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Long-term soil nutrient and understory plant responses to post-fire rehabilitation in a lodgepole pine forest

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ABSTRACT

Wildfires and other disturbances play a fundamental role in regenerating lodgepole pine forests. Though severe, stand-replacing fires are typical of this ecosystem, they can have dramatic impacts on soil properties and biogeochemical processes that influence the rate and composition of vegetation recovery. Organic soil amendments are often applied to manage post-fire erosion, but they can also improve soil moisture and nutrient retention and potentially alter the trajectory of post-fire revegetation. We compared change in soil nutrients, microbial communities, and understory plant cover and composition on six burned hillslopes treated with 1) biochar (20 t ha $^{-1}$), 2) wood mulch (37 t ha^{-1}), 2) biochar + mulch, and 4) an untreated control a decade after the 2010 Church's Park fire. Wood mulch increased soil moisture and N retention the first three years following treatment. Mulch and biochar were still visible when we resampled in 2023. Mulch continued to increase soil moisture compared to unamended controls, though it had few lasting effects on soil N or cations. Conversely, biochar added alone increased dissolved organic C in soil leachate, C:N in soil and leachate, and hosted microbial communities distinct from those in mulch and combined biochar and mulch treatments. Biochar also elevated various dissolved and extractable soil N forms but reduced net nitrification. The amendments had no general effect on total graminoid, forb, or shrub cover, but had plant species-specific impacts. For example, biochar doubled cover of the dominant shrub *Vaccinium scoparium*, and mulch reduced cover of the most common forb (*Oreochrysum parryi*) by more than 50 %. The combined biochar and mulch treatment had persistent, additive effects on both soil and plant responses that exceeded impacts of the individual treatments. As seen increasingly in western North America, conifer regeneration remains scarce in the Church's Park burn scar, and these findings suggest that mulch and biochar amendments may improve reforestation success following severe wildfires.

1. Introduction

Wildfires are increasing in frequency and severity across western North America, raising concerns about the resiliency of forest ecosystems in a warming climate (Westerling et al., 2006; Nelson et al., 2016). Lodgepole pine (*Pinus contorta* Dougl. ex. Loud. var. latifolia) is a fire-dependent species with serotinous cones that open with heat and typically regenerate into dense, uniform stands (Lotan et al., 1985). However, future warmer and drier climatic conditions are expected to alter the geographical distribution of this forest type (Davis et al., 2023); bioclimatic modeling predicts that 79 % of the suitable range of lodgepole pine in the Colorado Front Range will become unsuitable by 2060 (Fornwalt et al., 2024, in press). A review of 52 wildfires across the Rocky Mountains found that declining post-fire tree regeneration was linked to the drier conditions observed during recent decades (Stevens-Rumann et al., 2018). Near the Colorado-Wyoming border increased variability and patchiness in post-fire lodgepole pine density was attributed to post-fire climate and pre-fire stand conditions (Guz et al., 2021). However, simulations based on future climatic projections for Yellowstone National Park, Wyoming, USA found that post-fire tree regeneration was resilient to significant changes in climate and fire return interval and that regeneration failure was likely only when

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climate-related stresses were coupled with other factors, such as increased distance to a seed source (Hansen et al., 2018).

Severe wildfire can alter physical, chemical and biological soil properties and influence ecosystem recovery. During wildfires, the C and nutrients stored in vegetation and surface soil layers are released, and C and nutrient-rich ash and mineral soils are exposed to erosion (Certini, 2005; Ebel, 2012). Although N is lost during combustion and post-fire leaching (Wan et al., 2001), changes in the microbially mediated processes that regulate soil N cycling are long-lasting (Dove et al., 2020). Soil microbial biomass typically declines immediately after fire (Pressler et al., 2018), but alteration of microbial community composition can persist for decades (Caiafa et al., 2023; Nelson et al., 2024). Changes in soil resources regulate initial post-fire plant responses (Andrade et al., 2020), but their effect on longer-term vegetation development are not well understood. Better understanding of the linkages between soil and plant disturbance and recovery has implications for designing effective post-fire rehabilitation treatments (Heneghan et al., 2008).

Organic amendments, including various mulch types, are commonly applied to reduce post-fire soil erosion (Robichaud et al., 2014; Fernández and Vega, 2014; Prats et al., 2016) though these treatments may also facilitate soil and vegetation recovery. For example, the cover created by woody mulch applied to reduce erosion also increases infiltration, soil water and N retention (Jonas et al., 2019). Similarly, biochar, a byproduct of pyrolysis (Kuzyakov et al., 2018), has a high surface area and exchange capacity that retain moisture and nutrients (Hagemann et al., 2017; Edeh et al., 2020); thus, it may have utility for post-fire rehabilitation (Joseph et al., 2021). Though positive short-term impacts of mulch and biochar on soil moisture, nutrient retention and plant establishment have been observed (Fornwalt et al., 2017; Rhoades et al., 2017; Jonas et al., 2019), questions remain about their longer-term consequences.

A post-fire rehabilitation experiment established within the 2010 Church's Park fire scar near Fraser, CO provides an opportunity to evaluate decade-scale ecosystem recovery among various organic amendments (Rhoades et al., 2017). The fire burned lodgepole pine forests impacted by severe mountain pine beetle outbreaks (*Dendroctonus ponderosae* Hopkins) in the early 2000s (Chapman et al., 2012), creating a compound disturbance that is widespread in the Southern Rockies (Rodman et al., 2022). Research conducted in the Church's Park fire scar and other wildfires that burned nearby beetle-killed forests documents low tree seedling regeneration (Rhoades et al., 2018), reduced tree seed availability (Rhoades et al., 2022), and decreased ectomycorrhizal symbiont abundance (Caiafa et al., 2023). Initial research indicated that woody mulch, especially when combined with biochar, increased soil moisture, reduced nitrate (NO_3-N) movement, and increased cover of a common post-fire colonizer (*Chamerion angustifolium* (L.) Holub.; fireweed) (Rhoades et al., 2017). That short-term study suggested that these treatments may have the potential to enhance longer-term ecosystem recovery after this combination of disturbances. As the severity of wildfires and other climate-related disturbances increases in western North America, land managers seek effective approaches for rehabilitating soil and vegetation that can be applied widely.

In this study, we evaluate whether woody mulch and biochar treatments applied shortly after a severe wildfire have impacts on soil and plant recovery that are evident more than a decade after the fire. We expected that the initial impacts of the amendments on soil moisture and nutrient retention would continue during the intervening years and influence the composition of the current understory plant community. Combined with earlier work on this site, our current findings should help managers determine whether these rehabilitation treatments have utility for enhancing post-fire soil and vegetation recovery.

