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Indirect effects of soil amendments on plant traits and the microbiome in post-wildfire forest recovery

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ABSTRACT

As wildfires intensify across the western United States, understanding long-term ecosystem recovery is increasingly critical. Post-fire soil amendments, such as woody mulch or biochar, are commonly used to stabilize soils and promote vegetation recovery, yet their effects on plant functional strategies and plant–microbe interactions remain poorly understood. Thirteen years after a high-severity wildfire in Colorado, we evaluated the impacts of these treatments on soil properties, microbial communities, and plant functional traits, including plant height, specific leaf area (SLA), and leaf dry matter content (LDMC). While statistical means comparisons showed limited treatment effects on vegetation composition or plant traits, random forest and exploratory mediation models revealed complex, non-linear, and indirect relationships among soil chemistry, microbial community composition, and plant responses. Notably, microbial community shifts and soil nutrient changes, especially in nitrogen form, emerged as key drivers of plant trait variation. *Vaccinium scoparium* responded more strongly to NH_4^+ and ectomycorrhizal fungi, while *Oreochrysum parryi* was associated with NO_3^- and bacterial/archaeal diversity. Biochar increased soil carbon and microbial diversity, whereas mulch enhanced soil moisture and reduced NO_3^- availability, leading to contrasting effects on microbial and plant responses. These findings demonstrate that post-fire soil amendments can have meaningful yet indirect impacts on plant resource use strategies and microbial dynamics, which may not be captured using conventional analyses. Our results highlight the value of trait-based approaches and integrative modeling for guiding restoration strategies aimed at enhancing ecosystem function and resilience in fire-affected landscapes.

1. Introduction

Wildfires are becoming more frequent and severe across western North America, threatening forest resilience, soil stability, and water resources (Abatzoglou and Williams, 2016; Barnard et al., 2023; Kampf et al., 2022). High-severity fires alter vegetation structure and disrupt ecosystem services by transforming soil physical, chemical, and microbial properties (Caiafa et al., 2023; Nelson et al., 2022). While many forests in this region have evolved with stand-replacing fires, increasing fire intensity, compounded by warming and aridity, is now driving regeneration failures and ecosystem state shifts (Harvey et al., 2016; Roccaforte et al., 2012; Rother et al., 2015; Stevens-Rumann and Morgan, 2019). Although restoration treatments such as soil organic amendments are widely applied to promote recovery, we still lack a mechanistic understanding of how these treatments affect plant functional strategies and plant–microbe interactions over the long term. Therefore, a trait-based framework that links plant strategies to post-fire resource availability is needed to improve predictions of recovery and guide effective restoration (Aubin et al., 2024; Suding, 2011).

One key concern after wildfire is the alteration of soil properties and nutrient availability, which can limit vegetation recovery (Bormann et al., 2008; Certini, 2005; Homann et al., 2011). Fires alter soil chemistry by leaving behind nutrient-rich ash prone to erosion and nutrient leching (Ebel, 2012; Santín et al., 2015; Wan et al., 2001). High soil

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temperatures during fire also reduce living microbial biomass, disrupting nutrient cycling during early recovery (Dove et al., 2020; Nelson et al., 2022; Pressler et al., 2019). These microbial losses can alter the abundance of key functional groups such as nitrifiers and ectomycorrhizal fungi (EMF) that are critical for nutrient retention and plant symbioses, thereby constraining vegetation recovery (Caiafa et al., 2023; Nelson et al., 2024a). Restoration treatments such as mulch and biochar are commonly applied after high-severity fires to reduce soil erosion (Prats et al., 2016; Robichaud et al., 2017). They can also increase vegetation recovery, soil fertility, and soil moisture (Fornwalt et al., 2017; Jonas et al., 2019; Kaiser et al., 2025; Rhoades et al., 2017). Mulch increases surface roughness, enhancing infiltration and reducing nutrient loss, while biochar's high surface area helps retain water and nutrients (Bautista et al., 2009; Rhoades et al., 2017; Rhoades et al., 2025). Together, these amendments offer the potential to foster post-fire ecosystem recovery by improving belowground conditions critical for plant establishment and growth.

Many studies on post-fire organic soil amendments in the western United States have focused on vegetation composition and structure (e.g., Bontrager et al., 2019; Fornwalt et al., 2017; Jonas et al., 2019), with little attention given to plant functional strategies. However, there is increasing interest in trait-based approaches to better understand functional plant responses relevant to restoration and ecosystem recovery (Aubin et al., 2024). Plant functional traits, such as plant height, specific leaf area (SLA), and leaf dry matter content (LDMC), integrate plant allocation and stress responses, and can help predict fitness and community composition across environmental gradients (Brudvig and Mabry, 2008; McGill et al., 2006). Specific leaf area typically increases with resource availability, while LDMC tends to rise under stress, indicating conservative growth strategies (Niklas et al., 2023; Westoby and Wright, 2006). These traits often vary within and among species depending on environmental context and life-history strategy, such as resprouting versus seeding after fire (Anacker et al., 2011; Blumenthal et al., 2020; Perez-Harguindeguy et al., 2016). Understanding how post-fire amendments influence trait expression across species and landscapes may reveal more nuanced effects on recovery than community composition alone.

In 2010, the Church's Park fire burned 200 ha of lodgepole pine (*Pinus contorta*) forest northwest of Fraser, CO. Lodgepole pine is a key forest species across western North America with a broad but declining distribution (Stanke et al., 2021). In 2014 research plots were established to investigate the impacts of organic soil amendments (mulch, biochar, mulch + biochar) on soil moisture and nutrients (Rhoades et al., 2017). The goal of the current study was to revisit these sites thirteen years after the fire and nine years after soil amendment applications to assess longer-term effects on soil moisture and nutrients, vegetation and microbial community, and plant functional traits across a range of landscape factors. To evaluate plant trait responses, we focused on two abundant species with contrasting life-history and regeneration strategies: Parry's goldenrod (*Oreochrysum parryi*) a basal-sprouting perennial forb which reestablishes via seed after fire, and grouse whortleberry (*Vaccinium scoparium*) a deciduous shrub which resprouts from rhizomes after fire.

Our objective was to assess how organic amendments and landscape variation influence plant communities, microbial functional groups, and plant traits. We hypothesized that trait and microbial responses would not manifest directly from treatment categories but would emerge through non-linear and indirect pathways mediated by changes in soil nutrients, moisture, and microbial composition. To test this, we applied a combination of random forest models to capture non-linear relationships and exploratory mediation (EM) analysis to disentangle mediators and direct and indirect effects. Specifically, we asked: (1) Do plant traits and community composition differ among treatments? (2) Which treatment, soil, or landscape factors are most strongly associated with plant trait and microbial variation? (3) Do treatment and landscape effects operate indirectly through changes in soil and microbial mediators?

2. Methods

2.1. Study site and statistical design

For this study, we revisited experimental plots within the Church's Park burn perimeter established in 2014 (Rhoades et al., 2017). The Church's Park fire burned 200 ha from 2438 to 3200 m elevation. 47 % of the total area was burned at moderate to high severity and 53 % at low severity (USFS, 2010). This area of Colorado receives on average 700 mm of precipitation annually, primarily as snow during the winter and spring, with sporadic convective rainstorms during the monsoon season in late summer (NRCS, 2013). Soils at the research sites are characterized by gravelly, sandy-loam Alfisols from alluvium and colluvium of granitic gneiss and schist parent materials (Alstatt and Miles, 1983). Prior to the fire, forest overstory was primarily lodgepole pine with scattered stands of quaking aspen (*Populus tremuloides*) (Huckaby and Moir, 1998). In the mid- to late-2000s, before the fire, an infestation of mountain pine bark beetles (*Dendroctonus ponderosae*) killed > 85 % of the overstory trees (Chapman et al., 2012).

A full description of the study design to test soil amendment effects is available in Rhoades et al. (2017). Briefly, organic treatment impacts were quantified on soil chemistry, nutrients, and physical properties and re-establishment of vegetation in areas that burned at high severity. The study design consisted of six blocks, each with four 5 × 5 m plots within a small area of the burn perimeter (Fig. 1**c-e**). The block locations were selected to include areas that had similar forest composition before the fire based on the following criteria: (1) > 75 % lodgepole pine with (2) > 85 % beetle mortality, (3) slope angles between 5 % and 15 %, (4) south-facing aspect. Within each block, plots were randomly assigned to one of four treatments: mulch, biochar, mulch + biochar, and control. The biochar used in this study was created through pyrolysis of local lodgepole pine chips at 400–550 degrees C and then applied at 20 t ha^{-1} and raked into the top 2–3 cm of mineral soil (Fig. 1c). The mulch was also chipped from local lodgepole pine and applied to create a 2 cm deep layer on the soil surface (equivalent to 37 t ha^{-1}) (Fig. 1d). In the combined treatment, mulch was applied on top of the biochar, with similar application methods and rates as for the individual mulch and biochar treatments (Fig. 1e). A trench was dug on the uphill side of each block to reroute surface runoff to not affect cover of the organic treatments.

2.2. Field data collection

2.2.1. Soil moisture, nutrients, and chemistry

We measured soil volumetric water content (VWC) monthly from June to September in each plot in the upper 15 cm of soil using a handheld, time-domain reflectometry probe (HydroSense II, Campbell Scientific, Logan, UT). In each plot at every sampling date, five readings were collected at intervals equally spaced on a line crossing the middle of each plot. To omit influences from surface litter and mulch, all material was carefully moved aside prior to collecting VWC measurements. Full VWC data are reported in Kaiser et al. (2025). For this study, we focused only on June VWC measurements because field observations indicated that leaves for both species had fully expanded by then and thus later VWC measurements would not be indicative of leaf development.

Soil samples were collected from each plot to characterize soil physical, chemical, and nutrient characteristics in June of 2023. Prior to soil sampling, any organic material, remnant mulch, and organic horizon was removed, and underlying mineral soil was collected at depths of 0–5 cm and 5–15 cm twice in each plot using a 6.4 cm diameter bulb corer that was sterilized between samples. The two samples from each depth were then combined. Roots and rocks were removed from samples in a sterile lab setting. One subsample was dried, sieved, and ground for

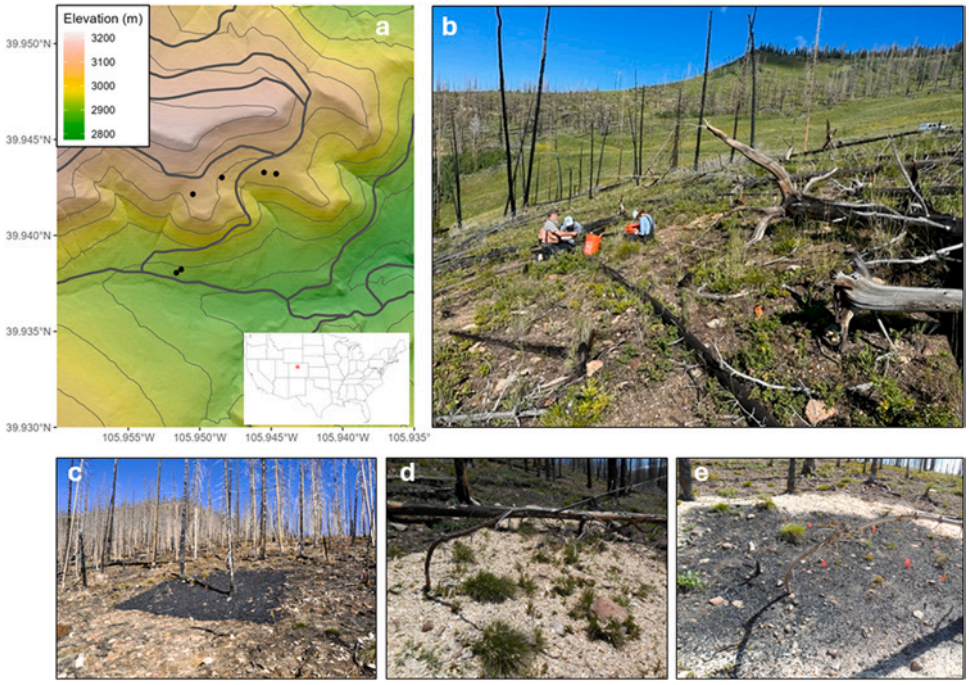

Fig. 1. Site map of experimental plots (a), site at 12 years post-fire showing minimal forest recovery (b), examples of treatments immediately after amendment application for biochar (c), mulch (d), and mulch + biochar (e). In panel a, grey lines represent dirt roads, black points are the study blocks, grey contour lines represent elevation increments of 50 m. For panel b note this image was take in June 2023, 13 years after the Chruch's Park fire, panels c-e were taken immediately after amendment application in 2014. Photo credits: D.M. Barnard (b) and C.C. Rhoades (c-e).

total C and N analysis via dry combustion and infrared detection (CN 802, Velp Scientifica, Deer Park, NY). Soil pH was assessed using a 1:1 soil-to-water slurry after one hour of agitation (Thomas, 1996; inMotion Pro, Mettler Toledo, Greifensee, Switzerland). Another subsample was taken to quantify water-soluble ions, nutrients, and C by shaking the sieved soils with deionized water (> 18 MΩ), filtering, and analyzing for dissolved organic C (DOC) and total dissolved N (TDN) after purging mineral carbon with 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 with an AS19A column for anions and CS12A column for cations (Integrion, Thermo Fisher, Waltham, MA). Detection limits for water-extractable ions were < 0.01 mg L^{-1} for Na^+, K^+, Na^+, Ca^{+2}, Mg^{+2}, NH_4^+-N, NO_3^--N, SO_4^-, and PO_4^+. Dissolved inorganic N (DIN) is then defined as the sum of NO_3^--N and NH_4^+-N. Soil texture was measured by standard methods using a Bouyoucos hydrometer (Gee, 1986).

