

RESEARCH ARTICLE

Stream restoration effectively alters functional diversity and composition of riparian plant communities in the southern Rocky Mountains, U.S.A.

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Channel incision degrades ecosystems by lowering water tables and disconnecting floodplains. Stream restoration often aims to reverse these impacts. However, projects typically receive minimal monitoring, and treatment effectiveness has not been validated. We used trait-based analysis to evaluate whether two stream restoration techniques—beaver dam analogs (BDAs) and plug-and-ponds—raised water tables and increased overbank flooding, whether these altered environmental filters facilitated recovery of riparian plant communities, and how reassembly impacted the representation of traits that influence ecosystem function. We report on a before-after-control-impact study and Bayesian analysis that estimated the probability that treatments affected riparian plant functional diversity and composition. We found a high probability (0.99 and 0.97, respectively) that BDAs decreased functional dispersion by $\geq 50\%$ and plug-and-ponds decreased dispersion by $\geq 30\%$. Both treatments increased the relative abundance of high moisture use plants, wetland plants, and plants with high anaerobic tolerance. For example, BDAs increased the relative abundance of obligate wetland plants by 100%, and plug-and-ponds increased the relative abundance of facultative wetland plants by 105%, on average. These results suggest treatments modified environmental filters and recovered riparian plant communities. Ecosystem function was likely altered as the streamside plant community reassembled. Small increases in functional divergence suggest both treatments increased resource use efficiency, and we found a high probability of small treatment effect sizes ($<20\%$) related to changes in community-level C:N and nitrogen fixation. Our results demonstrate trait-based analysis can detect a rapid response to restoration and offer a cost-effective monitoring approach to compare treatments across space and time.

Key words: Bayesian analysis, beaver dam analog, before-after-control-impact, meadow rewetting, plug-and-pond, pond-and-plug, process-based restoration, streams and rivers

Implications for Practice

- Trait-based approaches, including analysis of functional diversity and community-weighted trait values, are a useful tool for understanding whether stream restoration successfully modifies environmental filters in the floodplain and reassembles desired riparian communities across watersheds with differing hydrologic regimes, climate, geology, elevation, and plant community types.
- Before-after-control-impact experimental design and Bayesian analysis are powerful and intuitive approaches for the detection of restoration impacts and provide managers a probability of restoration effect size to be considered when balancing trade-offs between different management actions.
- Decreases in functional dispersion and richness signify stronger environmental filters and responses to treatment, suggesting that reduced functional diversity is an appropriate target for restoration depending on the system.

Introduction

Channel incision impacts the structure and function of aquatic and riparian ecosystems worldwide (Shields et al. 1994; Duncan

et al. 2011; Johaneman et al. 2023). Streambed erosion occurs when natural phenomena or human activities alter the balance between sediment supply and transport capacity (Galay 1983; Simon & Rinaldi 2006). As entrenchment progresses, alluvial water tables lower and lateral connectivity with the floodplain is lost (Shields et al. 1994; Schilling et al. 2004, 2006; Duncan et al. 2011). This process alters water availability and flooding that control the establishment, growth, and survival of riparian plant

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communities (Auble et al. 1994; Stromberg et al. 1996). Consequently, hydrologic changes caused by channel incision contribute to the loss of riparian vegetation, which further destabilizes streambanks, reduces shading, and increases water temperatures (Stromberg et al. 1996; Loheide & Gorelick 2007; Johaneman et al. 2023).

Degradation of floodplain habitats and loss of ecosystem services due to widespread channel incision has alarmed land managers and scientists (National Research Council [U.S.] 1995, 1996; Kauffman et al. 1997). In response, billions of dollars have been spent on stream restoration (Bernhardt et al. 2005; Wohl et al. 2015) including projects that aim to reverse the effects of channel incision and recover riparian plant communities (González et al. 2015). Despite massive investment, many stream restoration projects fail (Bernhardt et al. 2005; Wohl et al. 2015), with varying success in reestablishing riparian plant communities (González et al. 2015). Most restoration projects lack properly designed or funded monitoring plans, and recovery of riparian vegetation may be overestimated as published studies favor “positive” results (González et al. 2015).

A critical question is how best to assess the performance of stream restoration treatments? Trait-based analyses of streamside vegetation offer a valuable, but underused, method (Laughlin 2014; Carlucci et al. 2020). Functional traits are measurable characteristics of individuals that determine the response of an organism to the environment (i.e. response traits) or describe the effect on ecosystem function (i.e. effect traits) (Suding et al. 2008). Community assembly occurs as ecological filters—factors such as disturbance, resource availability, or competition—eliminate species with traits that are unsuitable for that environment (Keddy 1992; Laughlin 2014). For example, frequent inundation limits the establishment of plants lacking response traits such as high specific leaf area that allows a plant to withstand submergence or flexible stems that limit loss of aboveground biomass during flooding (Diehl et al. 2017). The resulting community affects ecosystem function depending on the representation of effect traits such as nitrogen fixing capacity or growth rate (Suding et al. 2008). Dominant filters can be identified, and their strength assessed using community-weighted values for functional traits and functional diversity indices that measure the distribution of a community’s species and their abundances in trait space (Hedberg et al. 2013, 2014; Lozanovska et al. 2018).

Stream restoration is well suited to trait-based analysis. Aquatic-terrestrial ecotones have steep environmental gradients with variable resource distribution (Diehl et al. 2017). Clear patterns in plant traits that provide adaptation to flooding and drought exist as a function of distance from and elevation above the channel (Diehl et al. 2017). Trait-based approaches have been used to understand how environmental filters control the distribution of riparian vegetation (McCoy-Sulentic et al. 2017; Palmquist et al. 2017), to determine environmental flows required to sustain riparian vegetation (Merritt et al. 2010; Stromberg & Merritt 2016), and to understand how altered flow regimes shift the dominance of hydriplant versus xerophyte species (Lytle et al. 2017; Scott & Merritt 2020). Water availability and fluvial disturbance (overbank flooding, erosion, and deposition) are the dominant filters through

which streamside plant communities assemble (Hough-Snee et al. 2015; Diehl et al. 2017). Successful stream restoration of incised channels modifies these filters by raising water tables and increasing the frequency, duration, or magnitude of overbank flooding. Treatment effectiveness can therefore be evaluated by examining changes in functional diversity and community-level traits of streamside vegetation (Laughlin 2014).

In this study, we applied a trait-based analysis to evaluate the effectiveness of two techniques used to restore incised channels: plug-and-ponds and beaver dam analogs (BDAs). Plug-and-ponds (i.e. meadow rewatering or pond-and-plugs) have been used to address channel incision in California’s meadows since the 1990s (Loheide & Gorelick 2007; Rodriguez et al. 2017). This technique involves building a series of ponds by excavating local alluvial material from the degraded stream, using that material to construct plugs within the channel, and redirecting stream flow onto the adjacent floodplain (Loheide & Gorelick 2007; Hammersmark et al. 2009). Plug-and-ponds are applied to reestablish hydrologic connectivity, slow run-off and trap sediment, raise water tables, and recover wet meadow habitats and riparian plant communities (Pope et al. 2015; Rodriguez et al. 2017). Although most plug-and-pond projects receive minimal monitoring (Pope et al. 2015; Rodriguez et al. 2017), past work demonstrates that these treatments can raise groundwater levels, increase floodplain inundation, recover wet meadow habitat, and increase vegetative productivity, biomass, and recruitment (Loheide & Gorelick 2007; Hammersmark et al. 2009; Pope et al. 2015; Rodriguez et al. 2017). However, local factors such as climate, hydrology, and topography influence meadow response to restoration (Rodriguez et al. 2017) and some plug-and-pond-treated meadows show no improvement compared to untreated meadows (Pope et al. 2015). Negative results raise questions regarding plug-and-pond efficacy, prompting Natali and Kondolf (2018) to caution against the widespread application of this technique without additional research.

BDAs are a relatively new stream restoration approach (Pilliod et al. 2018; Lautz et al. 2019) that attempts to reestablish natural physical, chemical, and biological processes by mimicking the effects of beaver dams (Pollock et al. 2014). Project designs vary (Pilliod et al. 2018), but this technique generally involves constructing permeable low-head dams made of branches, rocks, and sediment woven between wooden posts driven into the stream bed (Lautz et al. 2019; Pearce et al. 2021). Thousands of BDAs are being installed in streams (Pilliod et al. 2018), but few projects include rigorous monitoring and evaluation (Pilliod et al. 2018; Lautz et al. 2019; Nash et al. 2021). BDA projects often aim to reduce vertical erosion, raise water tables, and improve riparian habitat (Nash et al. 2021). BDAs can trap sediment, aggrade channels, and raise water tables (Bouwens et al. 2016; Orr et al. 2020; Scamardo & Wohl 2020; Munir & Westbrook 2021). Yet, these effects have not been consistently observed, and responses vary depending on site conditions and treatment configuration (Scamardo & Wohl 2020; Munir & Westbrook 2021). Riparian vegetation productivity and survival, and growth of willows (*Salix* spp.) can increase following BDA treatment (Silverman et al. 2019; Orr et al. 2020), but these effects may be temporary (Orr et al. 2024). Effects of BDAs on spatial

extent or composition of streamside vegetative communities remain unknown (Lautz et al. 2019).

The goals of our study were to determine whether stream restoration, as implemented by plug-and-pond or BDA treatments, altered functional diversity and community-level traits of streamside vegetation, evaluate whether these shifts indicated that treatments modified water availability and fluvial disturbance, and determine whether restoration recovered a riparian plant community. We used a before-after-control-impact (BACI) experimental design and Bayesian statistical analysis to determine treatment effect size and quantify the probability that BDAs and plug-and-ponds altered functional richness (FRic), evenness (FEve), dispersion (FDis), or divergence (FDiv), as well as community-weighted mean (CWM) values for functional traits related to water availability and fluvial disturbance. If stream restoration treatments modified environmental filters by raising water tables and increasing overbank flooding, we expected to observe high probabilities that traits associated with greater water availability and frequent fluvial disturbance would be dominant within the streamside plant community following treatment. Additionally, if BDAs and plug-and-ponds recovered high water tables and overbank flooding, treatments would be expected to intensify the filter of anoxia. Because stronger filtering acts on specific adaptive traits, only species that possess those traits persist, and functional diversity is reduced as a result. We therefore expected a high likelihood of lower functional diversity following treatment.

Methods

Study Site

We completed this study at two stream restoration sites on National Forest lands in northern New Mexico, United States: San Antonio Creek and Vidal Creek (Fig. 1). Livestock overgrazing and timber harvest contributed to channel incision, lowered water tables, and encroachment of upland vegetation at San Antonio Creek (Fig. 2A; USDA Forest Service 2011). BDAs were constructed in San Antonio Creek in August 2020 (Fig. 2B). Vidal Creek experienced channel incision, lowered water tables, and loss of riparian vegetation because of livestock overgrazing and mining (Fig. 2C; The Quivira Coalition 2005). The Coronavirus Disease of 2019 (COVID-19) pandemic delayed installation of plug-and-ponds in Vidal Creek (Fig. 2D) until August 2021 (Table 1), resulting in fewer post-treatment sampling events.

Experimental Design

We applied a BACI design to quantify treatment effects. BACI evaluates perturbation effects when random assignment of treatments is not possible (Eberhardt 1976; Osenberg et al. 2006). BACI is commonly applied to assess restoration because actions cannot be replicated or implemented randomly due to land ownership, limited potential restoration sites, and cost (Osenberg et al. 2006; Conner et al. 2016). BACI sampling requires the establishment of paired impact

and control sites. Impact sites receive restoration treatment during the study period. Control sites are in comparable condition to the pre-treatment impact site and are not restored during the study. Repeated and simultaneous sampling of control and impact sites prior to and following restoration allows BACI designs to distinguish the impact of treatments from differences between the sites or temporal effects shared by all sites (Osenberg et al. 2006).

We established two 100-m control and impact reaches at each restoration site in 2019 (Fig. 1). We acquired geospatial data describing planned restoration from the Santa Fe and Carson National Forests. The downstream end of impact reaches was randomly selected from streams with restoration planned for August 2020. Two impact reaches were established in a one-mile (1.6-km) section of San Antonio Creek with planned BDA treatments, and two impact reaches were established within a one-mile section of Vidal Creek with planned plug-and-pond restoration. Following field visits to impact sites, we identified locations for controls from nearby degraded streams with similar characteristics (i.e. comparable streamside vegetation communities and hydrological and geomorphological conditions, including amounts of channel incision) to the impact sites. We established two BDA control sites along a one-mile section of Rio Cebolla in the subwatershed neighboring San Antonio Creek. Control reaches for plug-and-ponds were established in Vidal Creek upstream of all planned restoration, as well as in Comanche Creek within the same subwatershed as impact sites (Fig. 1).

Each reach included three transects that extended perpendicularly on both sides of the channel at 0 (downstream), 50, and 100 m (upstream). Permanent 1-m² plots were placed at 1, 5, and 10 m from the channel on each transect, for a total of 18 plots distributed across six transects. During each sampling effort, we estimated the percent cover for any vegetation species with at least 5% cover within each plot. Data were collected once per month from May to September at BDA sites and July to October at plug-and-pond sites. Some sampling efforts were disrupted by National Forest closures (plug-and-ponds September 2021, BDAs May 2022), snow (BDAs May 2021, plug-and-ponds October 2021 and 2022), or COVID-19 exposures within the field crew (BDAs September 2021, plug-and-ponds July 2022), resulting in gaps in the dataset. We grouped estimates of percent cover within each plot into six cover classes: 0–5, 5–24, 25–49, 50–74, 75–94, 95–100% and used the calculations in Coulloudon et al. (1999) to compute species abundance for each transect. Species' abundance was entered into a matrix for analysis in R (R Core Team 2021), with each row characterizing a vegetation community based on site, sampling date, and transect.

Functional Trait Analysis

We retrieved functional trait data for plant species from the USDA Plant List of Accepted Nomenclature Taxonomy and Symbols (PLANTS) database (USDA, NRCS 2024), with a focus on response traits that reflect adaptation to water availability and fluvial disturbance (e.g. moisture use, height-at-maturity,

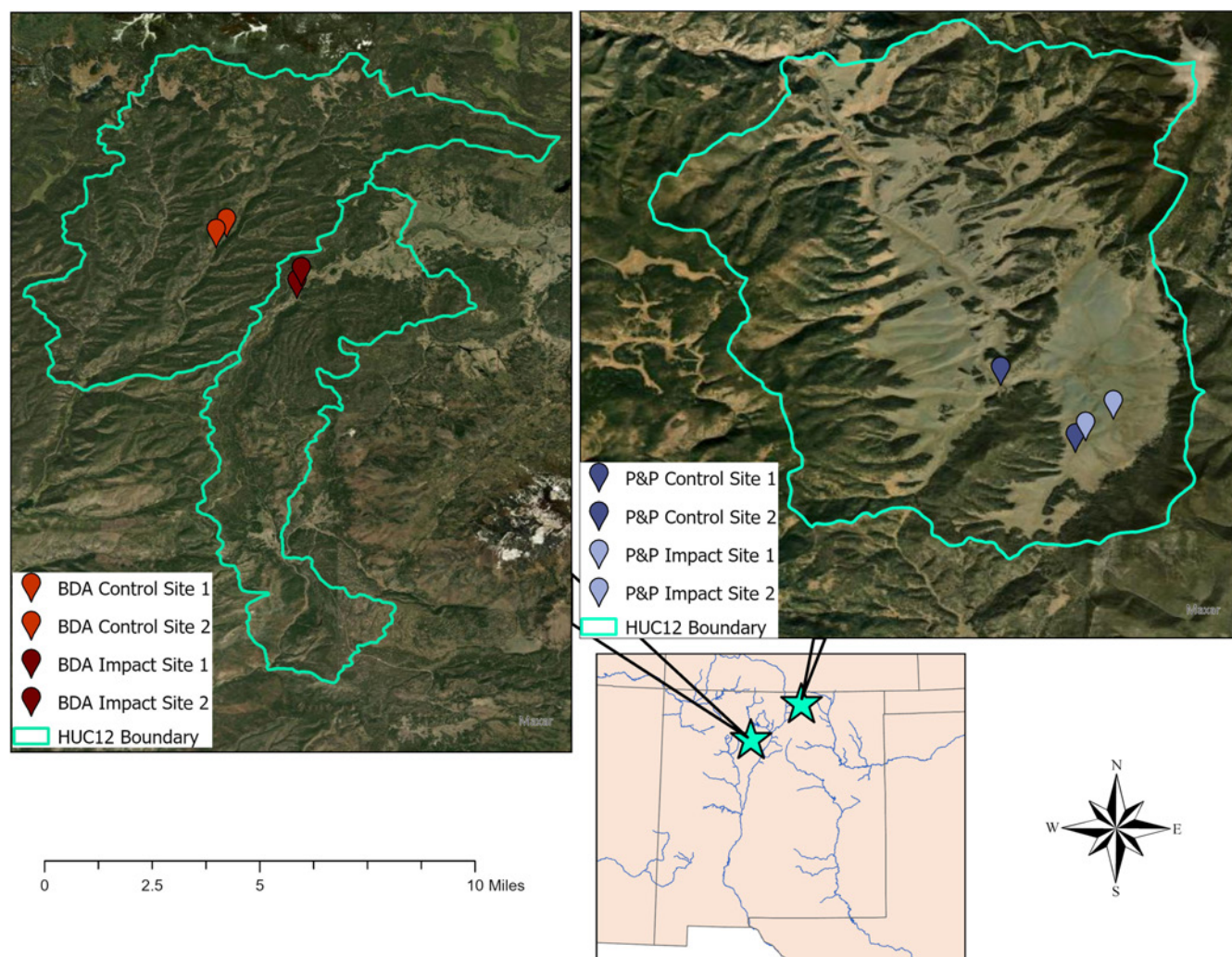


Figure 1. Study site locations, including control and impact reaches, at stream restoration sites in northern New Mexico. BDA control sites (lat 35°58'23.2"N, long 106°39'30.3"W; lat 35°58'10.7"N, long 106°39'42.8"W) are in the Headwaters Rio Cebolla subwatershed. BDA impact sites (lat 35°57'09.4"N, long 106°38'05.2"W; lat 35°57'24.3", long 106°37'60.0"W) are in the Outlet San Antonio Creek subwatershed. Plug-and-pond impact (lat 36°44'35.8"N, long 105°14'58.8"W; lat 36°44'53.7"N, long 105°14'35.7"W) and control sites (lat 36°45'21.6"N, long 105°16'09.5"W; lat 36°44'26.1"N, long 105°15'07.3"W) are in the Little Costilla watershed.

rooting depth, adaptation to various soil textures, wetland indicator status, and anaerobic tolerance), as well as effect traits that influence ecosystem function (e.g. growth rate, C:N, and nitrogen fixation rate) and tolerance to drought, fire, or anaerobic conditions (Table 2). For species lacking trait information, we used traits from closely related plants in the southwestern United States (Palmquist et al. 2017). We were unable to acquire trait data for 21 unidentified species and 10 identified species. These plants generally accounted for less than 5% of relative abundance, except for two unknown grass species that occurred at BDA control and impact sites. The relative abundance of unknown grass 1 ranged from 6 to 15% across sampling dates in 2020, and the relative abundance of unknown grass 2 was 19% in June 2020. Trait data for identified species across all sites were arranged into a species-by-trait matrix for analysis in R.

To calculate functional diversity, we selected five non-correlated traits that influence riparian functional groupings

(Hough-Snee et al. 2015): growth rate, height-at-maturity, moisture use, rooting depth, and adaptation to one, two, or three soil textures (coarse, medium, and/or fine). We used the dbFD function of the FD package (Laliberté et al. 2023) to calculate FRic, FEve, FDis, and FDiv for the plant community at each transect on each sampling date. We used the functcomp function in the FD package to compute CWMs for each transect on each sampling date for the following traits: growth rate, height-at-maturity, moisture use, rooting depth, adaptation to one, two, or three soil textures, anaerobic tolerance, drought tolerance, fire tolerance, C:N, nitrogen fixation rate, and wetland indicator status (Table 2). The functcomp algorithm quantifies CWMs as the mean trait value of all species in the community, weighted by relative abundance (Laliberté et al. 2023). For ordinal and nominal traits, the abundance of each individual class was returned.

The dbFD function uses a distance-based framework to calculate multidimensional functional diversity indices (Laliberté &



Figure 2. (A) Pre-treatment conditions at BDA restoration sites; (B) post-treatment conditions 2 years after BDAs were installed in San Antonio Creek; (C) pre-treatment conditions at plug-and-pond restoration sites; and (D) post-treatment conditions 1 year after plug-and-ponds were installed in Vidal Creek.

Table 1. A description of study sites analyzed using a BACI framework, including control reaches, applied treatments, and before and after periods.

<i>Impact reach</i>	<i>Control reach</i>	<i>Treatment</i>	<i>Restoration date</i>	<i>Before period</i>	<i>After period</i>
San Antonio	Rio Cebolla	BDAs	August 2020	May–August 2020	September 2020 June–Aug 2021 June–Aug 2022
Vidal Creek	Vidal Creek, Comanche Creek	Plug and Pond	August 2021	July–October 2020 July 2021	August–October 2021 July–September 2022

Legendre 2010). Two indices provide information on the degree of environmental filtering: FRic and FDis. FRic is the amount of trait space occupied by a community and is calculated using convex hull volume (Mason et al. 2005). FDis measures trait dissimilarity within a community by quantifying the distribution of traits around the centroid of all trait values. It is calculated as the mean distance of each species to the community centroid, weighted by relative abundance (Laliberte & Legendre 2010). Low FRic and FDis show that strong environmental filtering is limiting trait heterogeneity and species are functionally similar and clustered in trait space (Hedberg et al. 2014). To compare across communities, we standardized FRic by the hull volume occupied by all species in this study (Mason et al. 2005).

FEve and FDiv provide information on competition and resource use (Mason et al. 2005). FEve uses a minimum

spanning tree to measure the uniformity of community biomass distribution in trait space (Villéger et al. 2008). High FEve suggests an even distribution of species and efficient use of available niches. FDiv measures the extent to which functional characteristics' dissimilarity is maximized by the distribution of abundance in trait space by calculating the deviation of species' traits from the community's centroid (Villéger et al. 2008). High FDiv indicates that abundant species are functionally distinct, occupying specialized niches and maximizing resource use.

Statistical Analysis

We used Bayesian analysis to estimate treatment effect size and the probability of achieving various effect sizes using BDA

Table 2. Descriptions of traits used for functional diversity and composition analysis in this article and plant-environment associations in the valley bottom setting.

<i>Trait</i>	<i>Variable type</i>	<i>Levels</i>	<i>Description (USDA NRCS 2024)</i>	<i>Plant-environment associations in the riparian environment (from Hough-Snee et al. 2015)</i>
Growth rate	Categorical	Slow, moderate, rapid	Growth rate after successful establishment relative to other species with the same growth habit	Biomass production from photosynthetic carbon gains minus respiration costs
Moisture use	Categorical	Low, medium, high	Ability to use (i.e. remove) available soil moisture relative to other species in the same (or similar) soil moisture availability region	Required moisture to support transpiration and maintain whole plant water balance
Soils	Categorical	One, two, three	Adaptation to one, two, or three soil types (coarse, fine, or medium textured soils); can plant establish and grow in soil with coarse, medium, and/or fine textured surface layer	Seed dispersal, germination, and plant water relations in alluvial substrate
Height-at-maturity	Continuous		Expected height (in feet) of plant at maturity; an estimate of the median mature height of all plants of a species	Ability to acquire atmospheric light and CO ₂ ; response to flooding and fluvial shear stress
Rooting depth	Continuous		The minimum depth of soil (in inches) required for good growth	Potential for an individual to acquire soil resources: moisture, nutrients, etc.
Anaerobic tolerance	Categorical	None, low, high	What is relative tolerance to anaerobic soil conditions	Depth, duration, and timing of soil saturation from overbank flooding
Drought tolerance	Categorical	None, low, high	What is relative tolerance of the plant to drought conditions compared to other species with the same growth habit from the same geographic region. Drought tolerance is defined based on whether species are more frequently found in areas with heavy soils and higher soil moisture versus areas with coarse soils and lower soil moisture	Response to seasonal soil drying and moisture deficit
Fire tolerance	Categorical	None, low, high	What is the relative ability to resprout regrow, or reestablish from residual seed after a fire	Ability for stems to resprout and/or seeds to disperse or germinate following fire
C:N	Categorical	Low, medium, high	The percentage of organic carbon divided by the percentage of total nitrogen in organic material; low: less than 23; medium: 23–59; high: greater than 59	Leaf-level photosynthesis, tissue construction and maintenance from soil nutrition and atmospheric light, H ₂ O, CO ₂
Nitrogen fixation	Categorical	None, medium, high	How much nitrogen is fixed by this plant in monoculture; none: 0 lb N acre ⁻¹ yr ⁻¹ ; 0 < low < 85; medium: 85–160; high: greater than 160	Symbiotic relationships with atmospheric nitrogen-fixing bacteria in plant roots allows nitrogen acquisition in nutrient-poor alluvial substrates
Wetland indicator status	Categorical	Obligate wetland (OBL), facultative wetland (FACW), facultative upland (FACU), obligate upland (UPL)	Classifications from the National Wetland Plant List for the Western Mountains, Valleys, and Coast Geographic Area	Designate a plant species' preference for occurrence in a wetland or upland

and plug-and-pond restoration (Conner et al. 2016). This approach combines Bayesian modeling and Markov chain Monte Carlo (MCMC) sampling to generate estimates of the response parameter before and after restoration was applied in impact and control reaches. That output is used to estimate the probability of increases or decreases in the response variable driven by restoration. Bayesian inference applied to BACI data provides a probabilistic estimate and reduces type I and type II error rates (Conner et al. 2016).

We quantified the effect of BDAs and plug-and-ponds using BACI ratios calculated from Bayesian posterior distributions of estimates in impact and control reaches before and after treatments were applied (Conner et al. 2016). These estimates were generated from a model including an interaction between binary predictors for period (before or after) and treatment (impact or control). We built and analyzed models using a Gibbs sampler algorithm (JAGS—Plummer 2017) implemented in the R program rjags (Plummer et al. 2023) and used weakly informative prior distributions for all parameters. We ran the model for each site and period using 15,000 MCMC samples after discarding the first 1500 samples as burn-in for each of 10 chains. To reduce autocorrelation between samples, we thinned by saving every third sample; thus, retaining 50,000 samples. We assessed convergence using visual inspection of traceplots and the Gelman-Rubin statistic (Gelman et al. 2004; Conner et al. 2016).

We calculated BACI ratios for FRic, FDiv, FEve, FDis, and CWMs by dividing the posterior distribution for impact sites by the posterior distribution for control sites to generate $R_{i|c}$ —the ratio of the impact to control—for the before ($R_{i|c \text{ before}}$) and after ($R_{i|c \text{ after}}$) periods (Conner et al. 2016). To determine the average treatment effect size, we calculated a BACI ratio ($R_{\text{BACI}} = \bar{R}_{i|c \text{ after}} / \bar{R}_{i|c \text{ before}}$). A BACI ratio less than 1 indicates a negative treatment effect (i.e. the response variable decreased, on average, at the impact site relative to the control following treatment) and a BACI ratio greater than 1 indicates a positive treatment effect (i.e. the response variable increased, on average, at the impact site relative to the control following treatment) (Conner et al. 2016). To estimate the probabilities of achieving treatment effects of various sizes, we divided the $R_{i|c \text{ after}}$ posterior distribution by the posterior distribution for $R_{i|c \text{ before}}$ to generate a posterior distribution of BACI ratios (R_{BACI} —Conner et al. 2016).

Results

Functional Diversity

BDAs and plug-and-ponds altered the functional diversity of streamside plant communities. FDis declined at impact sites relative to controls by, on average, 95% post-BDA treatment and 59% following the installation of plug-and-ponds (Table 3). We observed small increases in FDiv following both treatments (Table 3). FRic decreased by 38% and 2%, on average, at impact sites relative to controls following the installation of plug-and-ponds and BDAs, respectively (Table 3). Changes in FEve were negligible following either treatment (Table 3).

Table 3. Mean BACI ratio describing the average treatment effect size at the impact site relative to the control after restoration was implemented using BDA ($R_{\text{BACI BDA}}$) or plug-and-pond ($R_{\text{BACI plug-and-pond}}$) treatment.

		$R_{\text{BACI BDA}}$	$R_{\text{BACI plug-and-pond}}$
Functional diversity	Dispersion	0.05	0.41
	Divergence	1.04	1.05
	Richness	0.98	0.62
	Evenness	0.99	1.01
Growth rate	Rapid	0.62	0.96
	Moderate	1.37	0.97
	Slow	1.12	1.05
Moisture use	High	1.36	2.20
	Medium	0.80	0.63
	Low	1.26	0.67
Soils	One	0.86	0.54
	Two	1.00	1.21
	Three	0.52	0.85
Plant height		1.11	1.04
Rooting depth		0.88	1.00
Wetland indicator status	Obligate wetland	2.00	1.33
	Facultative wetland	1.03	2.05
	Facultative upland	1.36	0.46
	Obligate upland	1.56	1.29
C:N ratio	High	1.42	1.16
	Medium	1.29	1.08
	Low	0.90	1.03
N fixation	High	0.83	1.16
	Medium	1.12	1.54
	None	1.05	0.99
Anaerobic tolerance	High	1.64	1.58
	Low	0.76	0.60
	None	1.30	0.74
Drought tolerance	High	1.23	1.09
	Low	0.69	1.23
	None	1.37	1.02
Fire tolerance	High	1.18	1.00
	Low	1.10	1.14
	None	1.05	1.15

BACI ratio posterior distributions showed a high probability of large effect sizes related to the impacts of BDAs and plug-and-ponds on the functional diversity of the streamside plant community. The probabilities were high (0.99 and 0.97, respectively) that FDis decreased by $\geq 50\%$ following the installation of BDAs and by $\geq 30\%$ after plug-and-ponds were applied (Table S1). Both treatments likely increased FDiv by less than 20% (Table S1). FRic likely declined by $\geq 20\%$ at plug-and-pond-treated sites (Table S1).

Community-Weighted Means

Following the installation of BDAs, the relative abundance of obligate wetland, facultative wetland, facultative upland, and obligate upland plants increased by, on average, 100, 3, 36, and 56%, respectively, at impact sites compared to controls (Table 3). At plug-and-pond treated sites, the relative abundances of obligate wetland, facultative wetland, and obligate upland plants increased by, on average, 33, 105, and 29%, respectively (Table 3). The relative abundance of facultative

upland plants decreased by 54%, on average, following the installation of plug-and-ponds (Table 3).

Of the traits that influence riparian plant functional groupings (growth rate, moisture use, soils, height-at-maturity, and rooting depth), BDAs affected the CWMs of all five, and plug-and-ponds affected the CWMs for moisture use and soils. Following BDA treatment, the relative abundances of plants with slow and moderate growth rates increased, and the relative abundance of plants with rapid growth rates decreased at impact sites relative to controls (Table 3). The relative abundances of plants with low or high moisture use increased, and the relative abundance of plants with medium moisture use decreased at BDA-treated sites (Table 3). BDAs reduced the relative abundance of plants adapted to one or three soil textures and did not affect the relative abundance of plants adapted to two soil textures (Table 3). At plug-and-pond treated sites, the relative abundance of plants with high moisture use increased by 120%, and the relative abundances of low and medium moisture use plants decreased by greater than 30% at impact sites relative to controls (Table 3). The relative abundance of plants adapted to two soil textures increased, and the relative abundances of plants adapted to one or three soil textures decreased at plug-and-pond treated sites (Table 3). Plug-and-ponds had a negligible effect on community-level growth rate, height-at-maturity, and rooting depth (Table 3).

Stream restoration shifted CWMs for effect traits that influence ecosystem function. BDAs increased community-level C:N and decreased community-level nitrogen fixation rates. At BDA-treated sites, the relative abundances of plants with medium and high C:N increased, and the relative abundance of plants with low C:N decreased (Table 3). The relative abundances of plants with high nitrogen fixation rates decreased, and plants with medium nitrogen fixation rates increased at BDA-treated sites (Table 3). Average changes in community-level C:N and nitrogen fixation were smaller at plug-and-pond treated sites, apart from an increase of 54% in the relative abundance of plants with medium nitrogen fixation rates (Table 3).

BDAs and plug-and-ponds shifted CWMs for traits related to tolerance of anaerobic conditions, fire, and drought. The relative

abundance of plants with high anaerobic tolerance increased by 64% and 58%, on average, at BDA-treated and plug-and-pond-treated sites, respectively (Table 3). BDAs also increased the relative abundance of plants with no anaerobic tolerance, high or no drought tolerance, and high, low, or no fire tolerance (Table 3). At plug-and-pond treated sites, the relative abundance of plants with high, or low drought tolerance increased, as well as the relative abundance of plants with low or no fire tolerance (Table 3). Both treatments reduced the relative abundance of plants with low anaerobic tolerance (Table 3).

BACI ratio posterior distributions showed a high probability of large effect sizes related to changes in CWMs for wetland indicator status and traits that determine riparian plant functional groupings. We found a high probability that the relative abundance of obligate wetland plants increased by $\geq 30\%$ following BDA treatment and the relative abundance of facultative wetland plants increased by $\geq 20\%$ at plug-and-pond-treated sites (Table 4). BDAs likely increased the relative abundance of high moisture use plants by $\geq 20\%$ (Table 5). The relative abundance of plants with rapid growth rates and plants adapted to three soil textures likely decreased by $\geq 20\%$ following the installation of BDAs (Table 5). We found high probabilities of small BDA treatment effects ($< 20\%$) on community-level plant height and rooting depth (Table 5). At plug-and-pond treated sites, the relative abundance of plants with high moisture use likely increased by $\geq 50\%$, and probabilities were also high that the relative abundance of plants with medium moisture use or plants adapted to one soil type decreased by $\geq 20\%$ (Table 5). We found high probabilities of small plug-and-pond treatment effects on the relative abundance of plants adapted to two soil textures, which likely increased by less than 20%, and plants with low moisture use, which likely decreased by less than 20% (Table 5).

We found a high probability of small effect sizes for the CWMs of traits that influence ecosystem function (Table 6). BDAs likely increased the relative abundance of plants with high C:N and plants with no nitrogen-fixing capacity by less than 20%. The probability was also high that BDAs increased the relative abundance of plants with medium C:N by $\geq 20\%$.

Table 4. Estimates of the probability that community-weighted means for wetland indicator status classifications increased or decreased a given percentage following restoration using BDAs and plug-and-pond treatments.

	BDAs					Plug-and-ponds				
	> 0 %	≥ 20 %	≥ 30 %	≥ 50 %	≥ 100 %	> 0 %	≥ 20 %	≥ 30 %	≥ 50 %	≥ 100 %
Increase										
Obligate wetland	0.99	0.95	0.91	0.82	0.51	0.77	0.59	0.50	0.35	0.12
Facultative wetland	0.53	0.40	0.35	0.26	0.13	0.86	0.78	0.73	0.64	0.44
Facultative upland	0.90	0.70	0.57	0.35	0.06	0.02	0.00	0.00	0.00	0.00
Obligate upland	0.74	0.66	0.62	0.55	0.41	0.57	0.48	0.44	0.37	0.24
Decrease										
Obligate wetland	0.01	0.00	0.00	0.00	0.00	0.23	0.09	0.05	0.00	0.00
Facultative wetland	0.47	0.33	0.25	0.11	0.00	0.14	0.07	0.05	0.01	0.00
Facultative upland	0.10	0.02	0.00	0.00	0.00	0.98	0.93	0.87	0.59	0.00
Obligate upland	0.26	0.18	0.14	0.06	0.00	0.43	0.32	0.26	0.14	0.00

Table 5. Estimates of the probability that community-weighted means for five functional traits related to water availability and fluvial disturbance increased or decreased a given percentage following restoration using BDAs and plug-and-pond treatments.

		BDAs					Plug-and-ponds				
		> 0 %	≥ 20 %	≥ 30 %	≥ 50 %	≥ 100 %	> 0 %	≥ 20 %	≥ 30 %	≥ 50 %	≥ 100 %
Increase											
Growth rate	Rapid	0.04	0.01	0.00	0.00	0.00	0.44	0.24	0.17	0.09	0.01
	Moderate	1.00	0.90	0.70	0.19	0.00	0.36	0.01	0.00	0.00	0.00
	Slow	0.59	0.48	0.42	0.33	0.18	0.47	0.36	0.32	0.25	0.13
Moisture use	High	0.95	0.76	0.62	0.34	0.03	1.00	1.00	1.00	0.97	0.68
	Medium	0.11	0.01	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
	Low	0.75	0.58	0.50	0.35	0.13	0.13	0.06	0.04	0.01	0.00
Soils	One	0.44	0.31	0.25	0.17	0.07	0.09	0.05	0.03	0.02	0.00
	Two	0.53	0.08	0.02	0.00	0.00	0.93	0.53	0.28	0.04	0.00
	Three	0.01	0.00	0.00	0.00	0.00	0.30	0.14	0.09	0.04	0.00
Plant height		0.89	0.19	0.04	0.00	0.00	0.74	0.01	0.00	0.00	0.00
Rooting depth		0.00	0.00	0.00	0.00	0.00	0.49	0.00	0.00	0.00	0.00
Decrease											
Growth rate	Rapid	0.96	0.82	0.65	0.19	0.00	0.56	0.31	0.19	0.03	0.00
	Moderate	0.00	0.00	0.00	0.00	0.00	0.64	0.04	0.00	0.00	0.00
	Slow	0.41	0.28	0.21	0.09	0.00	0.53	0.40	0.33	0.18	0.00
Moisture use	High	0.05	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	Medium	0.89	0.47	0.20	0.00	0.00	0.99	0.89	0.71	0.13	0.00
	Low	0.25	0.10	0.06	0.01	0.00	0.87	0.71	0.59	0.27	0.00
Soils	One	0.56	0.39	0.30	0.12	0.00	0.91	0.82	0.74	0.49	0.00
	Two	0.47	0.03	0.00	0.00	0.00	0.07	0.00	0.00	0.00	0.00
	Three	0.99	0.94	0.85	0.42	0.00	0.70	0.44	0.29	0.06	0.00
Plant height		0.11	0.00	0.00	0.00	0.00	0.26	0.00	0.00	0.00	0.00
Rooting depth		1.00	0.00	0.00	0.00	0.00	0.51	0.00	0.00	0.00	0.00

Table 6. Estimates of the probability that community-weighted means for two functional effect traits related to ecosystem function increased or decreased a given percentage following restoration using BDAs and plug-and-pond treatments.

		BDAs					Plug-and-ponds				
		> 0 %	≥ 20 %	≥ 30 %	≥ 50 %	≥ 100 %	> 0 %	≥ 20 %	≥ 30 %	≥ 50 %	≥ 100 %
Increases											
C:N	High	0.75	0.63	0.58	0.48	0.30	0.51	0.41	0.37	0.30	0.19
	Medium	0.99	0.78	0.49	0.06	0.00	0.79	0.12	0.02	0.00	0.00
	Low	0.38	0.16	0.10	0.03	0.00	0.51	0.36	0.30	0.20	0.07
N fixation	High	0.46	0.36	0.31	0.24	0.13	0.50	0.44	0.41	0.36	0.27
	Medium	0.59	0.52	0.48	0.42	0.30	0.63	0.55	0.52	0.45	0.33
	None	0.85	0.00	0.00	0.00	0.00	0.40	0.00	0.00	0.00	0.00
Decrease											
C:N	High	0.25	0.15	0.10	0.03	0.00	0.49	0.38	0.32	0.18	0.00
	Medium	0.01	0.00	0.00	0.00	0.00	0.21	0.00	0.00	0.00	0.00
	Low	0.62	0.29	0.15	0.01	0.00	0.49	0.31	0.21	0.07	0.00
N fixation	High	0.54	0.42	0.34	0.19	0.00	0.50	0.42	0.37	0.26	0.00
	Medium	0.41	0.32	0.27	0.16	0.00	0.37	0.28	0.23	0.13	0.00
	None	0.15	0.00	0.00	0.00	0.00	0.60	0.00	0.00	0.00	0.00

Plug-and-ponds likely increased the relative abundance of plants with medium C:N by less than 20%.

BACI ratio posterior distributions indicate high probabilities of varying BDA and plug-and-pond treatment effect sizes for traits related to tolerance of anaerobic conditions, fire, or drought. The relative abundance of plants with high anaerobic tolerance likely increased by ≥30% at BDA and plug-and-pond treated sites (Table S2). The probability was high that BDAs

reduced the relative abundance of plants with low drought tolerance by ≥20% and plug-and-ponds reduced the relative abundance of plants with low anaerobic tolerance by ≥30% (Table S2). We found high probabilities of small BDA and plug-and-pond treatment effects related to community-level drought and fire tolerance. BDAs likely increased the relative abundance of plants with high fire tolerance by less than 20% (Table S2). Plug-and-ponds likely increased the relative

abundance of plants with low drought tolerance by less than 20% (Table S2).

Discussion

We analyzed changes in functional diversity and community-level traits to draw conclusions regarding stream restoration efficacy. Lower FDis and FRic, as well as changes in CWMs for height-at-maturity, rooting depth, moisture use, and anaerobic tolerance, indicate BDAs and plug-and-ponds strengthened environmental filters by raising water tables and increasing overbank flooding. Modified filters acted on traits that respond to increased water availability and fluvial disturbance. Plants lacking traits that provide adaptation to anoxic conditions imposed by high water tables and frequent inundation declined in abundance following restoration. Large increases in the abundance of wetland plants confirm BDAs and plug-and-ponds altered floodplain habitats and recovered riparian vegetation. Additionally, shifts in the streamside plant community resulted in small changes in the representation of traits that influence ecosystem function and resilience to disturbance. These changes occurred quickly following restoration, suggesting BDAs and plug-and-ponds can rapidly recover riparian ecosystems and that trait-based approaches can capture short-term indicators of success.

The strength of environmental filters that affect community assembly can be detected and measured by FDis and FRic (Hedberg et al. 2014). FDis is sensitive to flood intensity, with lower values associated with more frequent, larger, or longer floods (Lawson et al. 2015; Brice et al. 2016; Lozanovska et al. 2018). Our study shows both treatments drove large declines in FDis. We also found a high likelihood of large decreases in FRic at plug-and-pond-treated sites. These results provide a clear sign that BDAs and plug-and-ponds modified environmental filters by raising water tables and increasing fluvial disturbance. Higher water tables and more frequent, larger, or longer overbank flooding increase the occurrence, extent, and duration of soil saturation. This stronger filtering excludes a larger range of traits and yields an assemblage dominated by functionally similar flood-adapted plants that plot near each other in trait space. This result is consistent with past studies that have found lower FRic and FDis in wetland plant communities growing in locations with restored or intact hydrology than in communities exposed to altered hydrologic regimes (Hedberg et al. 2014; Lawson et al. 2015).

A suite of morphological and physiological characteristics, captured by the “anaerobic tolerance” trait (USDA, NRCS 2024), allows riparian plants to survive anoxic conditions or escape stress imposed by flooding (Garssen et al. 2015; Diehl et al. 2017). Other traits, including height-at-maturity, rooting depth, and moisture use, respond to water availability and fluvial disturbance (Merritt et al. 2010; Stromberg 2013; Stromberg & Merritt 2016). We found increases in the relative abundance of plants with high anaerobic tolerance and high moisture use, as well as increases in the CWM for height-at-maturity following both treatments. Additionally, the rooting depth of the streamside vegetation community decreased at BDA-treated sites. Increased height of riparian vegetation communities is associated with

reduced depth-to-groundwater and enables plants to continue gas diffusion by emerging above flood waters (Luo et al. 2016; Stromberg & Merritt 2016; Lozanovska et al. 2018). Rooting depths are shallowest for wetland plants, intermediate for facultative upland species, and deepest for obligate upland plants (Stromberg 2013). Lastly, consistent access to groundwater allows riparian plants to maintain high transpiration rates, resulting in classification as high moisture use. Our results, therefore, indicate that BDAs and plug-and-ponds raised water tables and increased flooding, and that these modified filters helped recover riparian vegetation.

Plant species are assigned to wetland indicator categories based on the estimated probability of occurrence in wetlands (Lichvar et al. 2012). Obligate wetland plants grow in standing water or seasonally saturated soils 99% of the time. Facultative wetland plants occur in areas where soils are seasonally saturated. Facultative and obligate upland plants occur where soil is rarely or never saturated. Channel incision, lowered water tables, and less overbank flooding shift streamside vegetation to more xeric, dry-adapted species (Johaneman et al. 2023). Our results show stream restoration can rapidly reverse this process. We observed increases in the abundance of obligate wetland plants following both BDA and plug-and-pond restoration. Additionally, the relative abundance of facultative wetland plants increased at plug-and-pond-treated sites. The high probability of large treatment effects of BDAs on obligate wetland plants and plug-and-ponds on facultative wetland plants suggests both treatments expanded or created habitats with standing water or saturated soils. Large decreases in facultative upland plants at plug-and-pond-treated sites indicate that wetlands expanded into formerly dry areas dominated by upland plants. In addition to increases in obligate wetland plants, we observed increases in the relative abundance of upland plants following the installation of BDAs. We attribute this result to an increase in plant cover and a decrease in bare ground in plots far from the stream or elevated above the channel at BDA-treated sites. The cover of deep-rooted dry-adapted species likely increased in these locations because they benefited from higher water tables but did not experience increased fluvial disturbance.

As streamside plant communities reassembled in response to modification of environmental filters, the representation of effect traits that influence ecosystem function was also affected. Altered ecosystem function can be detected using FDiv, FEve, and CWMs for effect traits. FDiv and FEve provide information on competition and resource use (Mason et al. 2005). Neither treatment affected FEve, but FDiv increased slightly following both treatments. Higher divergence occurs when species with extreme traits make up a greater proportion of total abundance and is indicative of niche differentiation, lower competition, and increased ecosystem function due to efficient use of resources (Mason et al. 2005; Kuebbing et al. 2018). We found high probabilities of small BDA and plug-and-pond treatment effects on CWMs for nitrogen fixation, growth rate, C:N, and moisture use. These changes could have major impacts on ecosystem function (Lavorel & Garnier 2002). For example, declines in community-level rates of nitrogen fixation or growth and/or increases in community-level C:N could limit nutrients, reduce productivity, affect carbon

sequestration, slow nutrient cycling, and alter species interactions. Increased moisture use by the plant community could affect productivity or alter hydrologic processes. Future work should include field measurements to confirm the effects of stream restoration on ecosystem function.

Restoration projects often aim to recover ecosystem function (Palmer et al. 2014). Common function-based goals include stabilized trophic dynamics, the removal of nitrogen to improve water quality, and increased plant productivity to reduce erosion and provide forage. Although BDAs and plug-and-ponds likely resulted in increased resource-use efficiency, as demonstrated by higher FDiv, and affected CWMs for growth rate, nitrogen fixation, moisture use, and C:N, we found that treatment effect sizes were small compared to changes in FDis, FRic, and response trait CWMs. This result is consistent with past work that reported links between longer recovery times and restoration of complex ecosystem function (Power 1998). On their own, BDAs and plug-and-ponds may not be sufficient to recover ecosystem functions within a desired time frame. Combining the application of treatments with revegetation that targets plant species with specific traits may result in a more rapid recovery of ecosystem function (Sutton-Grier et al. 2010).

Shifts in streamside vegetation that occurred following restoration likely impacted resilience to disturbance. At plug-and-pond-treated sites, we found increases in the relative abundance of plants with low drought tolerance and/or high anaerobic tolerance and decreases in the relative abundance of plants with no or low anaerobic tolerance. This result indicates that, as expected, plug-and-ponds shifted the plant community to one that is less tolerant of drought and more tolerant of flooding. In contrast, BDAs increased the relative abundance of plants with high anaerobic tolerance, high drought tolerance, and/or high fire tolerance. This unexpected result was partially related to the decrease in bare ground and the increase in vegetative cover explained above. However, this finding is also related to the greater abundance of flood-adapted plants that are capable of resprouting, regrowing, or reestablishing after fire. At BDA-treated impact sites, we found large increases in the cover of species with high anaerobic and high fire tolerance (e.g. *Carex utriculata*, *Juncus longistylis*, and *Salix exigua*). These plants appear to replace species with no or low tolerance for anaerobic conditions and fire (e.g. *Festuca arizonica*, *Ipomopsis aggregata*, and *Potentilla hippiana*). Plug-and-pond-treated sites lacked substantial bare ground prior to treatment, and plants with high anaerobic and high fire tolerance replaced other plants with similar trait values. For example, we found increases in the abundance of *C. utriculata*, *Iris missouriensis*, and *J. longistylis* and decreases in *C. elynoides*, *Deschampsia cespitosa*, and *Hordeum brachyantherum* at plug-and-pond-treated sites. These species all have high anaerobic and high fire tolerance. Given greater threats from larger and more severe wildfires (Pausas & Keeley 2021), this result is relevant for managers who want to increase the fire resiliency of riparian ecosystems without losing wetland plant communities. Future work should aim to understand the mechanisms by which plants with specific trait combinations replace species with similar or different traits post-treatment.

Our results show that the probability of achieving restoration targets—including modified environmental filters, recovery of riparian vegetation, improved ecosystem function, or increased resiliency—through application of BDAs and plug-and-ponds in similar systems is high. Nonetheless, this study captures short-term changes in functional diversity and CWMs of the streamside plant community. Because plug-and-pond installation was delayed by the COVID-19 pandemic, our dataset is limited to one season of post-treatment sampling at plug-and-pond sites. This shorter post-treatment period may explain generally smaller effect sizes and lower probabilities of change at plug-and-pond-treated sites compared with BDA sites, where we completed two seasons of post-treatment sampling. More work is needed to assess whether the short-term responses observed in this study are maintained over longer time periods.

In this study we relied on the PLANTS database. This approach has limitations, including missing trait data and potential discrepancies between field-measured values and values in PLANTS. We excluded 21 unidentified and 10 identified species from our analysis due to a lack of trait data. Even though these species generally made up a small proportion of the plant community, removing them from the analysis could impact calculations of functional diversity if the removed species were outliers in terms of their trait values. Measuring trait values in the field is one method to address missing trait data. Field measurements are important as measured trait values can differ from values reported in trait databases; however, field measurements can be data or time intensive (Hedberg et al. 2013; Johaneman et al. 2023). Several past studies have used PLANTS to characterize riparian plant communities (Hough-Snee et al. 2015; Palmquist et al. 2017; Scott & Merritt 2020) and our use of this database demonstrates that these accessible trait values can be used to monitor restoration treatments even if resources to complete field measurements are lacking.

Managers are addressing lost ecosystem services and extensive floodplain degradation by increasing the pace and scale of stream restoration (Palmer et al. 2014). Prior to widespread implementation, the impacts of treatment on hydrology and ecology must be quantified and efficacy confirmed (Natali & Kondolf 2018; Lautz et al. 2019). Many stream restoration projects aim to raise water tables, increase overbank flooding, and aggrade channels. Therefore, understanding whether treatments recover hydrological and geomorphological processes is important, and future work should focus on this topic. Recovery of riparian vegetation is also a common restoration target (González et al. 2015). In this study, we addressed treatment effects on the functional diversity and composition of streamside plant communities. There are many benefits to trait-based evaluation of restoration. Functional traits are universal and not associated with a specific region (D'Astous et al. 2013). Focus on traits, as opposed to species, therefore allows comparison across sites that differ in climate, elevation, geology, aspect, or plant community type (D'Astous et al. 2013). Secondly, vegetation cover data is often collected at stream restoration sites. These data can easily be combined with trait values from databases like PLANTS to provide a simple and low-cost

method for measuring shifts in environmental filters, ecosystem function, or resiliency. Our results demonstrate that trait-based approaches can capture a rapid response to restoration and indicate that treatments are having desired effects on a short time frame. As most stream restoration projects receive little or no monitoring (González et al. 2015; Pilliod et al. 2018), the adoption of functional traits could improve understanding of treatment effectiveness across regions and provide managers with a tool to measure short-term response.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. Estimates of the probability that streamside plant functional diversity indices increased or decreased a given percentage following restoration using BDAs and plug-and-pond treatments.

Table S2. Estimates of the probability that community-weighted means for three functional effect traits related to resiliency increased or decreased a given percentage following restoration using BDAs and plug-and-pond treatments.

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