2. Methods

2.1. Study Site and Experimental Design

This research was conducted on experimental plots established within the Church's Park burn perimeter (Rhoades et al., 2017). The fire burned 200 ha on predominantly south-facing slopes with 47 % at moderate to high severity and 53 % at low severity (USDA USFS, 2010). The fire scar extends from 2438 to 3200 m elevation in an area that receives an average of 700 mm of precipitation annually, primarily as snow (USDA NRCS, 2013). Soils at the site are gravelly, sandy-loam mixed, typic Cryoboralfs (Alfisols) derived from colluvium and alluvium of granitic gneiss and schist parent materials (Alstatt and Miles, 1983). Permeability and available water capacity of these soils are moderate with more than 150 cm of effective rooting depth on average. The pre-fire forest overstory was predominately lodgepole pine interspersed with small (< 1 ha) patches of quaking aspen (*Populus tremuloides* Michx), that comprised less than 3 % of overstory tree density (Collins et al., 2011). Mountain pine bark beetles killed over 85 % of the overstory trees in the area before the Church's Park fire (Chapman et al., 2012).

The study was designed to evaluate the impacts of organic treatments on soil productivity and post-fire plant re-establishment compared to untreated, burned areas. Six blocks consisting of four 5 ×5 m plots were established in 2014 in areas that burned at high severity; severity was determined primarily by the degree of vegetation mortality and soil organic layer combustion (Parson et al., 2010). The blocks were located on mid-slope positions with similar slope (5–15 %), aspect (south--facing) and pre-fire forest composition (>75 % lodgepole pine, >85 % bark beetle related mortality). Plots were arranged side-by-side along the slope contour with the following treatments assigned at random: 1) untreated control, 2) wood mulch, 3) biochar, 4) biochar + mulch. Wood mulch was created locally from chipped, beetle-killed lodgepole pine and applied at a 2 cm deep surface layer, equivalent to 37 t ha^{-1}. Chips were $\leq$ 2 cm in diameter and $\leq$ 1 cm thick. Biochar was created from the chipped lodgepole pine feedstock using a two-step pyrolysis process that combined an O_2-limited step (700–750˚C, <1 minute) followed by an O_2-free step (400–550˚C, 10–15 minutes). Biochar had a pH of 9.4 and consisted of 87.2 % carbon (C), 1.4 % 0, 0.4 % N, 9.4 % ash, and 1.1 % water (Rhoades et al., 2017). Biochar was applied at 20 t ha^{-1} and hand-raked into the upper 2–3 cm of the mineral soil. Mulch was applied on top of biochar in the combined treatment. Trenches were hand dug upslope of plots to reroute surface runoff and cleaned out periodically to limit erosion during the first study. The initial study began four growing seasons after the Church's Park Fire, after significant post-fire overland flow had abated. See Rhoades et al., 2017 for additional study design details. Due to concerns over low tree regeneration after the Church's Park fire (Rhoades et al., 2018), the US Forest Service replanted trees; no trees were planted within or near the experimental plots.

2.2. Sampling and Analysis

The experimental plots were resampled in summer 2023 to measure soil and plant recovery 10 years after the organic amendments were applied.

2.3. Soil Water, Nutrients and Chemistry

Volumetric moisture content (VMC) was measured monthly from June to September 2023 using a hand-held, time-domain reflectometry probe (HydroSense II, Campbell Scientific, Logan, UT). At each sample date, five replicate readings were measured at equally spaced intervals along a line crossing the middle of each treatment plot (5 replicates x 4 treatments x 6 blocks) within the upper 15 cm of the mineral soil. Residual mulch or other organic material was carefully moved before sampling, then replaced. Sample locations were offset slightly to avoid cumulative soil disturbance.

In July 2023, the middle of the growing season, we sampled mineral soils for nutrient, chemical and microbial analyses. O-horizon and remnant woody mulch was removed then two replicate mineral soil subsamples were collected 1 m apart near the center of each 5 ×5 m plot and composited for the 0–5 and 5–15 cm depths (n = 6 per treatment and depth). Soils were collected with a 6.4 cm diameter bulb corer that was sterilized with ethanol between samples. Roots and rocks were removed by hand and soils were mixed; all soils were transported and stored at 4℃ and analyzed within 7 days. Extractable soil inorganic nitrogen was measured by extracting 20 g subsamples with 100 mL of 2 M KCl solution, shaking for 60 minutes, filtering, and analyzing for nitrate (NO_3-N) and ammonium (NH_4-N) using a flow injection analyzer via colorimetry (QuikChem 8500, Lachat Company, Loveland, CO). To convert concentrations to a dry weight basis, gravimetric soil water content was calculated after oven-drying samples at 105℃ for 24 hours.

A second subsample of these soils was dried (24 hours at 105℃), sieved to 2 mm, ground to a fine powder on a roller mill, and analyzed for total C and N by dry combustion and infrared detection (CN 802, Velp Scientifica, Deer Park, NY). Soil pH was analyzed on a 10 g subsample in a 1:1 soil-to-deionized water slurry after one hour of agitation (Thomas, 1996; inMotion Pro, Mettler Toledo, Greifensee, Switzerland).

Another subsample was used to quantify water-soluble ions, nutrients, and carbon. Sieved soils were added to 100 mL of deionized water, shaken for one hour, then filtered through 0.45 μm mesh membrane filters (Millipore Durapore PVDF). Dissolved organic C (DOC) and total dissolved N (TDN) concentrations were determined in the water extracts using a Shimadzu TOC-VCPN total organic carbon analyzer, after purging of mineral C with 2 M HCl (Shimadzu Co., Columbia, MD). Detection limits for water-extractable DOC and TDN were <0.05 mg L^{-1} and <0.01 mg L^{-1} respectively. Water soluble ions were determined by ion chromatography using electrical conductivity detection, and AS19A columns for anions and CS12A columns for cations (Integrion, Thermo Fisher, Waltham, MA). Detection limits for water-extractable ions were <0.01 mg L^{-1} for K, Na, Ca, Mg, NH_4-N, NO_3-N, SO_4, and PO_4.

Mineralization and nitrification assays were used to measure inorganic N production. Another subsample of the soils described above were incubated for 28 days at 20℃ with soil moisture maintained at 60 % of field capacity (Hart et al., 1994, Linn and Doran, 1984). Post-incubation soil extractable NH_4-N and NO_3-N concentrations were measured as described above. Net transformations were calculated as follows: net mineralization = $(NH_4\text{-N} + NO_3\text{–N})t_{28d}$ – $(NH_4\text{-N} + NO_3\text{-N})t_{0d}$ and net nitrification = $(NO_3\text{-N})t_{28d}$ – $(NO_3\text{-N})t_{0d}$ (Hart et al., 1994).

2.4. Microbial analyses

Subsamples from each soil sample described above were placed into sterile Whirlpak bags for microbial analyses. Samples were stored a 4 °C during transport, then transferred to a −80 °C freezer until further processing. DNA was extracted using a Zymo Soil/Fecal kit. Soil bacterial communities were amplified using the V4 region of the 16S rRNA gene using the primers 515 F (5'-GTGYCAGCMGCCGCGGTAA-3') (Parada et al., 2016) and 806 R (5'-GGACTACNVGGGTWTCTAAT-3') (Apprill et al., 2015). Soil fungal communities were amplified via the first internal transcribed spacer (ITS1) of the ribosomal DNA using the primers ITS1f (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2 (5′-GCTGCGTTCTTCATCGATGC-3′) (White et al., 1990). All samples were sequenced on the Illumina MiSeq Platform with 251 bp paired-end sequencing chemistry at Microbial Community Sequencing Lab (University of Colorado Boulder).