2.2.2. Microbial sampling

Soil samples were collected to characterize microbial community and functional groups using the same protocol described above for soil nutrient and chemistry analyses. Samples were placed in sterile Whirl-pak bags and stored at 4 °C during transport before being placed in a −80 °C freezer until processing. Microbial DNA was extracted using the Zymo Research Quick-DNA Fecal/Soil Microbe kit according to the manufacturer's instructions. Archaeal/bacterial communities were characterized by sequencing the V4 region of the 16S rRNA gene (Apprill et al., 2015; Parada et al., 2016) using the Earth Microbiome Project (EMP) suggested primers of 515 F (5′-GTGYCAGCMGCCGCGGTAA-3′) and 806 R (5′-GGACTACNVGGGTWTCTAAT-3′) while fungal communities were profiled using the first internal transcribed spacer (ITS1) region with ITS1F (5′-CTTGGTCATTTAGAGGAAGTAA-3′) and ITS2 (5′GCTGCGTTCTTCATCGATGC-3′) primers (White et al., 1990). Sequencing was peformed on an Illumina MiSeq Platform with 251 bp paired-end sequencing chemistry at Microbial Community Sequencing Lab (University of Colorado Boulder). To process the reads, we used QIIME2 (2021.2) and discarded low-quality ITS reverse reads. Demultiplexed 16S and ITS samples were merged, filtered, denoised, and binned to create amplicon sequence variants (ASVs) with DADA2. The read counts for 16S rRNA ranged from 20,952 to 68,942, while ITS counts varied from 9875 to 206,218. Bacterial and archaeal ASVs were taxonomically classified using pre-trained SILVA (version 138: Quast et al., 2012; Robeson et al., 2021) classifiers, and fungal ASVs were classified with self-trained UNITE (version 9.0: Nilsson et al., 2019) database classifiers. Sequences not assigned to the appropriate kingdoms and ASVs classified as mitochondria or chloroplasts were discarded. The resulting reads were deposited in NCBI under BioProject PRJNA682830.

2.2.3. Plant community and trait sampling

In August 2023, we measured substrate and plant cover at peak herbaceous biomass. The cover of each species was measured within two, 1 m quadrats per 5 m plot (48 quadrats total) using a gridded point intercept method. We measured three plant functional traits, canopy maximum height (hereafter, 'height'), LDMC and SLA, for four individuals at each plot for two species that were abundant throughout the study area, *O. parryi*, a native perennial forb and *V. scoparium,* a native deciduous shrub (n = 96 per species). For each plant sampled, height was measured, and then the plant was clipped at ground level and placed in a pitcher of deionized water. The cut surface was immediately submerged, and the stem was cut again approximately 1 cm from the original cut with a sharp razor blade. While the cut was still submerged, the base of the stem was placed in a Falcon tube filled with deionized water. Plant samples were returned to the lab to rehydrate for 24 h. Then, fully hydrated leaves were clipped from the stem and weighed, scanned with a flatbed scanner at 600 dpi along with a red 2 × 2 cm square, dried in a drying oven at 70 degrees Celsius for 72 h, and then weighed again. Image processing software Image J (Schneider et al., 2012) was used to calculate leaf area. Each image was converted to greyscale, and individually thresholded until the leaves were fully

highlighted, using an intensity threshold between 150 and 190 relative intensity (unitless). A 2 × 2 cm square scanned with the leaves was used to set the scale for the leaf area in Image J. Total leaf area was then calculated in cm^2 by the software. LDMC and SLA were calculated as:

$$LDMC = \frac{Md}{Mw}_{*} \quad 1000 \tag{1}$$

$$SLA = \frac{Md}{LA} \tag{2}$$

Where *Md* is the oven-dried sample mass in mg, *Mw* is the rehydrated wet sample mass in g, and *LA* is the rehydrated leaf area in m^2.

2.3. Topographic data

Topographic attributes of each study block were calculated from a 10 m digital elevation model (DEM; Rabus et al., 2003). We calculated slope from the DEM using the *terra* R package (Hijmans et al., 2022). We calculated folded aspect (McCune and Keon, 2002) and topographic wetness index (TWI; Beven and Kirkby, 1979) using the *topomicro* R package (Mahood, 2024). Folded aspect is an index of how southwesterly a surface is, with low values being cold, northeast-facing aspects, and high values being closer to a warmer, southwest-facing aspect. Topographic wetness index is an indicator of how much water will drain to a given point and is calculated based on how much land area is upslope of that point.

2.4. Statistical analysis

Logistical constraints on study design and sampling produced a relatively small number of observations but many predictors. Approaches to analyzing and interpreting such datasets can become unwieldy using standard one-off approaches or possibly generate unstable results that may be statistically significant but misleading. To address these potential shortcomings, we used a multi-faceted approach to data analysis that included (1) analysis of variance, means testing, and linear regression to assess statistical differences among treatment groups, (2) ordinations to assess plant and microbial community composition and multivariate soil characteristics among treatments, (3) random forests to visualize non-linear univariate relationships between predictors and dependent variables, and (4) EM to identify variables that mediate the relationship between independent (treatment, landscape factors) and dependent variables (plant traits, microbial groups). All statistical analyses were done in R Core Team (2024).

2.4.1. Ordinations of microbial and plant community composition, and soil chemistry

To quantify how plant community composition responded to treatments, we performed a non-metric multidimensional scaling ordination (NMDS) (Minchin, 1987) on the species occurrence data averaged for each plot and used permutational multivariate analysis of variance (PERMANOVA) (Anderson and Santana-Garcon, 2015) to test the effect of sample year and treatment effects on community composition. To visualize how the treatments affected the microbial community composition, we performed an NMDS ordination on the microbial community matrix for both abundance and occurrence data in both sampling depths (0–5 and 5–15 cm). Finally, we ran a principal components analysis on all soil chemistry variables measured.

To complement the PERMANOVA analysis for treatment effects on the bacterial and fungal community composition, we performed a beta dispersion analysis to examine if variability within treatment groups drove significant differences in our ordinations. We used the *betadisper* function, which is a multivariate equivalent to Levene's test in the *vegan* package in R (Dixon, 2003). ITS sequences were linked to fungal guilds using the FUNGuild database (Nguyen et al., 2016), and individuals were grouped into the ectomycorrhizae functional group. To assess discriminant taxa between soil treatment groups, we performed a statistical analysis using the *MaAsLin2* R package, applying a multivariable linear model with treatment as a fixed effect and correcting for multiple testing using the Benjamini-Hochberg FDR method (Mallick et al., 2021). Putative nitrifiers were classified based on matching sequence taxonomy to known nitrifying bacteria and archaea. Both Simpson's and Shannon-Weiner's alpha diversity index (H; Shannon 1948) were calculated on the relative abundances of fungi (Hf) and the combined bacteria and archaea (Hba) using the R *vegan* package (Oksanen et al., 2007). Differences in Hf and Hba between soil depths and treatments were assessed using pairwise Wilcoxon signed-rank tests with Bonferroni p-value adjustments in the *ggpubr* and *stats* package (Kassambara, 2018). Microbial beta diversity was calculated using Bray-Curtis dissimilarity matrices, and treatment effects were tested using PERMANOVA (Anderson and Santana-Garcon, 2015). Both analyses were completed using the R *vegan* package (Oksanen et al., 2007).

2.4.2. Random forest models

Random Forests excel at capturing complex, non-linear relationships between variables (Breiman, 2001), which makes them particularly effective for analyzing univariate plant functional traits and microbial responses to soil, treatment, and microbial predictors. For plant traits, soil predictors were averaged across both sampling depths to represent bulk conditions and account for unknown variations in rooting depth and distribution. For microbial analyses, we ran separate random forest models with both the dependent variables and predictors stratified by sampling depth, and a third with measurements from both depths averaged together. We used subsets of different predictors for plant trait and microbial models, each with different (but limited) degrees of collinearity (Figs. S3, S4). Collinearity of predictors and mediators was mostly present in the microbial dataset between DIN and NH_4^+. Because DIN was explained primarily (90 %) by NO_3^-, it was removed from further analyses and NO_3^- was retained. Preliminary testing showed no discernable difference in random forest results whether colinear predictors were included or filtered out, and previous reports have shown random forest to be quite robust to multicollinearity (Chowdhury et al., 2022; Roy and Larocque, 2012) so all predictors except DIN were retained for modeling. Random forest models were trained on the dataset using the *randomForest* package in R (Breiman et al., 2018). Hyperparameters were fixed at 5000 individual trees in each model and the number of predictors assessed at each branch (mtry) was defined as the square-root of the total number of predictors. We then estimated variance explained for each model using a linear regression between observed and predicted data.

2.4.3. Exploratory mediation for indirect effects

To quantify indirect effects of treatments and landscape effects on plant traits and microbial functional groups, we performed EM using the *regsem* package in R (Jacobucci, 2017). Exploratory mediation uses regularized structural equation modeling to identify mediating variables that transmit effects from independent to dependent variables, using automated feature selection. We used the Elastic Net ('Enet') regularization, which is well-suited for datasets with a limited number of observations and potential multicollinearity among predictors (Zou and Hastie, 2005). Elastic Net combines the L1 (Lasso) penalty, which performs variable selection by shrinking some coefficients to zero, with the L2 (Ridge) penalty, which stabilizes coefficient estimates and helps manage collinearity. Despite the strengths of this regularization approach, we observed some instability in model estimates during preliminary runs. To improve robustness, we ran each model for 1000 iterations and calculated 95 % confidence intervals around standardized effect sizes, considering effects significant only if their intervals did not overlap zero. In each EM, we defined mulch and biochar cover, topographic wetness index (TWI), and percent clay as independent variables; soil chemistry and nutrient metrics as potential mediators; and either plant functional traits (SLA, LDMC, height) or microbial functional

groups (nitrifiers, EMF, Hba) as dependent variables. All variables for the plant trait and microbial models are shown in Figs. S3, S4.

3. Results

3.1. Vegetation dynamics and soil chemistry thirteen years after fire

Thirteen years after fire and nine years after soil amendment treatments, there was little evidence of lodgepole pine regeneration (Fig. 1b), and the understory plant community did not differ among treatments, but fungal and bacterial/archaeal communities did (Fig. 2; Table S1). Exotic plant cover was low (< 1 %) and was not significantly affected by treatment. Mulch treatments were associated with lower relative abundances of EMF and putative nitrifiers, and higher VWC and PO_4^+ (Fig. S1). Across treatments, NO_3^--N accounted for approximately 90 % of DIN. It was lowest in the 0–5 cm soil layer of biochar (6 %) and biochar + mulch (8 %) plots, and highest (22 %) at the 5–15 cm depth in mulch-only plots. In other treatments, NO_3^--N made up about 10 % of DIN. Total dissolved nitrogen was primarily composed of organic N forms, with DIN accounting for 8–46 % of TDN. DIN was highest in the biochar treatment and lowest in the control plots.

3.2. Mean comparisons of treatment effects on plant functional traits

Plant functional traits varied inconsistently among species and treatments (Fig. 3). There was less variability within treatments (intraspecific variation) than among species (interspecific variation) for LDMC, with the converse being true for SLA and height. All three traits exhibited similar levels of intraspecific trait variation among the two species. The coefficient of variation for LDMC was 10.6 % for *O. parryi* and 11.9 % for *V. scoparium*; for SLA it was 18.2 % for *O. parryi* and 17 % for *V. scoparium*; and for plant height it was 26.6 % for *O. parryi* and 32.1 % for *V. scoparium*. A two-way ANOVA indicated there were no differences between species means for SLA and height ($p = 0.16$, and $p = 0.24$, respectively), but LDMC was significantly higher in *V. scoparium* ($p < 0.001$). When accounting for species, a treatment effect was only observed in SLA between control and mulch plots ($p = 0.023$, Tukey's pairwise comparison). There was a significant interaction term ($p < 0.01$) between species and treatment for height, indicating the relationship between treatment and height varied between the *V. scoparium* and *O. parryi*. We then performed linear regression tests to assess relationships between plant traits to capture resource utilization tradeoffs. We only found significant linear relationships between LDMC and SLA; $p < 0.001$, $R^2 = 0.21$, and $p < 0.001$, $R^2 = 0.43$ for *V. scoparium* and *O. parryi*, respectively.

3.3. Non-linear responses of microbes and plant traits

Key differences in predictor importance, effect sizes, and effect shapes were evident between species and among plant functional traits, but with weak effects of mulch and biochar treatments (Fig. 4). Model performance was decent among all species and traits ($R^2 > 0.34$) except for LDMC in *V. scoparium* ($R^2 = 0.01$; Table 1). Traits from both species were driven largely by soil chemistry, with divergent responses between the species, and SLA and LDMC response shapes typically being inverted between species. *Oreochrysum parryi* was strongly affected by NO_3^- with threshold-like responses that were inverse for SLA and LDMC, and similar threshold-like responses to PO_4^+. On the other hand, *V. scoparium* was driven more by NH_4^+, especially height and with SLA and LDMC showing similar inverse responses as *O. parryi* to NO_3^-. Across all traits and species, NO_3^- was the strongest predictor overall with an average relative importance score of 0.65, followed by Hba (0.49), NH_4^+, and percent clay (both 0.39). Interestingly, NO_3^- remained the strongest predictor of trait variation when both species were pooled, but the explanatory strength of NO_3^- was stronger in *O. parryi*, whereas NH_4^+ was a stronger predictor in *V. scoparium*, indicating a potential species-level preference for specific forms of N or the associated microbes that affect them. This is further confounded by microbial nitrifiers having a much stronger effect in *V. scoparium* compared to *O. parryi*. Mulch and biochar cover had limited explanatory power except for with height in *O parryi*. Microbial predictors were also variable in shape and effect size across traits and species. For example, Hba was an important predictor for *O. parryi*, with height decreasing and LDMC increasing with increasing diversity. The relative abundance of EMF was less important than expected with threshold-negative responses to height in *O. parryi* and LDMC and height in *V. scoparium*. Random forest model performance for microbial variables differed between soil depths in the two diversity metrics, being stronger in the 0–5 cm depth, but was still quite strong in the model with the two depths pooled ($R^2 > 0.7$; Table 1). Hence, for simplicity, we'll refer to results of the pooled model of microbial groups

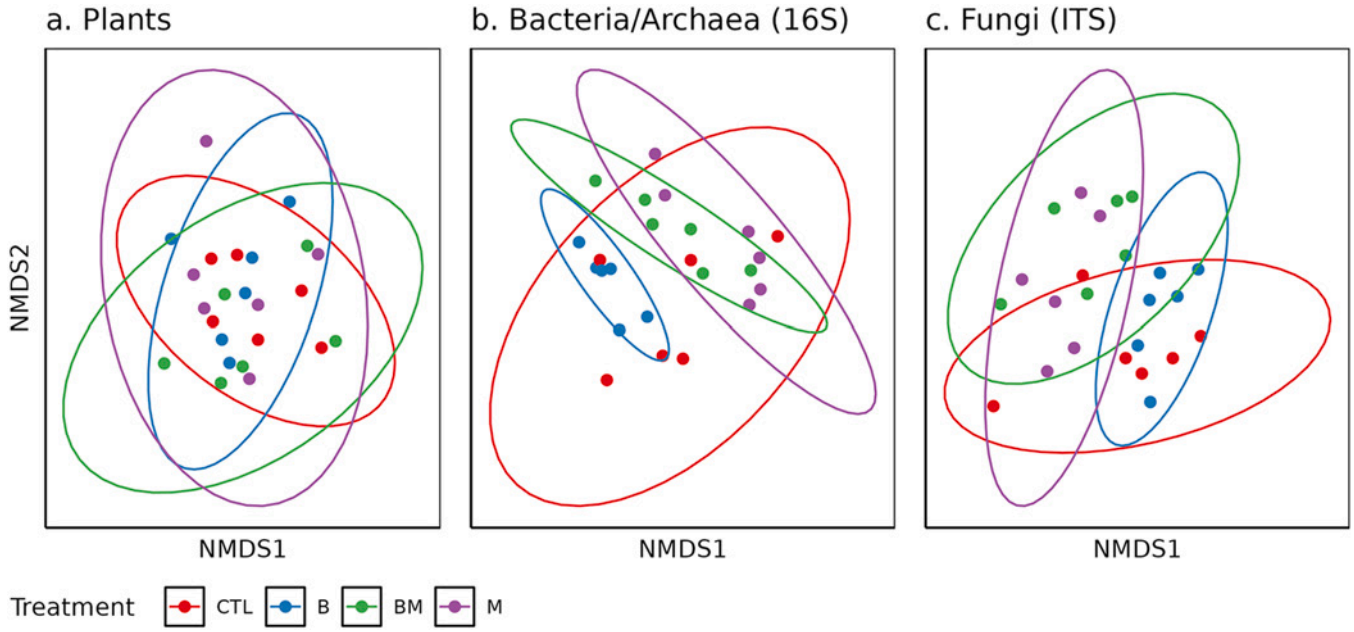

Fig. 2. Treatment effects on the plant community (a), treatment effects on bacterial/archaeal (b) and fungal (c) communities in 2023 at 0–5 cm depths.

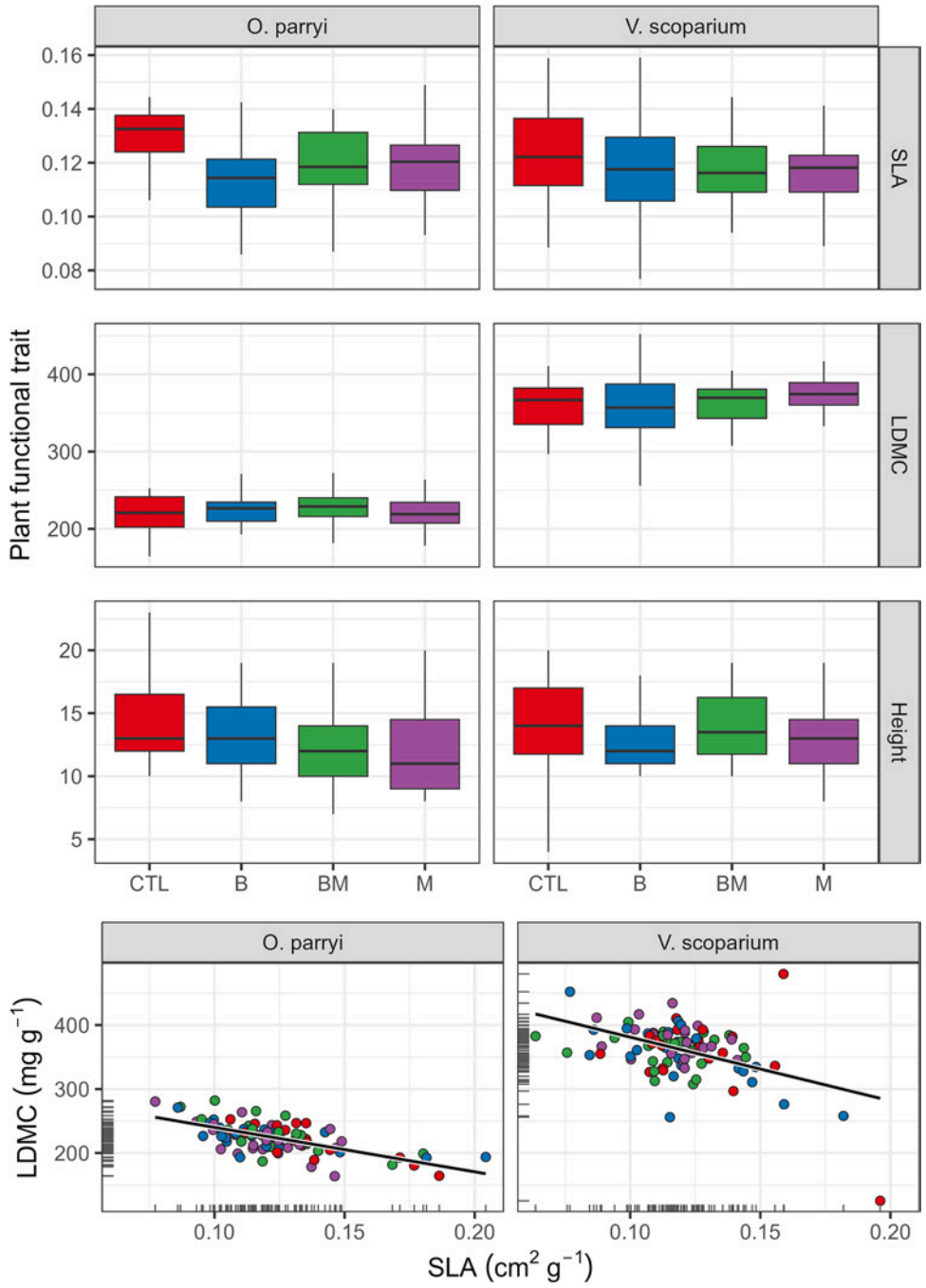

Fig. 3. Variation in specific leaf area (SLA; cm^2 g^{-1}), leaf dry matter content (LDMC; mg g^{-1}), and plant height (cm) among species and organic soil amendment treatments (a), and correlations between SLA and LDMC in Vaccinium scoparium and Oreochrysum parryi.

for the remainder of this paper.

There was little consistency in which predictors were most important among microbial groups, but there was more consistency in threshold-like and stepped response shapes (Fig. 5). Overall, EMF and nitrifiers showed the greatest standardized change among samples (>100 and 25 %, respectively), with Hf and Hba showing minimal variation (0.2 and 0.5 %, respectively). Biochar and soil pH were strong predictors, with both EMF and nitrifier relative abundance increasing non-linearly with residual biochar cover, but with opposite effects of pH. Variability in EMF was most strongly affected in a positive, but threshold-like manner, by NO_3^- and DIN, nitrifiers by biochar, Hba by VWC, and Hf by PO_4^+.

3.4. Direct and indirect effects of soil amendments and landscape factors

Exploratory mediation revealed different responses of plant traits and microbial functional groups to direct effects of treatments and landscape factors (Fig. 6). Overall, microbial functional group responses (as an absolute effect size) were driven primarily by indirect effects of treatments and landscape factors through soil chemistry and nutrient mediators with an average of 74.3 % of model variance explained by indirect effects and only 25.7 % explained directly by treatments and landscape factors. Plant traits responded differently to treatment versus landscape factors with treatment effects manifested more indirectly through soil mediators, but landscape factors caused slightly stronger direct effects (55.3 %) compared to indirect effects (44.6 %). It is

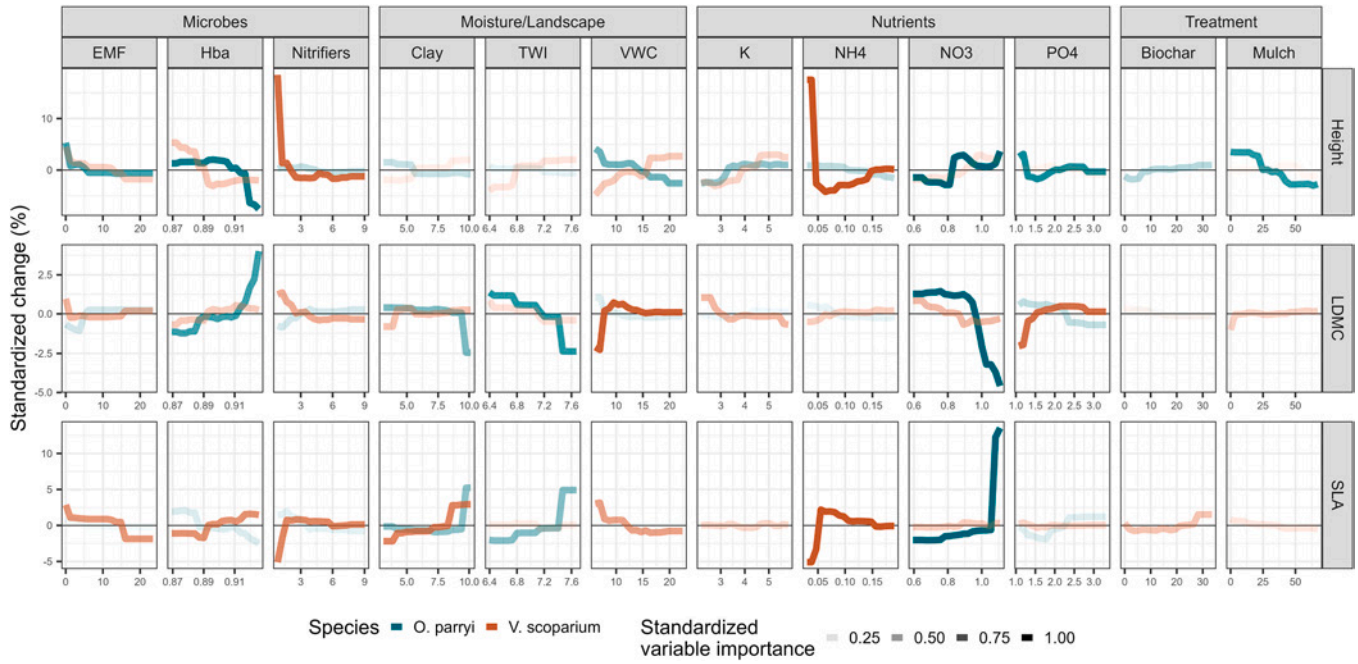

Fig. 4. Random forest partial dependence plots show the effect sizes and shapes of responses of plant functional traits to the 11 most important predictors. For visual clarity among species, the y-axis shows a standardized percent change from the mean of each functional trait. Similarly, the transparency of each line represents the standardized variable importance score for each predictor in each species, calculated as the increase in node purity for each predictor within a model, divided by the increase in node purity of the most important predictor, i.e. the darker and less transparent a line, the more important the predictor. Acronyms: ammonium (NH4), nitrate (NO3), potassium (K), phosphate (PO4), bacterial and archaeal diversity (Hba), ectomycorrhizal fungi (EMF), topographic wetness index (TWI), leaf dry matter content (LDMC), and specific leaf area (SLA), soil volumetric water content (VWC).

Table 1
Random forest model performance determined as the R^2 from a linear regression fit to predicted versus observed data for the dependent variables. Microbial random forests were run for each soil sampling depth and with values pooled across samples. Plant trait random forests were only run on the pooled depths.

	Trait	R^2 0–5 cm	R^2 5–15 cm	R^2 pooled depths
V. scoparium	SLA	-	-	0.37
	LDMC	-	-	0.01
	Height	-	-	0.46
O. parryi	SLA	-	-	0.46
	LDMC	-	-	0.34
	Height	-	-	0.37
Microbes	EMF relative abundance	0.94	0.87	0.71
	Nitrifier relative abundance	0.92	0.92	0.78
	Hba	0.96	0.14	0.83
	Hf	0.93	0.19	0.78

important to note that the analysis reports absolute effect sizes because opposing positive and negative indirect effects can sum near zero, potentially underrepresenting their true influence. For detailed directional effect sizes, refer to Figs. S5 and S6 for *V. scoparium* and *O. parryi*, respectively, and Fig. S7 for microbial groups.

Treatment and landscape factor effects on plant traits operated through various soil mediators, with responses differing by trait and species. Across sites, biochar generally increased microbial functional group diversity and relative abundance, as well as soil K^+, VWC, and NO_3^-. Mulch positively influenced PO_4^+, VWC, and Hba. Increasing TWI raised VWC, NO_3^-, K^+, and Hf, while higher clay content increased VWC, PO_4^+, and NO_3^- but decreased EMF and K^+. In *V. scoparium* specifically (Fig. 7), both increasing biochar cover and TWI had mostly negative effects on SLA due to changes in VWC, EMF, and Hba, although biochar did have a positive effect on SLA through increased Hba.div. Mulch and clay had more positive indirect effects on SLA increasing EMF and Hba. There was a strong negative indirect effect of increasing VWC in more clayey soils on SLA. Biochar and TWI had negative indirect effects on LDMC through changes to Hf and K^+, whereas both treatments and landscape factors had positive indirect effects on plant height through increases to VWC and NO_3^-. In *O. parryi* (Fig. 8), mulch had a strong negative indirect effect on SLA and strong positive effect on LDMC through changes to NO_3^-, with the converse being true for biochar. Despite increasing treatments and landscape factor values increasing VWC, these resulted in negative indirect effects to plant height.

Microbial responses to soil mediators were far more complex and diverse than plant trait responses (Fig. 9). The direct effects of treatments and landscape factors on mediators were like the plant trait models, but subsequent changes in soil mediators had many more indirect effects on microbial functional groups and diversity. Biochar had a strong negative indirect effect on EMF relative abundance through increased DOC, whereas mulch had a strong positive indirect effect on Hba.div through increased VWC, NO_3^- and DON. Mulch also had moderately strong negative indirect effects on the relative abundance of nitrifiers, Hf, and EMF through changes to VWC, DON, and PO_4^+. Clay had moderately strong negative indirect effects on nitrifiers, Hf, and EMF through changes to VWC, and PO_4^+, respectively.

4. Discussion

4.1. Post-fire succession and regeneration implications

This study provides new insight into forest recovery dynamics and possible regeneration failures after wildfire. Thirteen years after fire, tree regeneration remains minimal (Fig. 1b), likely due to low seed viability following pre-fire bark beetle mortality (Rhoades et al., 2022; Rhoades et al., 2018). While soil amendments significantly altered microbial communities and functional groups (Fig. 2; Kaiser et al., 2025), they did not produce significant changes in vegetation community

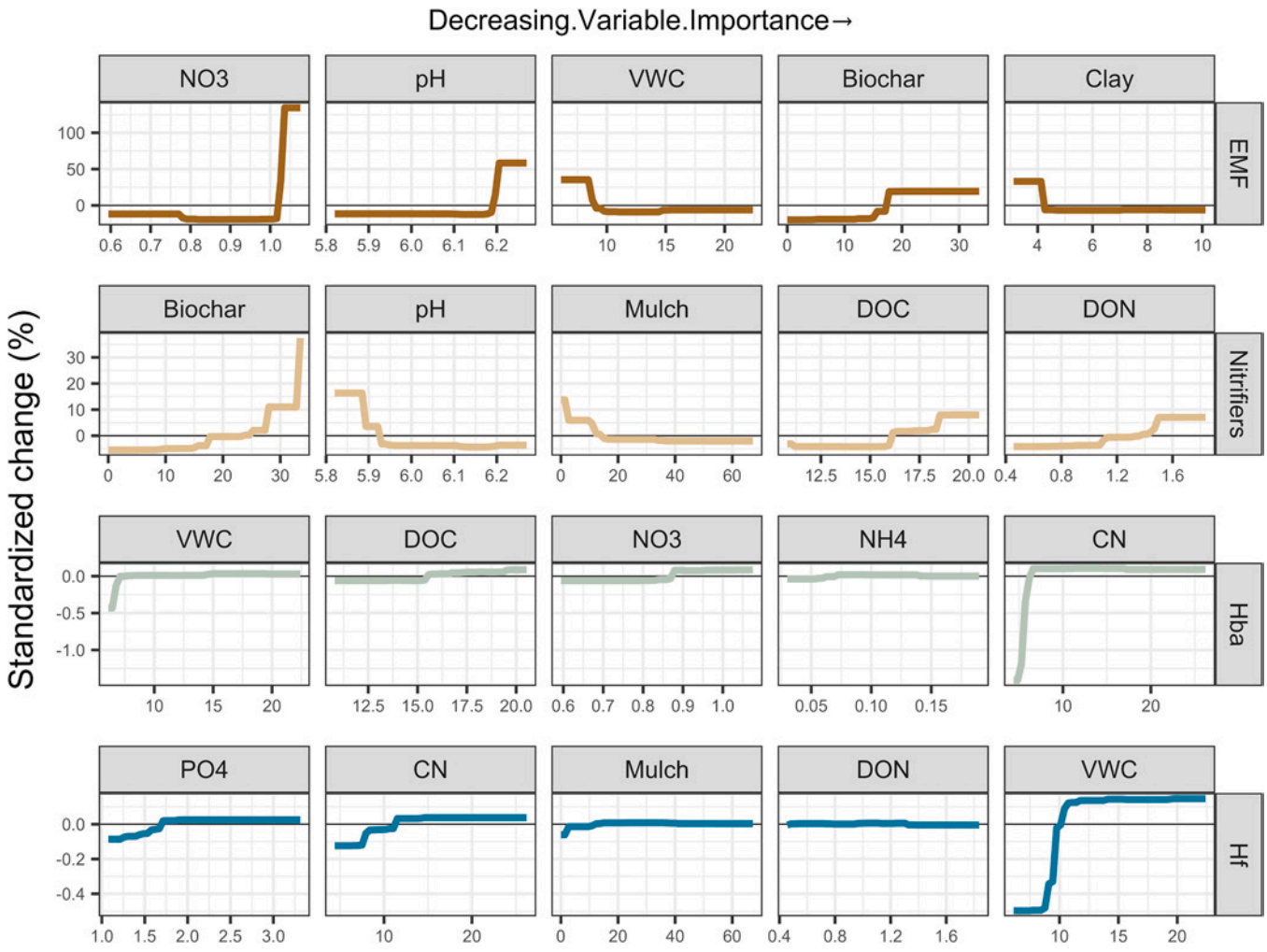

Fig. 5. Random forest partial dependence plots show the effect sizes and shapes of responses of microbial functional groups and diversity metrics to the five most important predictors, ordered from left-to-right by decreasing variable importance. For visual clarity among groups, the y-axis shows a standardized percent change from the mean of each functional trait. Acronyms: nitrate (NO3), volumetric water content (VWC), dissolved organic carbon (DOC), total dissolved nitrogen (TDN), total carbon (TotalC), bacterial and archaeal diversity (Hba), fungal diversity (Hf), ectomycorrhizal fungi (EMF), phosphate (PO4). Note the greater response of EMF and Nitrifiers to predictors as shown by a larger y-axis scale compared to the two diversity metrics.

composition (Fig. 2), consistent with previous research in similar forest types (Dodson and Peterson, 2010; Fornwalt et al., 2017; Jonas et al., 2019; Santana et al., 2014).

The limited overstory recovery has given rise to novel vegetation communities dominated by understory species, raising important questions about long-term ecosystem trajectories and management strategies (Edwards et al., 2015; Roccaforte et al., 2012; Wang and Kemball, 2005). Understory species like *V. scoparium* whose cover increases with biochar amendments (Fig. S2), may facilitate tree seedling establishment through microbial mutualisms, potentially accelerating forest regeneration (Perkins, 2015). Moreover, *V. scoparium* tends to thrive in areas with extensive canopy loss from bark beetles (Carter et al., 2022) where increased light availability may also boost fruit production, benefiting wildlife (Pengelly and Hamer, 2014). However, other research has shown that higher solar radiation in burn areas without overstory regeneration may constrain long-term persistence of *V. scoparium* (Fornwalt et al., 2024), especially in areas impacted by bark beetle mortality pre-fire (Andrus et al., 2020; Rodman et al., 2022; Stevens-Rumann et al., 2015). These conflicting findings highlight critical knowledge gaps, emphasizing the need for focused research on understory-overstory interactions to better predict forest resilience under compound disturbance regimes.

4.2. Treatment effects on soil nutrients, chemistry, and microbes

Soil amendment treatments had significant effects on soil physical, chemical, and microbial properties, and plant cover in the Church's Park burn area (Kaiser et al., 2025). Mulch treatments primarily increased total soil C, VWC, and reduced cover of *O. parryi* (Figs. S1, S2). Conversely, biochar increased total soil C, DOC, the C:N, while reducing net nitrification. The combined treatments (mulch + biochar) had unique soil and plant responses, increasing the diversity of soil bacterial and archaeal communities compared to control plots (Fig. 2). This increased microbial diversity is linked to improved nutrient cycling, crucial for plant recovery after fires (Bouskill et al., 2022), and especially shallowly rooted keystone species like *V. scoparium*. Additionally, higher soil carbon concentrations from the mulch and biochar treatment likely fostered beneficial microbial activity including increased Hba and relative abundance of nitrifiers (Fig. 5). Given the autotrophic metabolism of nitrifiers, these represent indirect effects mediated by soil amendments (Fig. 9). Regardless, soil amendments play an important role in post-fire soil rehabilitation, making them valuable tools for managers dealing with frequent and severe disturbances (Rhoades et al., 2017; Schuler, 2021).

Sorting microbial taxa into functional groups (i.e., putative nitrifiers, EMF) or summarizing their diversity provides valuable insights into the

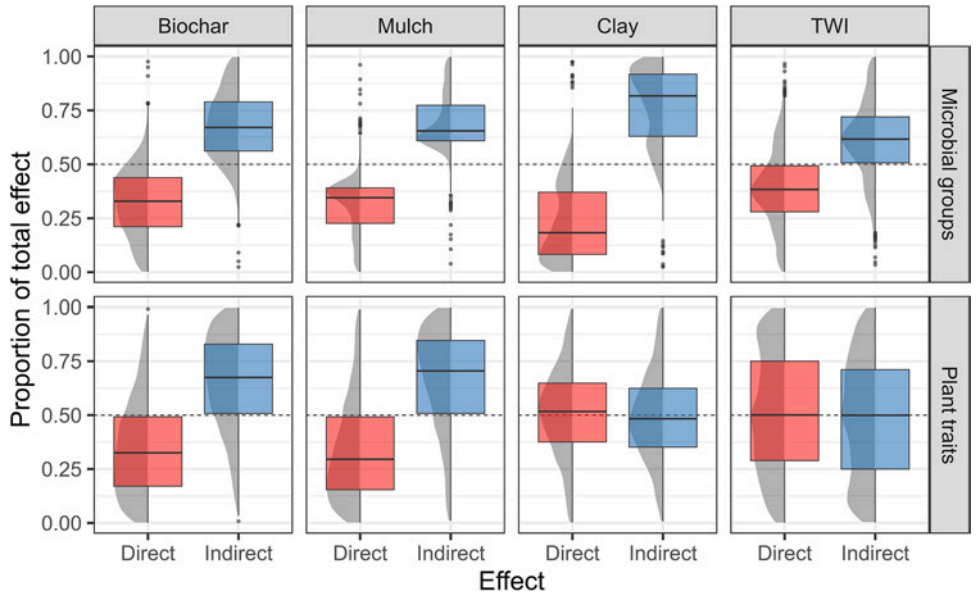

Fig. 6. Proportion of total effects in exploratory mediation models explained by absolute direct effect sizes of independent variables and total indirect effect sizes of soil mediators summarized over 1000 bootstrap iterations. Boxplots show data quartiles overlaid on probability density functions.

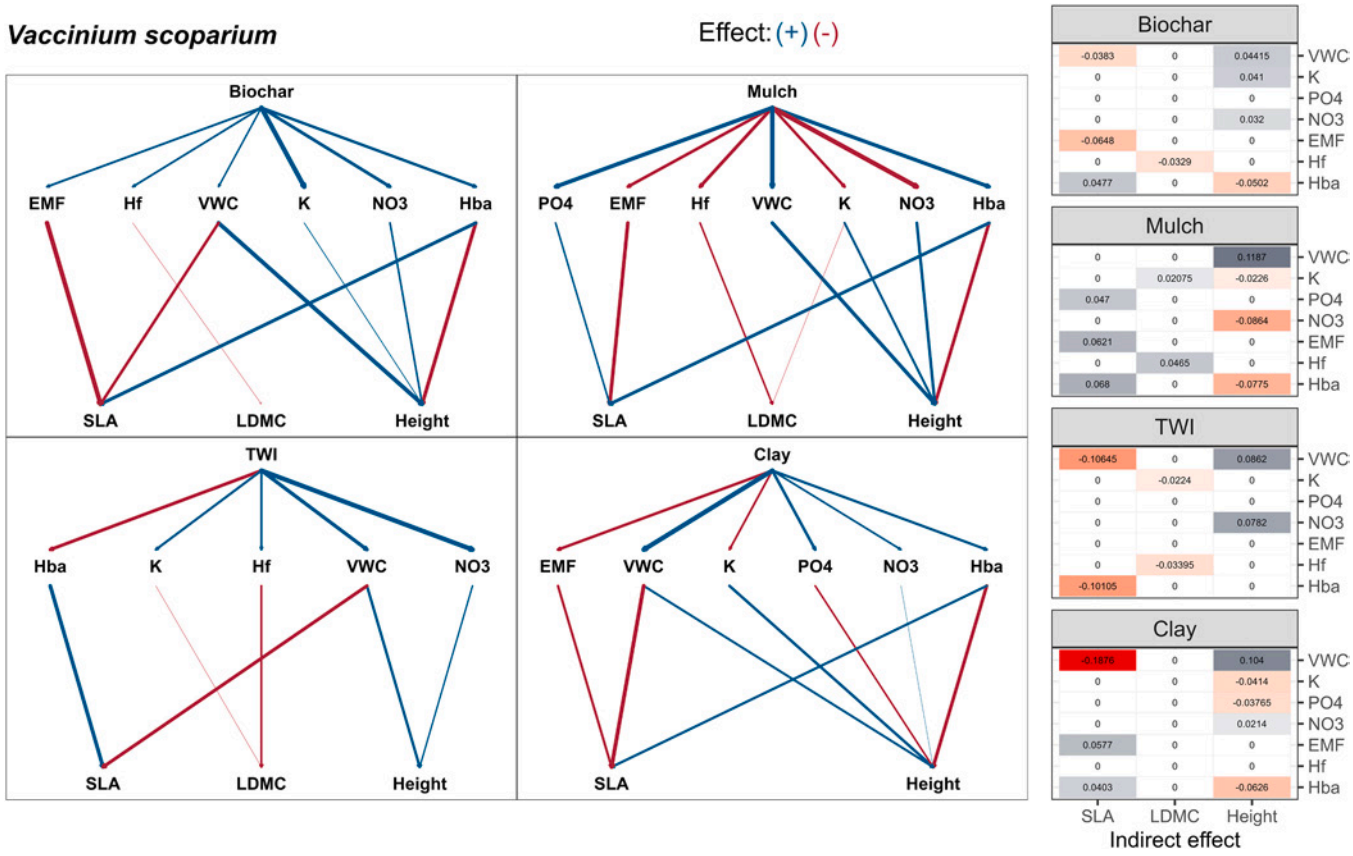

Fig. 7. Exploratory mediation of dependent variables through soil mediators for plant traits in Vaccinium scoparium. The middle row represents the soil mediators, and the bottom row are the plant trait dependent variables. Arrows connecting independent variables to mediators, and mediators to dependent variables, show the effect size (line width) and direction (blue/red) for each least squares regression. The right panel shows significant indirect effects calculated as the product of the independent variable to mediator and mediator to dependent variable effect sizes. Acronyms: ammonium (NH4), nitrate (NO3), phosphate (PO4), potassium (K), fungal diversity (Hf), bacterial and archaeal diversity (Hba), ectomycorrhizal fungi (EMF), topographic wetness index (TWI), leaf dry matter content (LDMC), and specific leaf area (SLA).

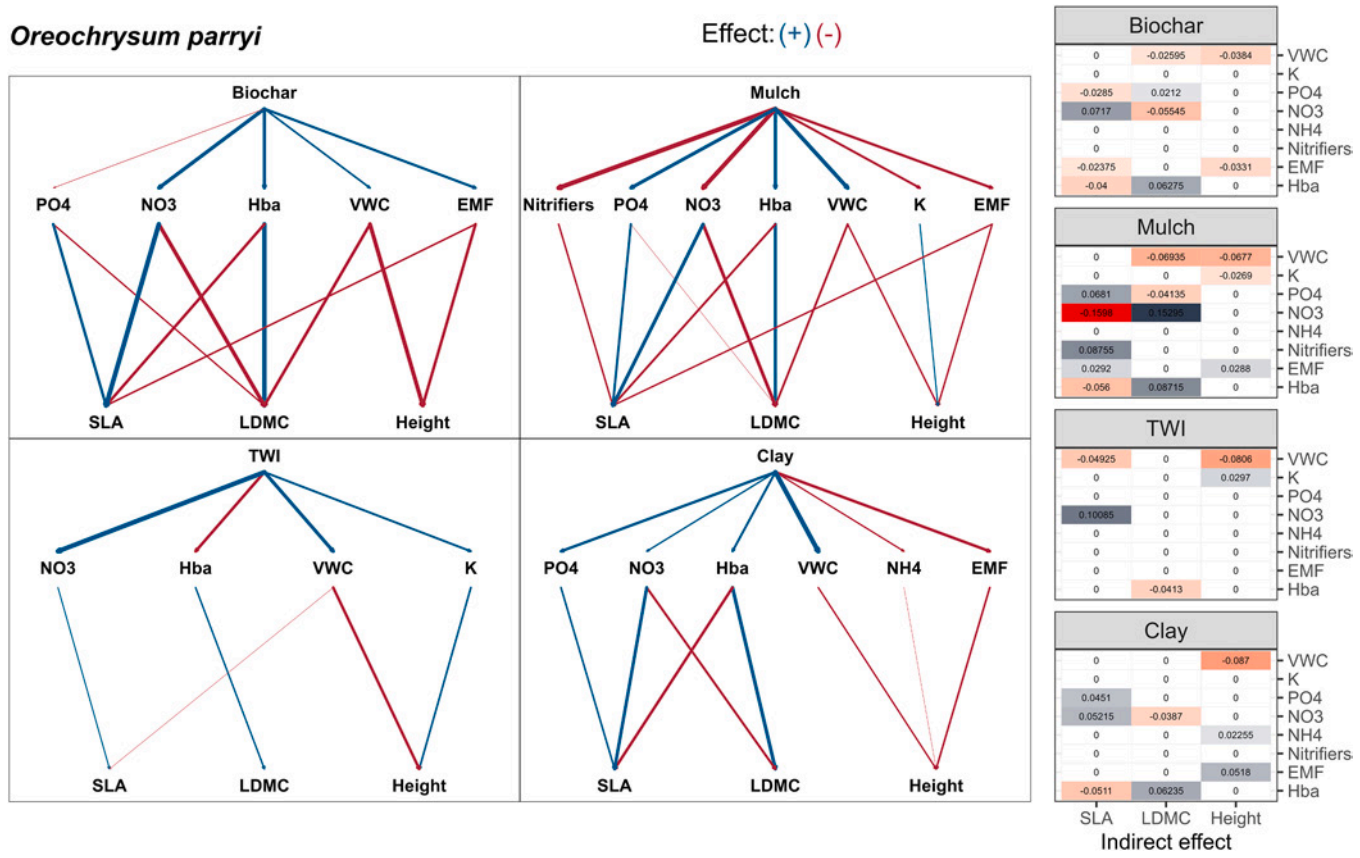

Fig. 8. Exploratory mediation of dependent variables through soil mediators for plant traits in Oreochrysum parryi. In each panel, the top row represents the treatment and landscape factor independent variables. The middle row represents the soil mediators, and the bottom row are the plant trait dependent variables. Arrows connecting independent variables to mediators, and mediators to dependent variables, show the size (line size) and direction (blue/red) for each least squares regression. The right panel shows significant indirect effects calculated as the product of the independent variable to mediator and mediator to dependent variable effect sizes. Acronyms: ammonium (NH4), nitrate (NO3), phosphate (PO4), potassium (K), fungal diversity (Hf), bacterial and archaeal diversity (Hba), ectomycorrhizal fungi (EMF), topographic wetness index (TWI), leaf dry matter content (LDMC), and specific leaf area (SLA).

direct and indirect effects of soil amendment treatments on microbes critical for ecosystem recovery (Figs. 5, 9). Indeed, our analyses show that summaries of microbial diversity or relative abundance of key functional groups improve functional understanding beyond analyses of the microbial community as a whole. Microbial responses were dominated almost entirely by indirect effects mediated through changes in soil properties (Fig. 6). Random forests identified important univariate and non-linear effects of biochar on increased nitrifier and EMF relative abundance (Fig. 5). Exploratory mediation models further revealed that these effects are mediated via biochar-induced changes in soil N, C, pH, and VWC. These complex and indirect effects may explain contradictory effects of biochar on nitrifier abundance and activity from previous studies (Luo et al., 2016; Rhoades et al., 2017; Yu et al., 2021) and wildfire effects on bacterial and archaeal communities (Fox et al., 2022). Mulch had similar non-linear effects for nitrifiers and Hf through soil mediated pathways involving N, C, and $PO_4^{\ddagger}$. These findings underscore the necessity of accounting for indirect soil-mediated mechanisms when assessing amendment effects and highlight the importance of targeting key microbial functional groups to refine forest management strategies. Future research should directly test these indirect pathways identified by our exploratory models in Fig. 9.

We also observed multiple indirect effects of soil amendment treatments on the microbiome through changes to soil characteristics. For example, both DOC and DON decreased with mulch but increased with biochar amendments (Fig. 9). This contrast suggests that mulch and biochar differentially influence N and P availability, both of which were key predictors of microbial abundance and diversity in our models (Figs. 5, 9). Mulch can also increase $PO_4^{\ddagger}$, which correlated negatively with Hf, consistent with a recent global meta-analysis (Ma et al., 2023). These amendment effects have important implications for nitrogen cycling during forest recovery, particularly through nitrifiers that can facilitate inorganic N supply to EMF and aboveground biomass. Mulch may reduce short-term N losses through leaching immediately post-fire (Rhoades et al., 2012), while biochar promotes longer-term N retention (Kaiser et al., 2025). Consistent with previous research, we found increased N availability positively influences EMF relative abundances when N-limited (Jörgensen et al., 2024), possibly because EMF can use NO_3^- as an energy source (France and Reid, 1983; Nygren et al., 2008; Plassard et al., 1994). Thus, combining mulch and biochar applications could optimally support EMF and nitrification processes by balancing short- and long-term nutrient retention.

This study further underscores the importance of EMF in the resilience of lodgepole pine and other western coniferous forests. Ectomycorrhizal fungi are critical symbionts for lodgepole pine (Caiafa et al., 2023) and *V. scoparium* (Perkins, 2015). Beyond the supply of N, mycorrhizal associations can reduce plant drought stress through direct water transport to plant roots (Kakouridis et al., 2022). These associations may be especially important after fire when decreased surface infiltration can reduce soil moisture (Holden et al., 2015). However, high-severity fire can reduce EMF relative abundance and diversity, thereby weakening potential interactions with aboveground biomass (Nelson et al., 2022; Nelson et al., 2024b). The soil amendments tested in this study could support greater EMF relative abundances through retention and addition of N and changes to soil pH, which in turn could enhance the mineral nutrition of conifers by promoting greater utilization of organic N (Abuzinadah and Read, 1986; Pelletier et al., 2016). In

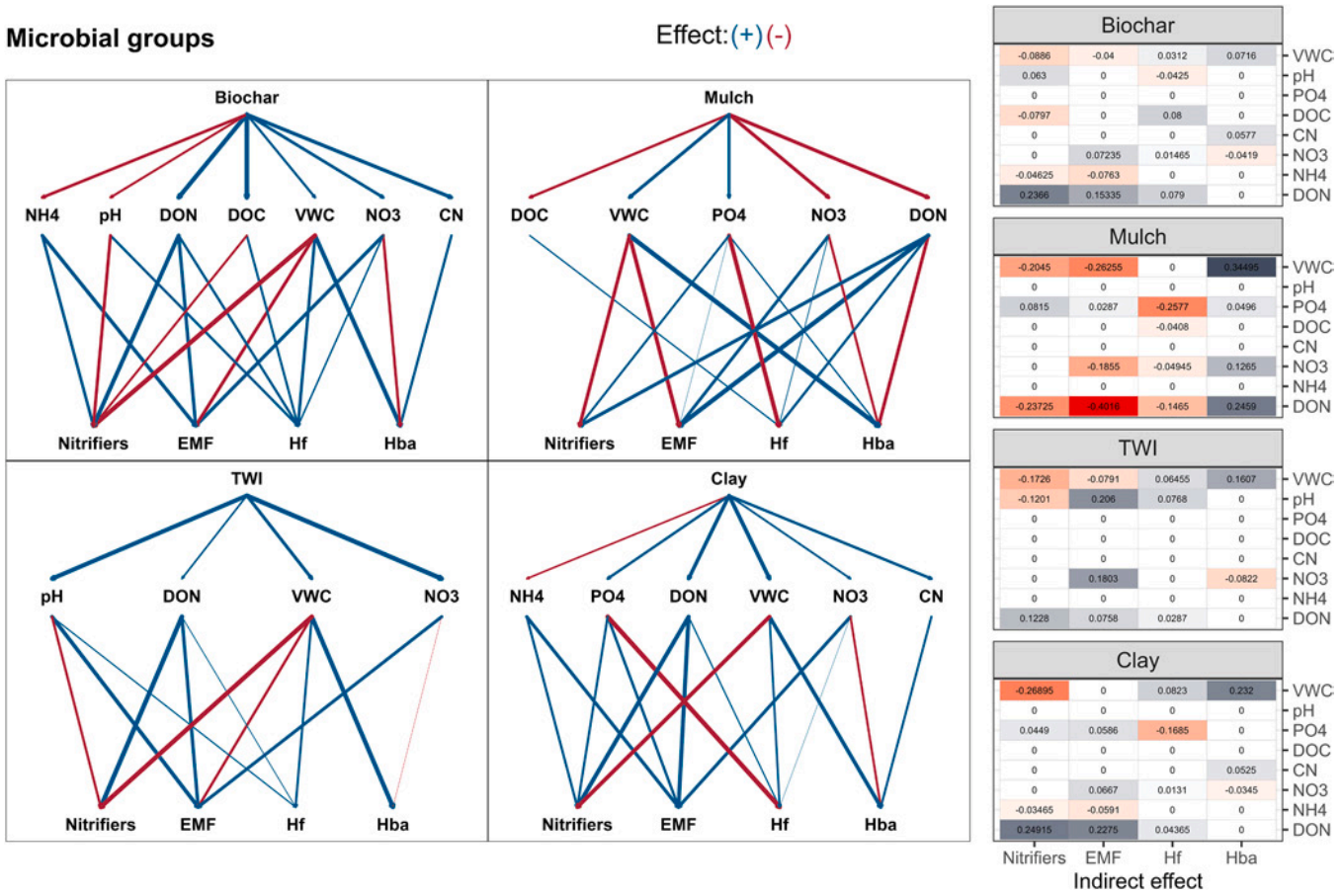

Fig. 9. Exploratory mediation of dependent variables through soil mediators for microbial functional and diversity groups. In each panel, the top row represents the treatment and landscape factor independent variables. The middle row represents the soil mediators, and the bottom row is the plant trait dependent variables. Arrows connecting independent variables to mediators, and mediators to dependent variables, show the size (line size) and direction (blue/red) for each least squares regression. The right panel shows significant indirect effects calculated as the product of the independent variable to mediator and mediator to dependent variable effect sizes. Acronyms: ammonium (NH4), nitrate (NO3), phosphate (PO4), dissolved organic nitrogen (DON), dissolved organic carbon (DOC), carbon to nitrogen ratio (CN), fungal diversity (Hf), bacterial and archaeal diversity (Hba), ectomycorrhizal fungi (EMF), topographic wetness index (TWI).

contrast, mulch may also inhibit EMF via increases in soil moisture and subsequent decreases in NO_3^- (Fig. 5). Previous work has shown the relative abundance of mycorrhizal fungi to increase in drier soils (de Vries et al., 2018; Lozano et al., 2021), which corresponds with negative relationships between EMF relative abundance and VWC in our random forest models, although these effects were not clear in the EMs (Figs. 5–8). Mulch has also been shown to result in 80 % lower NO_3^- compared to untreated soils after fire (Kaiser et al., 2025), potentially limiting an important energy source for EMF metabolism (France and Reid, 1983; Nygren et al., 2008; Plassard et al., 1994). Future research should disentangle soil moisture and nutrient effects to better understand their combined impacts on key microbial functional groups.

4.3. Plant functional traits respond indirectly to soil amendments

Plant functional trait responses to soil amendments were non-linear and dominated by indirect effects, highlighting the importance of our multifaceted analytical approach and confirming our overarching hypothesis that treatment effects would not manifest directly. While traditional ANOVA revealed no significant treatment effects, EM models show that indirect effects on plant traits were roughly twice the magnitude of direct effects (Figs. 3, 6). Random forest models further supported this, revealing consistent non-linear but weak relationships between soil amendments and plant traits (Fig. 4), mirroring patterns observed in microbial communities (Figs. 7, 8). Among species, *V. scoparium* exhibited significantly LDMC, suggesting a conservative strategy with tougher, longer-lived leaves compared to *O. parryi*. Specific leaf area was significantly lower in mulch plots for both species, indicating that heterogeneous soil conditions may enhance intraspecific variability and resilience. Interestingly, this result ran counter to our expectation that higher soil moisture (as observed in mulch plots) would correspond with higher SLA and growth rates. This contradiction might indicate 1) that these species have a drought escape strategy where faster growth is aimed at maximizing nutrient uptake prior to the onset of summer drought (Noy-Meir, 1973; Wolkovich and Cleland, 2014), or 2) that soil nutrients, such as N, are a more limiting resource.

Nitrogen form and microbial associations were key predictors of plant trait variation in the random forest models, with species-specific preferences evident. *V. scoparium* responded more strongly to NH_4^+, while *O. parryi* was more responsive to NO_3^- (Fig. 4). These trait responses often followed threshold-like, saturating curves with increasing nutrient availability, consistent with theoretical models of plant nutrient response (Ågren and Bosatta, 1988; Vitousek, 2004), especially leaf thickness and density (Jager et al., 2015). We found NH_4^+, was a much stronger predictor of plant trait variability in *V. scoparium* whereas *O. parryi* responded more strongly to NO_3^-. Nitrogen is often the most limiting nutrient for plant growth in temperate ecosystems and can interact with moisture limitations to affect growth (Drobnitch et al., 2024; Vitousek and Howarth, 1991), but uptake and metabolic pathways that lead to preferences for one form or the other are poorly understood at the species-level. In general, NH_4^+ uptake is less costly in terms of energetics (Salsac et al., 1987) but at ~10 % of DIN, NH_4^+ was

far less abundant in this study. NO_3^- is typically more abundant but also mobile and prone to leaching after fire, thereby less available for root uptake (Rhea et al., 2022; Rhoades et al., 2019).

Our results support a general understanding that ericaceous (acid adapted) shrubs such as *V. scoparium* prefer NH_4^+ as they lack the nitrate reductase enzyme to metabolize NO_3^-. However, studies have shown other *Vaccinium* species prefer a 2:1 NH_4^+ to NO_3^- ratio (Xu et al., 2021), suggesting a potential role of NO_3^- as energy sources for symbionts such as EMF which can convert NO_3^- to NH_4^+ for plant uptake (Nygren et al., 2008). The stronger leaf trait responses observed in *V. scoparium* relative to *O. parryi* may reflect this dual preference. Our models also indicated subtle but positive effects of NO_3^- on plant height, while *V. scoparium* showed negative associations between NO_3^- and both SLA and LDMC. This may reflect NO_3^-'s indirect role as an energy source for EMF, which in turn facilitates plant nutrient uptake and growth (France and Reid, 1983). In fact, EMF relative abundance was a key predictor of SLA in *V. scoparium,* suggesting that EMF increases its growth rate and corroborates documented reports of mutualism between *V. scoparium* and EMF (Perkins, 2015). Given that plant N-form preferences can be plastic and context-dependent (Harrison et al., 2007; Houlton et al., 2007; Wang and Macko, 2011), the interactions between N-form availability in the soil and the abundance of N cycling microbes such as nitrifiers and EMF warrants future investigation, especially with regards to post-fire soil amendments in forested ecosystems in the western US.

We also found strong but inconsistent effects of soil and topographic predictors on plant trait variability between and within species (Fig. 4), with similar contributions of direct and indirect effects (Fig. 6). Soil texture, specifically clay content, was an important random forest predictor for SLA in both species, and LDMC in *O. parryi.* The EMs indicate this is likely due to increased VWC in more clayey soils or in areas with higher TWI (Fig. 7). Although *O. parryi* has been shown to prefer wetter areas (Korb et al., 2007), we observed neutral or negative to increases in VWC. However, this species did respond positively to TWI and clay percent in the random forest models and to NO_3^- and Hba in the EMs. These responses suggest that landscape and edaphic factors that drive longer-term soil moisture dynamics may dominate over single time point VWC measurements.

Soil pH also played a significant role, particularly for LDMC in *V. scoparium* and for height in *O. parryi*, potentially due to its positive effects on foliar nitrogen and phosphorus concentrations, which are linked to enhanced photosynthetic rates (Maire et al., 2015). Lifecycle and growth strategy differences between the two species may also explain the divergent responses. While we found no significant difference in SLA between species (Fig. 3), LDMC was significantly higher in *V. scoparium* which, combined with the inverse relationship between SLA and LDMC, contradicts previous work showing higher SLA in resprouting species (i.e., *V. scoparium*) versus reseeding species (i.e., *O. parryi*) (Anacker et al., 2011). Although *O. parryi* is presumed to regenerate primarily from seed post-fire, based on its widespread presence and wind-dispersed seed morphology, its exact post-disturbance recruitment strategy remains uncertain (Fornwalt, 2009). In contrast, *V. scoparium* clearly resprouts from rhizomatous roots (Fischer, 1966). Nonetheless, this greater interspecific variability in traits (specifically LDMC) supports our expectations that recovering ecosystems may favor greater variability in functional traits to increase resilience to biotic and abiotic factors (Henn et al., 2018; Jung et al., 2010).

Despite our multifaceted analytical approach, substantial uncertainty remains in identifying the drivers of post-fire plant functional trait responses to soil organic amendments. While SLA and LDMC are widely recognized as inversely responsive to nutrient and moisture availability, intraspecific variation can often be lower than interspecific variation (Siefert et al., 2015), possibly confounding our findings. Several important factors not accounted for in this study could further contribute to uncertainty. First, we did not include root traits, which represent an additional axis of the plant economics spectrum and are essential to understanding belowground nutrient acquisition strategies (Weigelt et al., 2021). Second, the plant economics spectrum is classically defined for high-light conditions (Wright et al., 2004), but both *O. parryi* and *V. scoparium* are shade adapted species and may produce unexpected patterns of functional strategies when exposed to high-light conditions after fire, such as the novel environment both species must adapt to in this study. Third, we did not consider leaf nutrient concentrations such as N or P, which may show more robust direct responses to soil amendments. Finally, our soil samples represent bulk conditions rather than rhizosphere-specific communities that may capture plant-microbe interactions more explicitly. Recently, de Vries et al. (2023) theorized that increased mycorrhizal abundance in the rhizosphere during drought conditions may alter plant traits or physiological processes that attract mutualists or decrease susceptibility to pathogens. Nonetheless, we did observe an expected negative relationship between LDMC and SLA in both species (Fig. 3) and inverse response shapes to soil chemistry (Fig. 4) consistent with expectations about tradeoffs between these traits under varying resource availability (Blumenthal et al., 2020; Ocheltree et al., 2020).

4.4. Management implications

Ecosystem rehabilitation is increasingly important as shifting climate patterns and increasing disturbances, such as wildfire, drive long-term shifts in ecosystem composition and function (Coop et al., 2020; Davis et al., 2019; Reilly et al., 2020; Roccaforte et al., 2012). Understanding the impacts of restoration treatments is essential to guiding future land management decisions. While restoration efforts often focus on measurable outcomes such as plant community composition or vegetation structure, our findings suggest that treatment effects, especially from soil amendments like mulch and biochar, may be subtle, non-linear, and primarily indirect. For instance, while amendments showed limited direct impact on plant community composition or plant traits in standard statistical tests (Figs. 2, 3), our EMs and random forest models revealed underlying effects that were non-linear and mediated by changes to soil chemistry, nutrient availability, and microbial communities (Figs. 4–9). This disconnect between observable outcomes and underlying processes has important implications for land managers. It suggests that the success of soil amendment treatments may be underestimated when only plant community composition and structure are considered. To improve restoration planning, managers should incorporate indicators of belowground processes, such as soil microbial diversity or nutrient cycling dynamics, into monitoring protocols. Although our study used a broad exploratory framework and a high number of models, it provides a roadmap for future hypothesis testing and highlights the importance of systems-based evaluation when assessing treatment efficacy.

As degraded forest ecosystems become more widespread, restoration strategies must prioritize resilience and the recovery of ecosystem functions and services, rather than aiming solely to recreate historical conditions (Kollmann et al., 2016; Merchant et al., 2023; Suding, 2011). Our findings contribute to a growing body of work advancing trait-based restoration, demonstrating how plant traits respond to soil amendments both directly and through interactions with edaphic and microbial factors (Figs. 4–9). Despite the increasing focus on trait-based approaches, operational barriers remain, particularly in linking plant traits to ecosystem services and translating research into on-the-ground decision-making (Aubin et al., 2024; Gornish et al., 2023; Merchant et al., 2023). Progress will require stronger integration between ecologists and practitioners, and better defined restoration goals to guide trait selection and prioritization (Fiedler et al., 2021).

Our findings emphasize that future studies would benefit from further focus on the impacts of post-fire soil amendments on ecosystem recovery and forest regeneration. Biochar is an increasingly used amendment and is relatively well understood for its impacts to soil fertility and water holding capacity, especially when combined with mulch (Kaiser et al., 2025). Biochar can moderate soil temperature

(Zhang et al., 2013), and increase soil P and K, thereby accelerating growth, albeit in a species-specific manner (Gale and Thomas, 2019), and can vary by biochar type, application amount and post-processing (Thomas, 2021). After fire, biochar can increase seedling survival without impacting growth (Marsh et al., 2023). There are several mechanisms by which biochar and other pyrogenic carbon can promote regeneration and affect forest recovery including the improving soil fertility, supporting the growth of fire-adapted species through improved soil fertility and the rapid release of labile nutrients (Gundale et al., 2016; Pluchon et al., 2014). Biochar also includes carbonates of K, Ca, and Mg that increases soil pH and base saturation, thus enhancing nutrient availability (Bodí et al., 2014). Mulch supplies C to the soil and can promote N immobilization, with the potential to reduce leaching and mitigate post-fire losses to streams (Homyak et al., 2008; Perry et al., 2010), but more effort is needed to guide careful placement on the landscape, especially when using aerial applications (Rhoades et al., 2025). Finally, we acknowledge that the application of treatments in this study occurred four years post-fire, and thus our findings may have missed treatment effects evident only during early generation stages. We therefore encourage future research to quantify these potential early treatment effects.

4.5. Conclusions

The long-term legacy of high-severity fire in the Church's Park burn area remains evident more than a decade later, with minimal tree regeneration and persistent shifts in vegetation composition. In this study, we found that post-fire soil amendments had limited direct effects on aboveground characteristics, such as vegetation community structure and plant functional traits. However, using exploratory mediation and random forest analyses, we uncovered complex, non-linear, and primarily indirect effects as plant traits and were mediated through changes in soil chemistry, nutrient availability, and microbial communities. These findings emphasize the need to evaluate restoration outcomes beyond basic means testing of treatment effects. Indirect and interactive relationships between soil, microbes, and plant traits may obscure treatment effects unless examined within a broader ecological framework. Importantly, our results suggest that intraspecific trait variation can help plants adapt to altered post-fire environments and may serve as a key mechanism linking restoration treatments to ecosystem function. To our knowledge, this is the first study to integrate soil amendments, microbial communities, and plant traits into a trait-based framework for post-fire forest restoration. This approach offers a foundation for designing management strategies that build ecosystem resilience by fostering plant communities with diverse and adaptive functional traits in the face of shifting climate and increasing disturbance.

CRediT authorship contribution statement

Barnard Dave M: Writing – original draft, Writing – review & editing, Validation, Resources, Investigation, Data curation, Visualization, Software, Methodology, Formal analysis, Supervision, Project administration, Funding acquisition, Conceptualization. **Macdonald Jacob A:** Writing – review & editing, Methodology, Visualization, Data curation, Writing – original draft, Formal analysis. **Mahood Adam L:** Writing – review & editing, Validation, Methodology, Data curation, Visualization, Resources, Formal analysis, Writing – original draft, Software, Investigation, Conceptualization. **Fegel Timothy S:** Writing – original draft, Methodology, Data curation, Writing – review & editing, Resources, Formal analysis, Validation, Investigation, Conceptualization. **Kaela K Amundson:** Software, Writing – review & editing, Formal analysis, Methodology. **Madeline Guimond:** Methodology, Resources, Data curation, Writing – review & editing, Formal analysis. **Gleason Sean M:** Writing – review & editing, Investigation, Methodology, Validation, Formal analysis. **Kya Sparks:** Writing – review & editing, Validation, Formal analysis, Visualization, Investigation, Conceptualization, Writing – original draft, Methodology, Data curation. **Kaiser Sophia:** Writing – review & editing, Investigation, Methodology, Validation. **Rhoades Charles C:** Visualization, Resources, Investigation, Data curation, Writing – original draft, Supervision, Methodology, Formal analysis, Writing – review & editing, Validation, Project administration, Funding acquisition, Conceptualization. **Wilkins Michael J:** Writing – original draft, Supervision, Methodology, Formal analysis, Writing – review & editing, Validation, Project administration, Funding acquisition, Conceptualization, Visualization, Resources, Investigation, Data curation.

Open research statement

Data and code are publicly available on GitHub at https://www.github.com/admahood/church_park.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT in order to improve readability and flow of the text. After using this tool/service, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

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.2025.122953.

Data availability

Data will be made available on request.

References

Abatzoglou, J.T., Williams, A.P., 2016. Impact of anthropogenic climate change on wildfire across western US forests. Proc. Natl. Acad. Sci. 113 (42), 11770–11775.
Abuzinadah, R., Read, D., 1986. The role of proteins in the nitrogen nutrition of ectomycorrhizal plants: III. Protein utilization by Betula, Picea and Pinus in mycorrhizal association with Hebeloma crustuliniforme. N. Phytol. 103 (3), 507–514.
Ågren, G.I., Bosatta, E., 1988. Nitrogen saturation of terrestrial ecosystems. Environ. Pollut. 54 (3-4), 185–197.
Alstatt, D. and Miles, R.L., 1983. Soil Survey of Grand County Area, Colorado.
Anacker, B., et al., 2011. Ecological strategies in California chaparral: interacting effects of soils, climate, and fire on specific leaf area. Plant Ecol. Divers. 4 (2-3), 179–188.
Anderson, M.J., Santana-Garcon, J., 2015. Measures of precision for dissimilarity-based multivariate analysis of ecological communities. Ecol. Lett. 18 (1), 66–73.

Andrus, R.A., Hart, S.J., Veblen, T.T., 2020. Forest recovery following synchronous outbreaks of spruce and western balsam bark beetle is slowed by ungulate browsing. Ecology 101 (5), e02998.
Apprill, A., McNally, S., Parsons, R., Weber, L., 2015. Minor revision to V4 region SSU rRNA 806R gene primer greatly increases detection of SAR11 bacterioplankton. Aquat. Microb. Ecol. 75 (2), 129–137.
Aubin, I., et al., 2024. Restoring forest ecosystem services through trait-based ecology. Environ. Rev. 32 (4), 498–524.
Barnard, D., et al., 2023. Wildfire and climate change amplify knowledge gaps linking mountain source-water systems and agricultural water supply in the western United States. Agric. Water Manag. 286.
Bautista, S., Robichaud, P.R., Bladé, C., 2009. Post-fire mulching. Fire effects on soils and restoration strategies. CRC press, pp. 369–388.
Beven, K.J., Kirkby, M.J., 1979. A physically based, variable contributing area model of basin hydrology/Un modèle à base physique de zone d'appel variable de l'hydrologie du bassin versant. Hydrol. Sci. J. 24 (1), 43–69.
Blumenthal, D.M., et al., 2020. Traits link drought resistance with herbivore defence and plant economics in semi-arid grasslands: the central roles of phenology and leaf dry matter content. J. Ecol. 108 (6), 2336–2351.
Bodí, M.B., et al., 2014. Wildland fire ash: production, composition and eco-hydro-geomorphic effects. EarthSci. Rev. 130, 103–127.
Bontrager, J.D., Morgan, P., Hudak, A.T., Robichaud, P.R., 2019. Long-term vegetation response following post-fire straw mulching. Fire Ecol. 15, 1–12.
Bormann, B.T., Homann, P.S., Darbyshire, R.L., Morrissette, B.A., 2008. Intense forest wildfire sharply reduces mineral soil C and N: the first direct evidence. Can. J. For. Res. 38 (11), 2771–2783.
Bouskill, N.J., Mekonnen, Z., Zhu, Q., Grant, R., Riley, W.J., 2022. Microbial contribution to post-fire tundra ecosystem recovery over the 21st century. Commun. Earth Environ. 3 (1), 26.
Breiman, L., 2001. Random forests. Mach. Learn. 45, 5–32.
Breiman, L., Cutler, A., Liaw, A., Wiener, M., 2018. Package 'randomforest'. University of California, Berkeley: Berkeley, CA, USA.
Brudvig, L.A., Mabry, C.M., 2008. Trait-based filtering of the regional species pool to guide understory plant reintroductions in Midwestern oak savannas, USA. Restor. Ecol. 16 (2), 290–304.
Caiafa, M.V., et al., 2023. Distinct fungal and bacterial responses to fire severity and soil depth across a ten-year wildfire chronosequence in beetle-killed lodgepole pine forests. For. Ecol. Manag. 544, 121160.
Carter, T.A., Fornwalt, P.J., Dwire, K.A., Laughlin, D.C., 2022. Understory plant community responses to widespread spruce mortality in a subalpine forest. J. Veg. Sci. 33 (1), e13109.
Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oecologia 143, 1–10.
Chapman, T.B., Veblen, T.T., Schoennagel, T., 2012. Spatiotemporal patterns of mountain pine beetle activity in the southern Rocky Mountains. Ecology 93 (10), 2175–2185.
Chowdhury, S., Lin, Y., Liaw, B., Kerby, L., 2022. Evaluation of tree based regression over multiple linear regression for non-normally distributed data in battery performance. 2022 International Conference on Intelligent Data Science Technologies and Applications (IDSTA). IEEE, pp. 17–25.
Coop, J.D., et al., 2020. Wildfire-driven forest conversion in western North American landscapes. BioScience 70 (8), 659–673.
Davis, K.T., et al., 2019. Wildfires and climate change push low-elevation forests across a critical climate threshold for tree regeneration. Proc. Natl. Acad. Sci. 116 (13), 6193–6198.
Dixon, P., 2003. VEGAN, a package of R functions for community ecology. J. Veg. Sci. 14 (6), 927–930.
Dodson, E.K., Peterson, D.W., 2010. Mulching effects on vegetation recovery following high severity wildfire in north-central Washington State, USA. For. Ecol. Manag. 260 (10), 1816–1823.
Dove, N.C., Safford, H.D., Bohlman, G.N., Estes, B.L., Hart, S.C., 2020. High-severity wildfire leads to multi-decadal impacts on soil biogeochemistry in mixed-conifer forests. Ecol. Appl. 30 (4), e02072.
Drobnitch, S., et al., 2024. Can nitrogen availability impact plant performance under water stress? A review of traits, mechanisms, and whole plant effects. Plant Soil. 123.
Ebel, B.A., 2012. Wildfire impacts on soil-water retention in the Colorado Front Range, United States. Water Resour. Res. 48 (12).
Edwards, M., Krawchuk, M.A., Burton, P.J., 2015. Short-interval disturbance in lodgepole pine forests, British Columbia, Canada: understory and overstory response to mountain pine beetle and fire. For. Ecol. Manag. 338, 163–175.
Fiedler, S., et al., 2021. Global change shifts trade-offs among ecosystem functions in woodlands restored for multifunctionality. J. Appl. Ecol. 58 (8), 1705–1717.
Fischer, W.C., 1966. US Department of Agriculture, Forest Service, Intermountain Research Station. Fire Eff. Inf. Syst. Use 'S. Guide 327.
Fornwalt, P.J., 2009. Disturbance impacts on understory plant communities of the Colorado Front Range. Colorado State University.
Fornwalt, P., et al., 2024. Chapter 5: Vulnerability of Major Colorado Front Range Tree Species to Climate Change. In: Hanberry, B. (Ed.), Colorado Front Range Climate Change Vulnerability Assessment for National Forests. General Technical Report RMRS-GTR-438. U. S Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fort Collins, CO.
Fornwalt, P.J., Rocca, M.E., Battaglia, M.A., Rhoades, C.C., Ryan, M.G., 2017. Mulching fuels treatments promote understory plant communities in three Colorado, USA, coniferous forest types. For. Ecol. Manag. 385, 214–224.
Fox, S., et al., 2022. Fire as a driver of fungal diversity-a synthesis of current knowledge. Mycologia 114 (2), 215–241.
France, R.C., Reid, C., 1983. Interactions of nitrogen and carbon in the physiology of ectomycorrhizae. Can. J. Bot. 61 (3), 964–984.
Gale, N.V., Thomas, S.C., 2019. Dose-dependence of growth and ecophysiological responses of plants to biochar. Sci. Total Environ. 658, 1344–1354.
Gee, G., 1986. Particle size analysis. Methods Soil Anal. /ASA SSSA.
Gornish, E.S., et al., 2023. Functional traits are used in restoration practice: a response to Merchant et al.(2022). Restor. Ecol. 31 (7), e13880.
Gundale, M.J., Nilsson, M.C., Pluchon, N., Wardle, D.A., 2016. The effect of biochar management on soil and plant community properties in a boreal forest. GCB Bioenergy 8 (4), 777–789.
Harrison, K.A., Bol, R., Bardgett, R.D., 2007. Preferences for different nitrogen forms by coexisting plant species and soil microbes. Ecology 88 (4), 989–999.
Harvey, B.J., Donato, D.C., Turner, M.G., 2016. Drivers and trends in landscape patterns of stand-replacing fire in forests of the US Northern Rocky Mountains (1984–2010). Landsc. Ecol. 31, 2367–2383.
Henn, J.J., et al., 2018. Intraspecific trait variation and phenotypic plasticity mediate alpine plant species response to climate change. Front. Plant Sci. 9, 1548.
Hijmans, R.J., et al., 2022. Package 'terra'. Maintainer, Vienna, Austria.
Holden, S.R., Berhe, A.A., Treseder, K.K., 2015. Decreases in soil moisture and organic matter quality suppress microbial decomposition following a boreal forest fire. Soil Biol. Biochem. 87, 1–9.
Homann, P.S., Bormann, B.T., Darbyshire, R.L., Morrissette, B.A., 2011. Forest soil carbon and nitrogen losses associated with wildfire and prescribed fire. Soil Sci. Soc. Am. J. 75 (5), 1926–1934.
Homyak, P.M., Yanai, R.D., Burns, D.A., Briggs, R.D., Germain, R.H., 2008. Nitrogen immobilization by wood-chip application: protecting water quality in a northern hardwood forest. For. Ecol. Manag. 255 (7), 2589–2601.
Houlton, B.Z., Sigman, D.M., Schuur, E.A., Hedin, L.O., 2007. A climate-driven switch in plant nitrogen acquisition within tropical forest communities. Proc. Natl. Acad. Sci. 104 (21), 8902–8906.
Huckaby, L.S., Moir, W., 1998. Forest communities at fraser experimental forest, Colorado. Southwest. Nat. 204–218.
Jacobucci, R., 2017. regsem: Regularized structural equation modeling. arXiv preprint arXiv:1703.08489.
Jager, M.M., Richardson, S.J., Bellingham, P.J., Clearwater, M.J., Laughlin, D.C., 2015. Soil fertility induces coordinated responses of multiple independent functional traits. J. Ecol. 103 (2), 374–385.
Jonas, J.L., Berryman, E., Wolk, B., Morgan, P., Robichaud, P.R., 2019. Post-fire wood mulch for reducing erosion potential increases tree seedlings with few impacts on understory plants and soil nitrogen. For. Ecol. Manag. 453, 117567.
Jörgensen, K., Clemmensen, K.E., Wallander, H., Lindahl, B.D., 2024. Ectomycorrhizal fungi are more sensitive to high soil nitrogen levels in forests exposed to nitrogen deposition. N. Phytol. 242 (4), 1725–1738.
Jung, V., Violle, C., Mondy, C., Hoffmann, L., Muller, S., 2010. Intraspecific variability and trait-based community assembly. J. Ecol. 98 (5), 1134–1140.
Kaiser, S., et al., 2025. Long-term soil nutrient and understory plant responses to post-fire rehabilitation in a lodgepole pine forest. For. Ecol. Manag. 575, 122359.
Kakouridis, A., et al., 2022. Routes to roots: direct evidence of water transport by arbuscular mycorrhizal fungi to host plants. N. Phytol. 236 (1), 210–221.
Kampf, S.K., et al., 2022. Increasing wildfire impacts on snowpack in the western US. Proc. Natl. Acad. Sci. 119 (39), e2200333119.
Kassambara, A., 2018. ggpubr:'ggplot2'based publication ready plots. R. Package Version. 2.
Kollmann, J., et al., 2016. Integrating ecosystem functions into restoration ecology-recent advances and future directions. Restor. Ecol. 24 (6), 722–730.
Korb, J.E., Daniels, M.L., Laughlin, D.C., Fulé, P.Z., 2007. Understory communities of warm-dry, mixed-conifer forests in southwestern Colorado. Southwest. Nat. 52 (4), 493–503.
Lozano, Y.M., Aguilar-Trigueros, C.A., Roy, J., Rillig, M.C., 2021. Drought induces shifts in soil fungal communities that can be linked to root traits across 24 plant species. N. Phytol. 232, 1917–1929.
Luo, Y., Yu, Z., Zhang, K., Xu, J., Brookes, P.C., 2016. The properties and functions of biochars in forest ecosystems. J. Soils Sediment. 16, 2005–2020.
Ma, X., et al., 2023. Global arbuscular mycorrhizal fungal diversity and abundance decreases with soil available phosphorus. Glob. Ecol. Biogeogr. 32 (8), 1423–1434.
Mahood, A.L., 2024. topomicro: Topography and Microclimate Tools R package version 0.4.1, https://www.github.com/admahood/topomicro.
Maire, V., et al., 2015. Global effects of soil and climate on leaf photosynthetic traits and rates. Glob. Ecol. Biogeogr. 24 (6), 706–717.
Mallick, H., et al., 2021. Multivariable association discovery in population-scale meta-omics studies. PLoS Comput. Biol. 17 (11), e1009442.
Marsh, C., Blankinship, J.C., Hurteau, M.D., 2023. Effects of nurse shrubs and biochar on planted conifer seedling survival and growth in a high-severity burn patch in New Mexico, USA. For. Ecol. Manag. 537, 120971.
McCune, B., Keon, D., 2002. Equations for potential annual direct incident radiation and heat load. J. Veg. Sci. 13 (4), 603–606.
McGill, B.J., Enquist, B.J., Weiher, E., Westoby, M., 2006. Rebuilding community ecology from functional traits. Trends Ecol. Evol. 21 (4), 178–185.
Merchant, T.K., Henn, J.J., de Silva, I., Van Cleemput, E., Suding, K.N., 2023. Four reasons why functional traits are not being used in restoration practice. Restor. Ecol. 31 (3), e13788.
Minchin, P.R., 1987. An evaluation of the relative robustness of techniques for ecological ordination. July 8–13, 1985 Theory and models in vegetation science: Proceedings of Symposium. Springer, Uppsala, pp. 89–107. July 8–13, 1985.
Nelson, A.R., et al., 2022. Wildfire-dependent changes in soil microbiome diversity and function. Nat. Microbiol. 1–12.

Nelson, A.R., et al., 2024b. Wildfire impact on soil microbiome life history traits and roles in ecosystem carbon cycling. ISME Commun. 4 (1), ycae108.
Nelson, A.R., et al., 2024a. Soil microbiome feedbacks during disturbance-driven forest ecosystem conversion. ISME J. 18 (1), wrae047.
Nguyen, N.H., et al., 2016. FUNGuild: an open annotation tool for parsing fungal community datasets by ecological guild. Fungal Ecol. 20, 241–248.
Niklas, K.J., Shi, P., Gielis, J., Schrader, J., Niinemets, Ü., 2023. Leaf functional traits: ecological and evolutionary implications. Front. Media SA 1169558.
Nilsson, R.H., et al., 2019. The UNITE database for molecular identification of fungi: handling dark taxa and parallel taxonomic classifications. Nucleic Acids Res. 47 (D1), D259–D264.
Noy-Meir, I., 1973. Desert ecosystems: environment and producers. Annu. Rev. Ecol. Syst. 4 (1), 25–51.
NRCS, U., 2013. Snowpack telemetry (SnoTel) precipitation data sites 335, 970, 1186, 1187, 9175. In: N.R.C.S. US Department of Agriculture (Editor).
Nygren, C.M., et al., 2008. Growth on nitrate and occurrence of nitrate reductase-encoding genes in a phylogenetically diverse range of ectomycorrhizal fungi. N. Phytol. 180 (4), 875–889.
Ocheltree, T., et al., 2020. Identification of suites of traits that explains drought resistance and phenological patterns of plants in a semi-arid grassland community. Oecologia 192 (1), 55–66.
Oksanen, J., et al., 2007. The vegan package. Community Ecol. Package 10 (631-637), 719.
Parada, A.E., Needham, D.M., Fuhrman, J.A., 2016. Every base matters: assessing small subunit rRNA primers for marine microbiomes with mock communities, time series and global field samples. Environ. Microbiol. 18 (5), 1403–1414.
Pelletier, J.D., et al., 2016. A gridded global data set of soil, intact regolith, and sedimentary deposit thicknesses for regional and global land surface modeling. J. Adv. Model. Earth Syst. 8 (1), 41–65.
Pengelly, I., Hamer, D., 2014. Grouseberry (Vaccinium scoparium Leiberg ex Coville) fruit production in forest openings in Banff National Park, Alberta. Can. FieldNat. 128 (4), 400–407.
Perez-Harguindeguy, N., et al., 2016. Corrigendum to: new handbook for standardised measurement of plant functional traits worldwide. Aust. J. Bot. 64 (8), 715–716.
Perkins, J.L., 2015. Facilitation of Pinus albicaulis seedling regeneration by Vaccinium scoparium. For. Ecol. Manag. 349, 55–65.
Perry, L.G., Blumenthal, D.M., Monaco, T.A., Paschke, M.W., Redente, E.F., 2010. Immobilizing nitrogen to control plant invasion. Oecologia 163, 13–24.
Plassard, C., Barry, D., Eltrop, L., Mousain, D., 1994. Nitrate uptake in maritime pine (Pinus pinaster) and the ectomycorrhizal fungus Hebeloma cylindrosporum: effect of ectomycorrhizal symbiosis. Can. J. Bot. 72 (2), 189–197.
Pluchon, N., Gundale, M.J., Nilsson, M.C., Kardol, P., Wardle, D.A., 2014. Stimulation of boreal tree seedling growth by wood-derived charcoal: effects of charcoal properties, seedling species and soil fertility. Funct. Ecol. 28 (3), 766–775.
Prats, S.A., Wagenbrenner, J.W., Martins, M.A., Malvar, M.C., Keizer, J.J., 2016. Hydrologic implications of post-fire mulching across different spatial scales. Land Degrad. Dev. 27 (5), 1440–1452.
Pressler, Y., Moore, J.C., Cotrufo, M.F., 2019. Belowground community responses to fire: meta-analysis reveals contrasting responses of soil microorganisms and mesofauna. Oikos 128 (3), 309–327.
Quast, C., et al., 2012. The SILVA ribosomal RNA gene database project: improved data processing and web-based tools. Nucleic Acids Res. 41 (D1), D590–D596.
Rabus, B., Eineder, M., Roth, A., Bamler, R., 2003. The shuttle radar topography mission-a new class of digital elevation models acquired by spaceborne radar. ISPRS J. Photogramm. Remote Sens. 57 (4), 241–262.
Reilly, M.J., et al., 2020. Repeated, high-severity wildfire catalyzes invasion of non-native plant species in forests of the Klamath Mountains, northern California, USA. Biol. Invasions 22, 1821–1828.
Rhea, A.E., Covino, T.P., Rhoades, C.C., Brooks, A.C., 2022. Use of geostatistical models to evaluate landscape and stream network controls on post-fire stream nitrate concentrations. Hydrol. Process. 36 (9), e14689.
Rhoades, C.C., et al., 2017. Examining the Potential of Forest Residue-Based Amendments for Post-Wildfire Rehabilitation in Colorado, USA. Scientifica 2017 (1), 4758316.
Rhoades, C.C., et al., 2019. The legacy of a severe wildfire on stream nitrogen and carbon in headwater catchments. Ecosystems 22 (3), 643–657.
Rhoades, C., Battaglia, M., Rocca, M., Ryan, M., 2012. Short-and medium-term effects of fuel reduction mulch treatments on soil nitrogen availability in Colorado conifer forests. For. Ecol. Manag. 276, 231–238.
Rhoades, C.C., Fegel, T.S., Hubbard, R.M., Chambers, M.E., 2022. Limited seed viability in long-dead serotinous lodgepole pine trees in the Southern Rockies, USA. For. Ecol. Manag. 526, 120565.
Rhoades, C.C., Pelz, K.A., Fornwalt, P.J., Wolk, B.H., Cheng, A.S., 2018. Overlapping bark beetle outbreaks, salvage logging and wildfire restructure a lodgepole pine ecosystem. Forests 9 (3), 101.
Rhoades, C.C., Richardson, M.J., Fegel, T.S., Kampf, S.K., 2025. Assessing the effects of woody mulch on post-fire soil and stream nitrogen at experimental and operational scales. For. Ecol. Manag. 578, 122490.
Robeson, M.S., et al., 2021. RESCRIPt: reproducible sequence taxonomy reference database management. PLoS Comput. Biol. 17 (11), e1009581.
Robichaud, P., Jennewein, J., Sharratt, B., Lewis, S., Brown, R., 2017. Evaluating the effectiveness of agricultural mulches for reducing post-wildfire wind erosion. Aeolian Res. 27, 13–21.
Roccaforte, J.P., Fulé, P.Z., Chancellor, W.W., Laughlin, D.C., 2012. Woody debris and tree regeneration dynamics following severe wildfires in Arizona ponderosa pine forests. