al., 2024; Fischer et al., 2021). This may point to a need for more active revegetation efforts in areas with LTPBR that are lacking pre-existing floodplain vegetation.

Fire and Floodplains

These results point to the overall resilience of floodplain vegetation in the face of disturbance and how restoring floodplain inundation disturbance regimes can further promote resiliency in the context of plant diversity. The weak biomass response across burn severity classes coupled with the overlap in ordination space of unburned plant communities suggests resilience of floodplain vegetation to fire and relatively rapid recovery of aboveground biomass within five years post-fire. Floodplain plant communities were largely structured by the legacy effects of disturbance, disturbance regimes, and species life history traits, rather than by short-term hydrologic variability.

Fire severity influenced community composition more strongly than biomass likely because species, such as perennial grasses or plants of Salicaceae, can rapidly resprout or expand clonally following fire (Ott et al., 2019; Gom & Rood, 2000), allowing biomass to recover even as relative species abundances shift. Low and moderate fire severity acted as an environmental filter that reorganized community composition without resetting community structure, maintaining conditions for wetland and riparian species to persist and compete. In contrast, high severity fire plots were associated with fast-colonizing, often non-native perennial pasture grasses, reflecting greater exposure of bare ground and reduced biotic pressures that clonal species readily take advantage of. The overlap among burn severity classes with unburned vegetation composition indicates that post-fire compositional changes largely occurred within the range of existing floodplain community states rather than representing transitions to novel assemblages, reflecting overall resilience. Given this shift in

composition to fire severity, this could point to compositional shifts in a world with more frequent and severe fire.

This study found no consistent pattern of movement across burn severity, flooding occurrence, LTPBR installation, or functional group changes between 2024 to 2025. Despite disturbances such as fire, restoration activities, flooding, sediment deposition, floodplains maintained ecosystem structure, as shown by the lack of directional shift in ordination space toward specific functional groups. These findings support our definition of resilience, which reflects a system's capacity to experience disturbance, reorganize, and maintain ecosystem function and structure (Holling, 1973). LTPBR facilitated the restoration of floodplain function by reintroducing the flood disturbance regime, yet overall community structure remains largely unchanged one-year post-installation, despite functional group variation among sites.

Plant community states represent long histories of competition and facilitation among plant species (Campbell & Keddy, 2022), grazing pressure (Kauffman et al., 2022; Krall & Roni, 2023), as well as flow and sediment regimes (Asaeda & Rashid, 2012; Capon, 2005; Rivaes et al., 2013). In a future with more frequent, severe fire, and increasing water demand, we may see community shifts toward more non-native pasture grasses if LTPBR does not shift the ecological trajectory to support a community composition of more native wetland species. While current floodplains exhibit resilience, future conditions may push communities toward non-native species establishment. Similar to our results, Jackson & Sullivan (2009) reported that severely burned plots had increased non-native cheatgrass (*Bromus tectorum*) cover, while low to moderate severity plots resembled unburned reaches. Despite uncertainty in long-term vegetation responses to LTPBR, restoring floodplain

hydrology and disturbance regimes can put floodplains on a trajectory to a more dynamic equilibrium.

Limitations & future directions

This study represents the first assessment of LTPBR effects on vegetation within burned watersheds in northern Colorado that integrates aboveground biomass responses, reach-scale plant community composition, and patch-scale vegetation establishment from sediment deposition. As LTPBR continues to gain traction as a restoration tool for enhancing channel-floodplain connectivity, evaluations of its ecological effects, especially on vegetation, remain limited.

This study has several limitations, most notably its limited temporal scope and replication. Vegetation responses to hydrologic change are often slow and may not be detectable over short monitoring periods, and more variability could be captured with a larger sample size. In addition, variation in LTPBR implementation methods and time since structure installation among sites may have influenced observed responses and limited our ability to isolate treatment effects.

Flooding extent was recorded as presence-absence and resurveyed later in the season. Consequently, variability in inundation depth, duration, and temporal dynamics may not have been fully captured: more frequent surveys and depth measurements would have improved characterization of overbank flooding. We also did not measure belowground biomass, and plants may have allocated growth to belowground root systems in response to early-season flooding (Martinez, 2025). In addition, measurements such as soil moisture or groundwater

elevation would have clarified whether these floodplains were water limited. Evaluating plant functional traits associated with tolerance to flooding and drought could further inform water availability because these traits vary with distance from and elevation above the stream (Diehl et al., 2017).

Finally, the placement and scale of the 100 m² vegetation plots may not have adequately represented large-scale variation in plant community composition to sediment deposition. Plots were stratified across the floodplain, but this variable was not a significant predictor in our models. Differences in sediment supply influenced sediment deposition, and because most 1 m² plots on fluvial deposits were located in Little Beaver, patch-scale community responses largely reflect conditions specific to that floodplain.

These limitations highlight the need for long-term monitoring of plant communities at restoration sites to better understand the drivers of compositional change and recovery trajectories in floodplains. Future research should examine how LTPBR alters groundwater flow paths and residence times, and how these hydrologic changes influence vegetation growth, plant functional traits, and resource allocation strategies under wetting and drying cycles within the floodplain. Future climate predictions will be necessary to examine plant community shifts under a changing climate with more allocation of water resources. Attention to willow growth, regeneration, and seedling establishment following disturbance will also be critical for evaluating longer-term riparian recovery and restoration success.

Conclusions

Although short-term vegetation responses to LTPBR were limited, our results suggest that floodplain vegetation is shaped primarily by long-term disturbance regimes rather than short-term hydrologic variability. Vegetation community compositions are a poor short-term metric of LTPBR success: community reorganization occurs on long timescales and is constrained by interacting abiotic, biotic and disturbance filters. The absence of immediate vegetation change does not imply a lack of longer-term effects because community reorganization is slow and often requires repeated disturbance and sustained channel-floodplain connectivity. Periodic overbank flooding and sediment deposition can act as a disturbance filter, selectively favoring floodplain-adapted and disturbance-tolerant species over time.

LTPBR can increase hydrologic connectivity when strategically designed, but it cannot substitute for the conservation of intact floodplains. Protecting river corridors that retain functional hydrologic and ecological processes is critical. Although short-term vegetation responses to LTPBR were modest, the rapid hydrologic responses observed within the first year following implementation at Little Beaver Creek and South Fork represent a meaningful restoration outcome and provide an optimistic foundation for longer-term ecological recovery trajectories.

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APPENDICES

Appendix A: Supplemental Figures

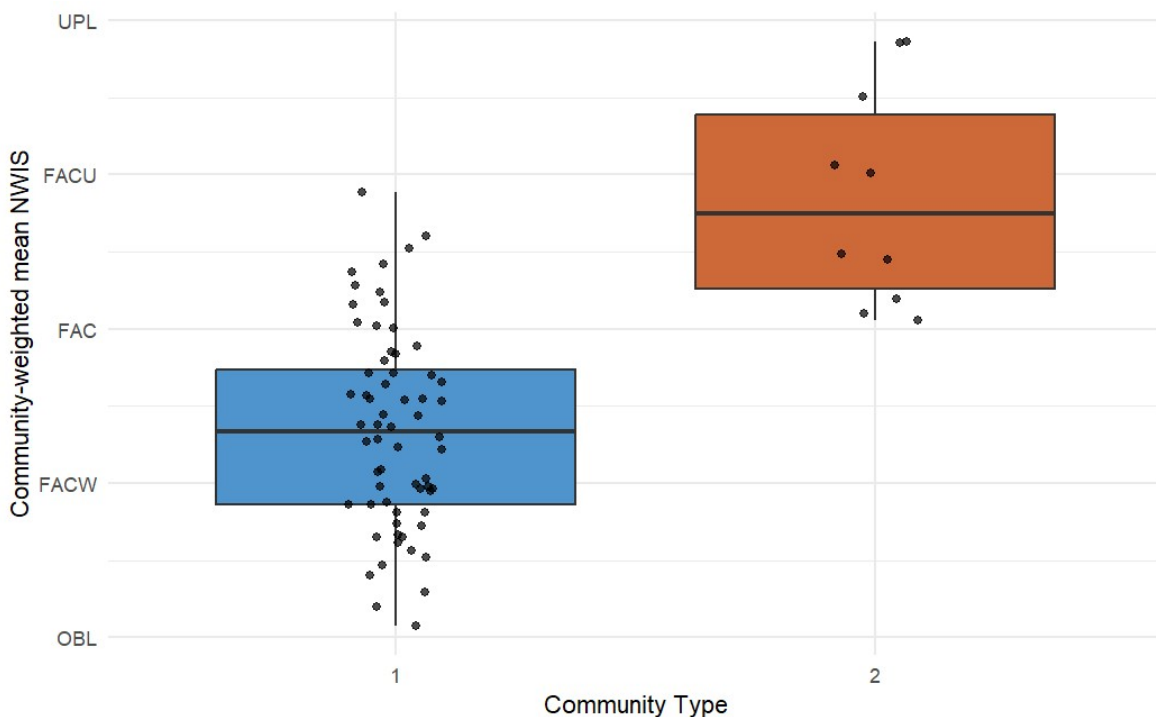


Figure 1. Dominant National Wetland Indicator Type of Community 1 and 2.

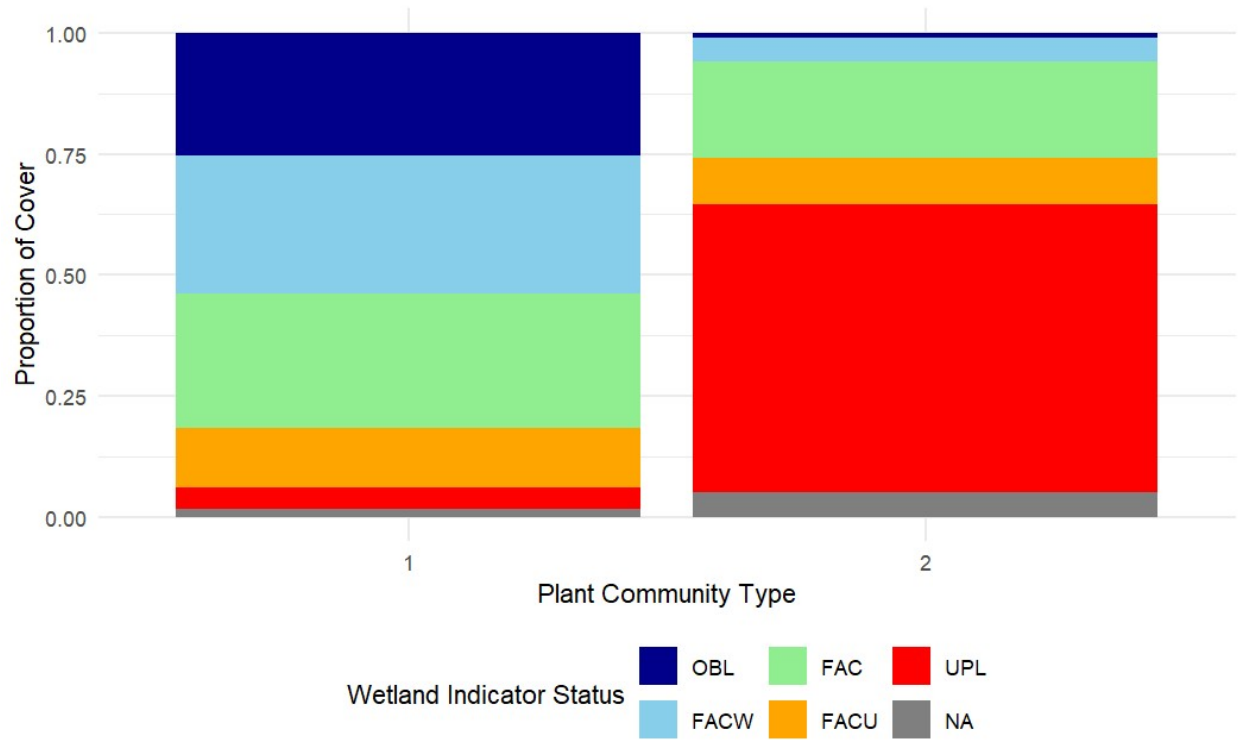


Figure 2. Proportions of cover by each National Wetland Indicator Type across plant communities. NA values represent plants that were not identified to species.

Table 1. Indicator species of each plant community type and their associated p-values and National Wetland Indicator Status (NWIS)

<i>Plant Community</i>	<i>Latin Name</i>	<i>p-value</i>	<i>NWIS</i>
Community 1	<i>Calamagrostis canadensis</i>	0.001	FACW
	<i>Carex aquatilis</i>	0.011	OBL
	<i>Carex utriculata</i>	0.002	OBL
	<i>Chamaenerion angustifolium</i>	0.035	FACU
	<i>Geum macrophyllum</i>	0.001	FAC
	<i>Heracleum maximum</i>	0.018	FAC
	<i>Mertensia ciliata</i>	0.004	FACW
	<i>Montia chamissoi</i>	0.003	OBL
	<i>Poa tracyi</i>	0.013	NA
	<i>Salix geyeriana</i>	0.001	FACW
	<i>Salix monticola</i>	0.001	OBL
	<i>Stellaria longipes</i> ssp. <i>longipes</i>	0.037	FACW
	<i>Androsace septentrionalis</i>	0.002	FACU
	<i>Anemone multifida</i>	0.002	FACU
	<i>Antennaria parvifolia</i>	0.001	UPL
	<i>Artemisia frigida</i>	0.001	UPL
	<i>Bromus inermis</i>	0.004	UPL
	<i>Campanula rotundifolia</i>	0.005	FACU
	<i>Collinsia parviflora</i>	0.047	UPL
	<i>Cymopterus lemmonii</i>	0.002	UPL
<i>Danthonia parryi</i>	0.002	UPL	
<i>Erigeron formosissimus</i>	0.013	UPL	
Community 2	<i>Eriogonum umbellatum</i>	0.001	UPL
	<i>Festuca idahoensis</i>	0.008	FACU
	<i>Heterotheca villosa</i>	0.001	UPL
	<i>Juncus arcticus</i> ssp. <i>balticus</i>	0.002	FACW
	<i>Pascopyrum smithii</i>	0.006	FACU
	<i>Potentilla hippiana</i> var. <i>hippiana</i>	0.005	UPL
	<i>Potentilla hippiana</i> X <i>pulcherrima</i>	0.001	UPL
	<i>Rosa acicularis</i> ssp. <i>sayi</i>	0.047	FACU
	<i>Sisyrinchium montanum</i> var. <i>montanum</i>	0.003	FAC
	<i>Thermopsis rhombifolia</i> var. <i>divaricarpa</i>	0.001	FAC
<i>Valeriana edulis</i>	0.001	FAC	

Table 2. Indicator species of plots in the 1 m² quadrat of vegetation plots or on sediment deposits and their associated p-values and functional groups

Location	Latin name	p-value	Functional Group
	<i>Poa pratensis</i>	0.001	Graminoid
	<i>Taraxacum officinale</i>	0.001	Forb
	<i>Achillea millefolium</i>	0.001	Forb
	<i>Cirsium arvense</i>	0.001	Forb
	<i>Geum macrophyllum</i>	0.001	Forb
	<i>Chamaenerion angustifolium</i>	0.001	Forb
	<i>Mertensia ciliata</i>	0.001	Forb
	<i>Montia chamissoi</i>	0.001	Forb
	<i>Juncus arcticus ssp. balticus</i>	0.001	Graminoid
	<i>Fragaria vesca</i>	0.001	Forb
	<i>Heracleum maximum</i>	0.001	Forb
	<i>Potentilla gracilis</i>	0.001	Forb
	<i>Salix geyeriana</i>	0.016	Shrub
	<i>Rosa acicularis ssp. sayi</i>	0.001	Subshrub
	<i>Stellaria longipes ssp. longipes</i>	0.001	Forb
	<i>Trifolium sp.</i>	0.037	Forb
	<i>Conioselinum scopulorum</i>	0.004	Forb
	<i>Geranium richardsonii</i>	0.005	Forb
Quadrat	<i>Dasiphora fruticosa</i>	0.010	Shrub
	<i>Bistorta bistortoides</i>	0.004	Forb
	<i>Carex praticola</i>	0.004	Graminoid
	<i>Erigeron glabellus</i>	0.007	Forb
	<i>Moehringia lateriflora</i>	0.004	Forb
	<i>Populus tremuloides</i>	0.006	Tree
	<i>Salix planifolia</i>	0.007	Shrub
	<i>Thermopsis rhombifolia var. divaricarpa</i>	0.005	Forb
	<i>Solidago gigantea</i>	0.043	Forb
	<i>Astragalus sp.</i>	0.018	Forb
	<i>Cymopterus lemmonii</i>	0.013	Forb
	<i>Senecio eremophilus var. kingii</i>	0.015	Forb
	<i>Carex microptera</i>	0.031	Graminoid
	<i>Collomia linearis</i>	0.039	Forb
	<i>Epilobium ciliatum</i>	0.029	Forb
	<i>Galium trifidum ssp. subbiflorum</i>	0.048	Forb
	<i>Salix bebbiana</i>	0.035	Shrub
	<i>Stellaria longifolia</i>	0.027	Forb
	<i>Trifolium hybridum</i>	0.035	Forb
Sediment	<i>Gnaphalium exilifolium</i>	0.001	Forb