To process resulting reads, we utilized QIIME2 (release 2021.2) (Bolyen et al., 2019). Due to low quality, ITS reverse reads were discarded. Demultiplexed 16S and ITS samples were merged, filtered/denoised, and binned to infer amplicon sequence variants (ASVs) using DADA2 (Callahan et al., 2016). Following these steps, 16S rRNA gene read counts ranged from 20,952 to 68,942 and ITS amplicon sequencing read counts ranged 9,875 to 206,218. Taxonomy was assigned to our resulting bacterial ASVs using scikit-learn pre-trained SILVA classifiers (version 138; Quast et al., 2013; Bokulich et al., 2018; Robeson et al., 2021) and our resulting fungal ASVs using self-trained UNITE database classifiers (Nilsson et al., 2019; Kõljalg et al., 2020). Fungal sequences not assigned to the Kingdom Fungi and bacterial sequences assigned to mitochondria or chloroplast by taxonomic assignment were discarded from ASV tables prior to downstream analysis. Resulting reads were deposited and are available at NCBI under BioProject PRJNA682830 (Supplemental File BioSampleObjects_NCBI_ChurchPark_KMS_May2024.xlsx). To assess differential taxonomic enrichment and depletion for bacterial and fungal communities between treatments, we performed MaAsLin2 (MaAsLin2- Microbiome Multivariable Association with Linear Models) using the MaAsLin2 R package (Mallick et al., 2021).

2.5. Understory Plant and Ground Cover

Substrate (litter/duff, mineral soil, mulch, biochar) and plant cover was measured in August 2023 near the peak of herbaceous plant biomass. Plant cover and species were measured within two 1 m^2 quadrats per plot using a gridded point-intercept method. Nomenclature, plant growth form (graminoid, forb, and shrub) and nativity were classified based on the PLANTS Database (USDA NRCS, 2024) and local botanical keys (Weber and Wittmann, 2001; Ackerfield, 2015).

2.6. Statistical analysis

Treatment effects on soil moisture and nutrients were compared using a one-way analysis of variance and Bonferroni corrected Tukey means separation tests (SPSS V. 22, IBM Co., Chicago, IL). To characterize how soil microbial communities differed by rehabilitation treatment and soil depth (0–5 cm, 5–15 cm), statistical analyses were performed using R version 4.1.2 (R Core Team, 2021). Levene's statistic was used to test for homogeneity of variance and non-normal and unequal variances were log-transformed before statistical analysis. Substrate and plant cover data was arcsine transformed before statistical analysis. Differences in Shannon's H index of microbial alpha diversity (e.g., $H = -\Sigma p_i * \ln(p_i)$, where p_i is the proportion of the community represented by species i) between distinct soil depths were assessed and tested using pairwise Wilcoxon signed-rank tests with a Bonferroni p-value adjustment for multiple tests using the function "stat_compare_means" and in the package ggpubr (Kassambara, 2023) and the function "pairwise.wilcox.test" in the package stats (R Core Team, 2021), and between treatments through Kruskal-Wallis tests using "stat_compare_means" and the function "kruskal.test" in the package stats. To test differences in bacterial and fungal community composition between rehabilitation treatments, nonparametric permutational multivariate analysis of variance (PERMANOVA) was performed (Anderson, 2001) using Bray-Curtis dissimilarity matrices and the "adonis2" function in the vegan package (Okansen et al., 2022) and visualized using Non-Metric Multidimensional Scaling (NMDS). All visualizations were produced using the package ggplot2 (Wickham, 2016). Significance was assigned at ρ values less than $\alpha = 0.05$, except where specified.

3. Results

3.1. Surface cover and soil properties

The organic amendments remained visible a decade after they were applied (Table 1) and they continued to influence soil moisture and chemistry. Mulch and biochar cover was 100 % when the treatments were initially applied. By 2023, mulch was present on 50 and 40 % of the mulch and mulch + biochar treatment combinations. Mulching reduced

Table 1
Substrate cover 10 years after rehabilitation treatments were applied following the 2010 Church's Park fire. Cover was measured in 1 m^2 quadrats in six replicate blocks of treatments. Letters denote significant differences between means at the α = 0.05 level.

		Control				Biochar				Mulch				Biochar + Mulch			
		Mean	SD	Max		Mean	SD	Max		Mean	SD	Max		Mean	SD	Max	
Litter / Duff	%	38.8	14.3	64	c	34.8	15.2	54	bc	20.6	21.8	80.0	ab	15.4	13.2	36	a
Mineral Soil	"	37.0	16.2	61	b	24.3	14.4	51	ab	12.8	12.4	38.0	a	15.3	13.1	36	a
Biochar	"	1.1	1.7	4	a	16.5	11.4	34	b	1.4	2.6	6.5	a	8.9	7.9	24	b
Wood Mulch	"	4.3	3.1	7	a	4.5	3.5	7	a	49.7	20.2	71.0	b	40.5	18.2	80	b

exposed mineral soil cover from 37 % in the control plots to 13 and 15 % in the mulch and biochar + mulch plots, respectively. Biochar was visible on 17 and 9 % of the individual biochar and combined biochar + mulch treatments.

Mulching increased volumetric soil moisture content (VMC) compared to the untreated controls (Fig. 1) and effects were greatest during early summer when soil moisture was generally highest. Mulch applied alone and in combination with biochar had similar effects, with 1.7- and 1.9-times more VMC than untreated soils. Biochar applied alone had no effect on VMC during any sample period. The general ranking of treatments was consistent as soils dried, though the treatments did not differ significantly during August and September.

Biochar combined with mulch increased total soil C three-fold in the upper soil depth compared to untreated soils, and more than doubled it in the lower depth. The C added in the biochar treatments increased C:N in both sample depths, with the greatest change in the combined treatment. The biochar treatment depressed soil pH by 0.4 units in the lower sampled depth (5–15 cm) compared to any of the other treatments. Mulch alone had no impact on these soil properties in either depth.

Concentrations of dissolved total and organic N (TDN and DON) and dissolved organic C (DOC) were higher in water soluble extracts from the upper soil layer in plots with biochar compared to untreated and mulched plots (Table 3). The effect of biochar added with mulch was intermediate between untreated and biochar-amended soil. Overall, biochar added alone or with mulch had 1.5-, 1.6- and 1.7-times more TDN, DOC and DON than untreated controls. Mulch depressed water soluble NO_3-N concentrations by 36 % compared to control soils, and biochar reduced them by 18 %. The two biochar treatments reduced the proportion of NO_3-N in total dissolved N compared to the control and mulch treatments (i.e., 16 vs 22 %).

Concentrations of KCl-extractable NO_3-N and the sum of inorganic soil N were elevated in the surface layer of biochar-amended soils (Table 4). Additionally, the sum of inorganic N in that depth was twice that of the untreated soils; NO_3-N was more than 3-times higher. The proportion of extractable inorganic soil N comprised by NO_3-N was higher in all the amended soils compared to the control plots. Differences were largest for biochar either added alone or with mulch. Net mineralization did not differ statistically among the treatments. Net nitrification in the two biochar treatments was roughly half that measured in the control and mulch plots.

Several soil cations (K, Ca, Mg) were elevated in the combined

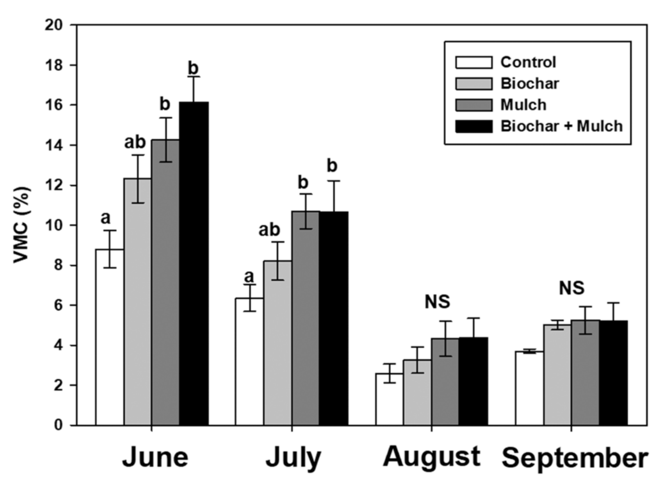

Fig. 1. Volumetric soil moisture content (VMC, 0–15 cm depth) measured in 2023, 10 years after rehabilitation treatments were applied following the 2010 Church's Park fire. Bars are means with standard errors for six study blocks. Within months, letters denote significant differences among Bonferroni adjusted treatments means at α = 0.05.

Table 2
Soil properties 10 years after establishment of rehabilitation treatments at Church's Park fire, Colorado. Data are means, standard deviations (SD) and range for six replicate blocks. Letters denote significant differences among treatment means at α = 0.05 level.

			Control				Biochar				Mulch				Biochar + Mulch			
		Depth (cm)	Mean	SD	Range		Mean	SD	Range		Mean	SD	Range		Mean	SD	Range	
Total C	%	0-5	1.0	(0.6)	[0.2-1.8]	a	1.6	(0.4)	[1.1-2.3]	a	1.1	(0.5)	[0.4-1.9]	a	3.0	(1.4)	[1.2-4.4]	b
	"	5-15	2.2	(0.7)	[1.3-3.3]	a	3.4	(1.1)	[2.1-4.8]	a	2.1	(0.8)	[0.9-3.2]	a	5.1	(1.4)	[3.0-7.1]	b
Total N	"	0-5	0.09	(0.03)	[0.06-0.15]		0.08	(0.03)	[0.03-0.11]		0.09	(0.03)	[0.06-0.12]		0.10	(0.03)	[0.07-0.15]	
	"	5-15	0.12	(0.03)	[0.09-0.15]		0.10	(0.03)	[0.06-0.14]		0.13	(0.06)	[0.07-0.22]		0.10	(0.04)	[0.06-0.16]	
C:N	–	0-5	10.6	(4.1)	[3.5-14.4]	a	24.5	(13.6)	[12.6-51.4]	ab	13.0	(5.0)	[5.9-18.7]	a	27.8	(12.2)	[15.4-48.8]	b
	–	5-15	18.1	(5.4)	[9.7-25.3]	a	35.6	(5.8)	[27.4-43.5]	b	16.4	(4.5)	[9.9-22.7]	a	53.9	(18.4)	[35.5-86.1]	c
pH	–	0-5	6.2	(0.1)	[6.1-6.3]		6.0	(0.2)	[5.8-6.2]		6.1	(0.1)	[5.9-6.2]		6.1	(0.1)	[6.0-6.2]	
	–	5-15	6.1	(0.2)	[5.8-6.2]	b	5.7	(0.3)	[5.2-6.0]	a	6.2	(0.2)	[6.0-6.5]	b	6.0	(0.2)	[5.8-6.2]	b

Table 3
Water soluble soil N and C concentrations 10 years after establishment of rehabilitation treatments at Church's Park fire, Colorado. Data are means, standard deviation (SD) and maximum (n= 6). Letters denote significant differences among treatment means at the α = 0.05 level.

			Control				Biochar				Mulch				Biochar + Mulch			
		Depth (cm)	Mean	SD	Max		Mean	SD	Max		Mean	SD	Max		Mean	SD	Max	
TDN	mg L^{-1}	0–5	6.9	0.8	8.2	a	10.5	2.0	12.5	b	5.9	1.2	7.3	a	7.7	1.5	8.9	a
	"	5–15	6.0	1.1	7.8		7.3	2.2	10.5		8.6	4.2	14.2		5.3	1.7	7.9	
NH_4-N	"	0–5	0.5	0.2	0.8		0.3	0.1	0.5		0.5	0.2	0.8		0.4	0.3	0.8	
	"	5–15	0.4	0.2	0.7		0.3	0.1	0.4		0.4	0.3	0.8		0.4	0.2	0.8	
NO_3-N	"	0–5	1.4	0.3	2.1		1.6	0.3	2.1		1.4	0.2	1.6		1.3	0.2	1.5	
	"	5–15	1.1	0.1	1.2	b	0.9	0.2	1.2	ab	0.7	0.4	1.4	a	1.1	0.2	1.4	b
DON	"	0–5	4.8	1.0	6.4	a	8.7	2.0	10.7	b	4.0	1.2	5.8	a	6.0	1.7	7.5	a
	"	5–15	4.5	1.1	6.2		6.1	2.2	9.4		7.5	4.3	13.5		3.8	1.5	6.0	
DOC	"	0–5	74.1	20.7	100.1	a	117.3	18.7	136.5	b	82.8	10.4	95.4	a	94.5	21.8	127.5	ab
	"	5–15	78.0	9.7	87.5		93.9	11.0	101.8		74.5	17.2	87.8		74.3	19.5	94.3	
DOC: TDN	–	0–5	10.7	2.6	15.3		11.2	1.3	13.3		14.5	2.6	19.0		12.8	3.8	16.1	
	–	5–15	13.1	1.3	14.8		13.5	3.0	17.3		10.1	3.4	14.7		14.5	3.1	17.6	
NO_3-N: TDN	–	0–5	0.21	0.04	0.28	ab	0.15	0.04	0.22	a	0.24	0.04	0.30	b	0.18	0.06	0.26	ab
	–	5–15	0.19	0.03	0.25		0.14	0.05	0.19		0.11	0.10	0.26		0.22	0.07	0.32	

Table 4
Extractable inorganic soil N and net N transformations 10 years after establishment of rehabilitation treatments at Church's Park fire, Colorado. Data are means, standard deviation (SD) and maximum (n= 6). Letters denote significant differences among treatment means at the α = 0.05 level.

			Control				Biochar				Mulch				Biochar + Mulch			
		Depth (cm)	Mean	SD	Max		Mean	SD	Max		Mean	SD	Max		Mean	SD	Max	
NH_4-N	mg N kg^{-1}	0–5	1.2	0.2	1.4		2.1	1.0	4.3		1.5	0.9	3.2		1.2	0.2	1.6	
	"	5–15	0.8	0.3	1.4	b	0.3	0.1	0.4	a	0.4	0.1	0.5	a	0.4	0.1	0.6	a
NO_3-N	"	0–5	0.3	0.2	0.5	a	1.1	0.3	1.4	c	0.7	0.2	1.0	b	1.0	0.2	1.5	bc
	"	5–15	0.1	0.1	0.2		0.2	0.1	0.3		0.1	0.1	0.2		0.1	0.1	0.2	
Sum of Inorganic N	"	0–5	1.5	0.3	2.0	a	3.1	1.1	5.3	b	2.2	0.8	3.7	ab	2.2	0.2	2.5	ab
(NH_4-N +NO_3-N)	"	5–15	0.9	0.3	1.4	b	0.4	0.1	0.6	a	0.5	0.2	0.7	a	0.5	0.2	0.7	a
NO_3-N: Sum N	%	0–5	21.5	7.9	28.0	a	35.5	9.7	46.0	ab	35.2	16.7	63.0	ab	45.6	8.0	60.0	b
	"	5–15	8.5	8.9	25.0	a	36.9	21.2	60.0	b	19.2	11.0	30.0	ab	23.5	11.6	37.0	ab
Net Mineralization	mg N kg^{-1} mo^{-1}	0–5	0.3	0.5	1.1		−0.8	1.1	1.3		−0.5	0.9	0.7		−0.3	0.4	0.3	
	"	5–15	0.8	0.3	1.4		0.9	0.3	1.3		0.9	0.4	1.4		0.7	0.4	1.3	
Net Nitrification	"	0–5	0.9	0.4	1.4		0.4	0.6	1.2		0.4	0.6	0.9		0.3	0.3	0.7	
	"	5–15	0.9	0.3	1.3	b	0.5	0.3	0.8	a	0.9	0.3	1.3	b	0.5	0.2	0.7	a

biochar + mulch treatment at 5–15 cm depth (Table 5). Concentrations of Ca and Mg were also elevated when mulch was applied alone. Overall, the highest mean concentrations of both Ca and PO_4 occurred in the surface soil layer of the biochar-treated plots. Concentrations of cations and anions generally decreased with depth except for SO_4 and PO_4 which increased with depth in the mulch and control treatments.

3.2. Understory plant cover and composition

Understory cover was 44 % overall in 2023 and was split relatively equally among graminoids (16 %), forbs (15 %) and shrubs (13 %). Sedges (primarily *Carex rossii* Boott.and *C. geyri* Boott.), the most abundant graminoid taxa, were present in 75 % of the sample plots and had 9 % cover (Table 6). *Oreochrysum parryi* (A. Gray) Rydb., Parry's goldenrod, was the most common forb species and was found in 69 % of the plots, with 5 % cover. The low-statured, ericaceous shrub *Vaccinium scoparium* Leiberg ex Coville represented 7 % of understory cover and occurred in 65 % of the sample plots.

Biochar and mulch amendments influenced cover and occurrence of specific taxa but not total understory cover. In the four study blocks where shrubs occurred, the individual and combined biochar treatments had more than double the total shrub cover compared to untreated plots (Fig. 2). Specifically, cover of the two most abundant shrubs (*V. scoparium* and *Rosa woodsii* Lindl.) were 2- and 4.6-times higher for biochar-amended plots than unamended plots, respectively ($p < 0.1$). Conversely, mulching reduced Parry's goldenrod cover relative to the untreated plots (Fig. 3). Its cover was 85 % lower in the combined biochar and mulch treatment compared to controls; mulch alone decreased it marginally. Graminoid cover was unaffected by the treatments.

3.3. Soil microbial communities

No significant differences in Shannon's H alpha diversity (a combination of richness and evenness) were observed for fungal communities in either the 0–5 cm or 5–15 cm depths across the rehabilitation treatments (Fig. 4A, B). In contrast, the Shannon's H for the 0–5 cm soil bacterial communities in the combined biochar + mulch treatment was significantly higher than biochar, mulch, and control treatments (Fig. 4C). In the deeper 5–15 cm samples, no significant differences in Shannon's H alpha diversity were observed across treatment conditions (Fig. 4D).

Beta diversity measurements revealed significant differences in the bacterial community composition across treatments and soil depth (Fig. 4E). Per ADONIS pairwise comparisons, biochar-treated surface soils hosted significantly different bacterial communities than either the mulch biochar/mulch, or control soils. No significant treatment differences were observed between bacterial communities in the deeper soils. Similarly, no significant differences were observed between depth or treatment in the fungal communities. To understand the discriminant features driving community differences between treatments, MaAsLin2 was used to identify specific taxa that were consistently enriched in biochar-amended soils relative to those from the other treatments (mulch, biochar + mulch). In particular, Chthoniobacteraceae (phyla Verrucomicrobiota), and other taxa within the orders Rhizobiales, Solirubrobacterales, and Chloroflexales were all discriminant for biochar-treated 0–5 cm soils.

4. Discussion

4.1. Ecosystem recovery after the Church's Park fire

After a period of rapid change the first years after the fire, changes in the soil environment and understory plant community in the Church's Park fire scar have begun to slow. Plant cover increased from near 0 % in 2010 to 14 % in 2013 then to 38 % in 2016 (Rhoades et al., 2017). Over

Table 5
Water soluble soil cation and anion concentrations 10 years after establishment of rehabilitation treatments at Church's Park fire, Colorado. Data are means, standard deviation (SD) and maximum (n= 6). Letters denote significant differences among treatment means at the α = 0.05 level.

			Control				Biochar				Mulch				Biochar + Mulch			
		Depth (cm)	Mean	SD	Max		Mean	SD	Max		Mean	SD	Max		Mean	SD	Max	
K	mg L^{-1}	0–5	20.8	5.5	29.4		26.2	6.0	34.6		23.1	10.7	44.1		32.5	6.7	42.9	
	"	5–15	17.4	4.4	24.7	ab	20.5	6.8	31.8	ab	13.1	3.6	18.1	a	22.6	4.0	28.2	b
Ca	"	0–5	12.3	1.8	14.8	ab	16.8	3.6	22.4	c	10.4	2.9	14.0	a	15.2	2.1	18.1	bc
	"	5–15	7.8	3.0	11.1	a	9.9	1.5	11.7	a	13.9	3.8	21.3	b	14.6	2.0	17.9	b
Mg	"	0–5	2.9	0.4	3.2		3.5	0.2	3.8		4.0	2.4	8.5		3.4	0.8	4.9	
	"	5–15	2.6	0.2	2.8	ab	2.1	0.6	2.6	a	3.5	1.2	5.2	b	3.3	0.1	3.5	b
Na	"	0–5	3.5	0.8	4.6		3.1	0.6	3.9		3.0	0.7	4.2		3.6	1.3	5.5	
	"	5–15	3.6	0.9	5.4		3.5	0.6	4.2		3.1	0.9	4.8		3.1	0.8	4.3	
SO_4	"	0–5	6.3	2.1	10.1		6.8	2.9	11.9		10.4	4.8	19.0		10.6	2.2	12.9	
	"	5–15	6.8	1.9	8.8	a	6.4	1.8	8.4	a	15.0	3.8	19.1	b	5.7	1.4	7.5	a
PO_4	"	0–5	7.2	4.8	12.1	a	14.4	2.3	17.1	b	13.9	4.2	21.1	b	10.0	4.3	16.4	ab
	"	5–15	12.1	1.7	14.1	c	2.9	1.4	5.0	a	4.3	1.0	5.8	a	9.9	1.1	11.3	b

the past eight years, plant cover has increased only slightly (i.e., 40 % in 2023). Conversely, bare soil cover was nearly 100 % in the high severity patches after the fire, then decreased to 53 % by 2013 and has changed little since then (i.e., 48 % in 2023). Overall, O-horizon cover increased from 0 % to 39 % since the fire. In 2013, when the rehabilitation treatments were installed, wood mulch and biochar cover were both 100 %. Subsequently, mulch cover declined to 76 % by 2016 and 50 % in 2023. Biochar dropped to 60 % in 2016, then to 17 % at the time of the 2023 resampling.

During the initial post-fire period, understory plant cover was dominated by forbs (29 %) with lower but relatively equal amounts of graminoids (5 %) and shrubs (4 %) (Rhoades et al., 2017). Representation by forbs has declined since the fire, and by 2023 graminoid, forb and shrub cover were all similar. Fireweed (*C. angustifolium*), a wind-dispersed forb associated with post-fire environments, occurred in 94 % of the study plots in 2016. In 2023, it was found in 21 % of plots and had < 1 % cover. By 2023, *O. parryi* had replaced fireweed as the most abundant forb. The presence and cover of the two most common graminoids (*Carex* spp. and *Elymus glaucus* Buckley) and the most common shrub (*V. scoparium*) all increased between 2016 and 2023. Noxious plants were absent from the study plots, though forb and grass species locally common to disturbed and open habitats (e.g., *Achillea millefolium* L. and *Phleum pratense* L.) have increased since 2016 (Table 6). In general, the composition of the existing understory plant community reflects the high-light environment of the burn scar. Such conditions may not favor long-term persistence of the shade-tolerant shrub, *V. scoparium,* that prefers closed-canopy forests in the area (Fornwalt et al., 2018).

Conifers remain sparse in the Church's Park burn scar and were completely absent from our study plots in 2023. Pine seedling recruits were absent the first four post-fire growing seasons (Rhoades et al., 2018), and their low initial recruitment was attributed mainly to high cone consumption from high severity crown fire, though declining seed viability in serotinous cones of bark beetle-killed trees would also have limited seed inputs (Rhoades et al., 2022). Scarce post-fire tree regeneration has been observed in recent years across the western United States (Coop et al., 2016; Stevens-Rumann and Morgan, 2019), raising concerns about future resilience of coniferous forests and shifting species dominance (Andrus et al., 2021; Turner and Seidl, 2023).

The general interplay between soil biotic and abiotic conditions and post-fire vegetation ecosystem recovery are well-appreciated, though the specific implications for the Church's Park fire scar are less certain. Research conducted at Church's Park and other nearby fires has found significant reductions in soil microbial biomass and diversity and ectomycorrhizal fungi (Nelson et al., 2022; Caiafa et al., 2023), with potentially cascading effects on soil biogeochemical cycling and plant establishment (Nelson et al., 2024). A decade after the Church's Park fire, soils that experienced high severity burning fire had elevated inorganic and organic N and C pools compared to unburned forests (Nelson et al., 2024). Though there was no general loss of soil fertility, the depressed levels of soil ectomycorrhiza, crucial symbionts for lodgepole pine, may represent a significant barrier to post-fire tree regeneration (Caiafa et al., 2023).

4.2. Treatment effectiveness

4.2.1. Wood Mulch

Wood mulch and other organic amendments can supply C and stimulate soil N immobilization (Perry et al., 2010; Homyak et al., 2008). Such treatments have potential to limit N leaching, mitigate post-fire N losses to streams (Richardson, 2024) and disfavor ruderal plants (Reever-Morghan and Seastedt, 2002; Perry et al., 2010). For two consecutive years after application in the Church's Park burn scar, wood mulch decreased resin-exchangeable and KCl-extractable NO_3-N by 80 % and 75 % compared to untreated, burned soils (Rhoades et al., 2017). Since the effect of fresh mulch on soil N cycling is greater than

Table 6
Frequency and cover of the select understory species after the 2010 Church's Park fire. Data are means combined across rehabilitation treatments sampled within 1 m^2 quadrats (n = 48).

Scientific Name	Common Name	2016 Frequency	2016 Cover	2023 Frequency	2023 Cover
		%			
Graminoids					
Carex sp.	Unknown sedges	67	6	75	9
Elymus glaucus Buckley	Blue wildrye	17	1	50	4
Phleum pratense L.	Timothy	0	0	13	<1
Bromus marginatus Nees ex Steud.	Mountain brome	10	<1	0	0
Bromus inermis Leyss.	Smooth brome	8	<1		0
Forbs					
Oreochrysum parryi (A. Gray) Rydb.	Parry's goldenrod	42	4	69	5
Gayophytum diffusum Torr. & A. Gray	Spreading groundsmoke	69	3	35	2
Lathyrus laetivirens Greene ex Rydb.	Aspen pea	27	3	33	3
Achillea millefolium L.	Yarrow	13	0	25	<1
Phacelia heterophylla Pursh.	Varileaf phacelia	35	2	23	<1
Chamerion angustifolium (L.) Holub.	Fireweed	94	10	21	<1
Shrubs					
Vaccinium scoparium Leiberg ex Coville	Grouse whortleberry	58	4	65	7
Rosa woodsii Lindl.	Wood's rose	6	<1	23	3
Mahonia repens (Lindl.) G. Don	Creeping Oregon grape	13	13	6	<1
Ceanothus velutinus Douglas ex Hook.	Snowbrush	4	<1	6	2
Shepherdia canadensis (L.) Nutt.	Canada buffaloberry	0	0	4	3

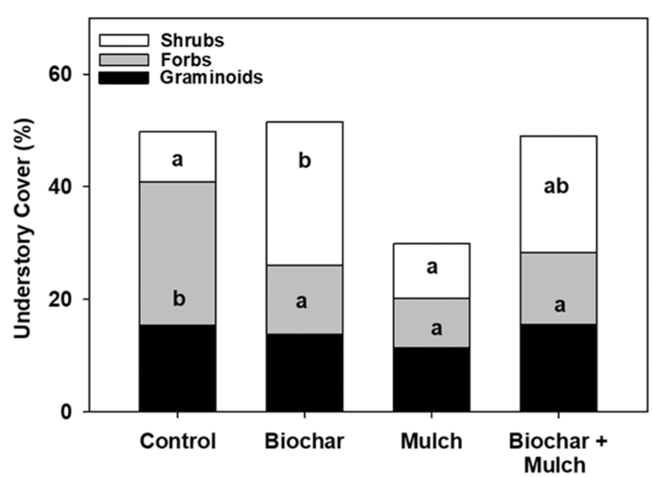

Fig. 2. Graminoid, forb, and shrub cover in the four study blocks where all three plant life forms occurred. Bars show mean cover from 1 m^2 quadrats with a gridded point-intercept method. Treatments were applied in 2012, 2 years after the 2010 Church's Park fire, Colorado, and resampled in 2023, 10 years after post-fire rehabilitation treatment. Within the forb and shrub groups, letters denote significant differences among Bonferroni adjusted treatments means at α = 0.05.

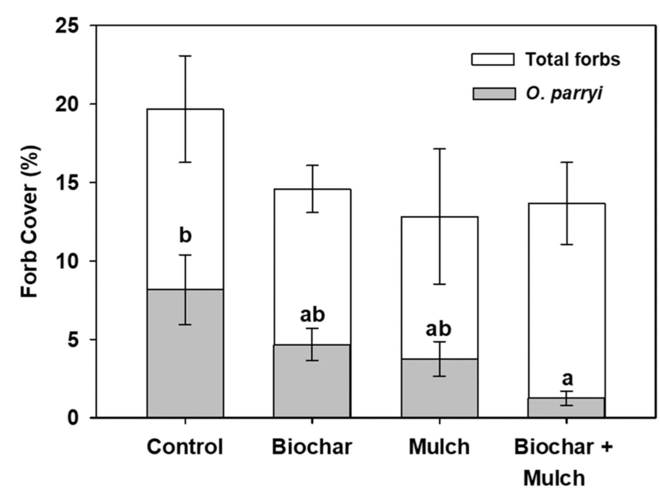

Fig. 3. Total forbs and Parry's Goldenrod (*Oreochrysum parryi*) cover in August 2023, 10 years after post-fire rehabilitation treatment establishment at the Church's Park fire, Colorado. Bars show means and standard error for six study blocks. Letters denote significant differences among Bonferroni adjusted treatments means at α = 0.05.

that of older material (Rhoades et al., 2012), it was uncertain whether effects would persist for a decade. In 2023, we found that mulch reduced water-soluble NO_3-N (Table 3) and KCl-extractable NH_4-N (Table 4), though other forms of N were higher or unchanged. Mulching also had no lasting impact on total C, soil C:N (Table 2), or DOC (Table 3), and no effect on net mineralization or nitrification (Table 4). There were mixed impacts on PO_4, Ca and Mg, but overall, a decade after treatment, mulch had minimal impacts on soil nutrients and chemistry.

Like early research on these plots, in 2023 we found higher soil moisture in mulched plots (Fig. 1), even though its cover had declined by half (Table 1). Though we did not specifically evaluate mulch losses, we observed that downslope movement was more prevalent than integration into the mineral soil profile. Surface mulching is known to have more short-term, positive effects on soil and plant responses compared to incorporated material (Fehmi et al., 2020). Thus, it is uncertain the extent to which the prolonged effect on soils relates to residual surface mulch versus material that has been integrated into the mineral soil.

The influence of mulch on understory plant communities is complex. Though mulch commonly enhances soil moisture (Santana et al., 2014; Jonas et al., 2019; Fehmi et al., 2020), it can also form a barrier to plant establishment (Facelli and Pickett, 1991). Since post-fire understory plant cover and composition responses often reflect soil moisture patterns (Andrade et al., 2020), we expected differences between mulched and unmulched plots. We found that mulch had no general effect on overall graminoid, forb or shrub cover, but that it altered the abundance of a least one dominant species, *O. parryi* (Fig. 3). It is unclear, if inhabitation of *O. parryi* is due to physical presence of the mulch layer, loss of bare soil cover, altered soil N, moisture, or other factors.

4.2.2. Biochar

Biochar is known to form stable compounds that are estimated to

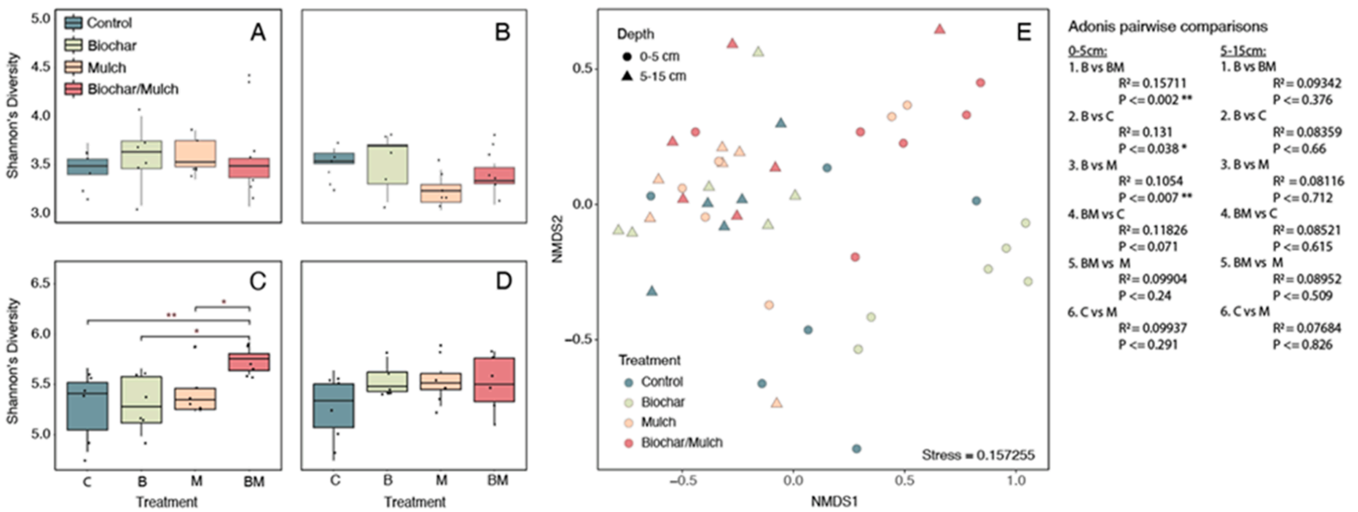

Fig. 4. Boxplots of Shannon's H alpha diversity (richness and evenness) across treatments (control, biochar, mulch, and biochar/mulch) for (A) fungal ITS 0–5 cm depth mineral soils, (B) fungal ITS 5–15 cm depth mineral soils, (C) bacterial 16S rRNA 0–5 cm mineral soils, and (D) bacterial 16S rRNA 5–15 cm mineral soils. Brackets represent Wilcoxon signed-rank tests with stars denoting significant differences. *: $p <= 0.05$ **: $p <= 0.01$ ***: $p <= 0.001$ ****: $p <= 0.0001$. Panel (E) shows a non-metric multidimensional scaling (NMDS) ordination plot using Bray-Curtis dissimilarity matrices for bacteria (16S rRNA gene). Point color denotes treatment and point shape denotes depth (0–5 cm or 5–15 cm). Panel E includes pairwise adonis statistics to assess differences between treatments, separated by depth.

reside in soils for millennia (Kuzyakov et al., 2014), often increasing soil total C (Santín et al., 2017) and pH. Its high surface area and reactivity can also retain soil N (Hagemann et al., 2017; Borchard et al., 2019; Wang et al., 2021). In 2013, the biochar treatment added 17.4 Mg C ha^{-1} and 0.1 Mg N ha^{-1} in the pH 9.4 material. Like other studies (Biederman and Harpole, 2012; Wang et al., 2021), biochar added shortly after the Church's Park fire increased soil pH, soluble NO_3-N, PO_4, K, and Ca (Rhoades et al., 2017) though it had no effect on total soil C or N.

Surface cover of biochar was greatly reduced in 2023 (Table 1), likely due to down-slope and down-profile movement (Major et al., 2010), though the treatment continued to impact soil and plant conditions. As observed earlier, biochar added alone did not alter total soil C or N (Table 2). However, it elevated soil C:N (Table 2), leachate DOC, TDN, and DON (Table 3) and extractable NO_3-N (Table 4). Soil pH was 0.4 units lower (Table 2) and net nitrification was roughly half that measured in untreated, burned soils in the lower depth of biochar-amended soils (Table 4). In contrast to our findings, charcoal addition to unburned ponderosa pine forest soils stimulated nitrification, potentially by tying up phenolic compounds that can inhibit nitrifier activity (DeLuca et al., 2006). The reduced nitrification we observed may have resulted higher microbial metabolism and N demand fueled by higher soluble C (Perry et al., 2010), inhibition of nitrifying bacteria at higher pH (Paul and Clark, 1996), or other factors. Beta diversity measurements indicated that bacterial communities in the surface soil layer of biochar-amended plots were distinct from the other treatments. Driving these differences in the biochar-amended surface soils, we measured enrichment of putative N-fixing bacteria associated with the order Rhizobiales that could have the potential to elevate plant-available soil N in these soils. We also detected enrichment of taxa affiliated with the order Chthoniobacterales, in the phyla Verrucomicrobiota, which comprise a significant fraction of soil bacteria in a range of ecosystems (Bergmann et al., 2011; Brewer et al., 2016). Given that bacteria within the Verrucomicrobiota are frequently depleted following wildfire (Nelson et al., 2022), their enrichment in these surface soils may be an indicator of microbiome recovery.

Like patterns documented the first three years after the treatments were established (Rhoades et al., 2017), in 2023 we found that biochar had an influence on soil moisture that fell between untreated and mulched soils (Fig. 1). Biochar has been shown to increase soil moisture, especially in coarse-textured soils (Fehmi et al., 2020; Razzaghi et al., 2020). We found cover of *V. scoparium,* a shrub that dominates the understory of closed-canopy conifer forests in the region (Fornwalt et al., 2018), was twice as high in biochar-amended compared to untreated plots (Fig. 2). The higher soil moisture in those plots may have contributed to this response, but *V. scoparium* and other common, local ericaceous shrubs are also favored by lower soil pH (Korcak, 1988). A decade after application, we found that biochar was influencing soil acidity, soluble C and N and shrub cover.

4.2.3. *Biochar + mulch*

As documented during the earlier phase of this study, the combination of biochar and wood mulch had the greatest effect on several soil and plant responses (Tables 2, 5 and Fig. 3). As seen elsewhere, this pattern indicates that the benefits of biochar may be optimized when combined with nutrients, microbial inoculants, or organic amendments (Hagemann et al., 2017; Joseph et al., 2021). Biochar characteristics and performance are linked to feedstock composition, pyrolysis conditions (McBeath et al., 2015), application rate and technique, and biochar composition must be matched to soil type, site limitations (Ippolito et al., 2020; Kerner et al., 2023) and management or restoration objectives (Heneghan et al., 2008; Thomas and Gale, 2015).

The combined treatment significantly increased total soil C and C:N in both sampled depths, relative to control soils or either biochar or mulch applied alone (Table 2). The extractable cations Ca, K, Mg were all highest in the combined treatment (Table 5). Unlike during the initial response, the combined treatment did not influence any soil N pool (i.e., total or inorganic N) or process (net mineralization or nitrification) more than biochar alone. Extractable NO_3-N was higher, but net nitrification was lower in the individual and combined biochar treatments (Table 4). Mulch cover may protect biochar from wind and water erosion, and the enhanced soil moisture may favor plant root production, the soil microbiome and soil C storage (Weng et al., 2017; Kerner et al., 2023), though the specific mechanisms responsible for the additive soil responses are unclear.

4.3. Management implications and conclusions

Prior to the mountain pine beetle outbreak and the Church's Park fire, the study site was dominated by mature, closed-canopy lodgepole pine forest. After 13 years, there is little evidence that the ecosystem will return to a similar pre-disturbance composition or structure within coming decades. Tree response to the organic amendments was not a focus of this plot-scale study, but some inferences may be relevant for reforestation efforts (Sarauer et al., 2019). For example, the independent and combined biochar treatments more than doubled shrub cover (Fig. 2), likely due to elevated soil moisture, potentially in combination with changes in soil C and nutrients. Biochar added to planting holes is known to increase post-fire conifer seedlings survival (Marsh et al., 2023) and thus may increase reforestation success. Similarly, organic amendments such as wood mulch have potential benefit post-fire seeding of understory species (Shaw et al., 2020). However, as observed after the Church's Park fire, the challenges of designing amendments that favor seed-based restoration will require species-specific information from well-replicated, long-term studies (Larson et al., 2023).

There is little known about the long-term effects of post-fire rehabilitation treatments. We found that after a decade, both mulch and biochar treatments were not only visible, but that they had persistent effects on soil properties and plant and microbial communities. The primary effect of wood mulch was to elevate soil moisture, whereas biochar increased total soil C, DOC and C:N and reduced net nitrification. Mulch dramatically reduced cover of the most common forb (*O. parryi*) and biochar doubled cover of the dominant shrub (*V. scoparium*). The combination of biochar and mulch had additive effects on several soil and plant responses. In general, the treatments increased the richness and evenness of the soil bacterial communities (as measured by Shannon's H') relative to control plots. The higher microbial diversity we observed has previously been associated with nutrient cycling processes that are critical for post-fire plant recovery (Tilman et al., 2014; Wagg et al., 2019). Furthermore, the increased soil C concentrations associated with the mulch + biochar treatment likely had other beneficial microbial outcomes; for example, other studies have found a positive relationship between soil C content and microbial biomass (Bastida et al., 2021). Overall, our long-term findings suggest that these organic amendments may contribute to post-fire soil rehabilitation and revegetation efforts and provide worthwhile options for managers confronting more frequent, severe and compound disturbances.

CRediT authorship contribution statement

Timothy S. Fegel: Writing – review & editing, Methodology, Investigation. **David M. Barnard:** Writing – review & editing, Supervision, Methodology, Investigation. **Sophia Kaiser:** Writing – review & editing, Writing – original draft, Investigation. **Adam L. Mahood:** Investigation. **Kya Sparks:** Investigation. **Kaela K. Amundson:** Investigation. **Michael J. Wilkins:** Writing – review & editing, Supervision, Resources, Investigation. **Charles C. Rhoades:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.foreco.2024.122359.

Data Availability

Data will be made available on request.

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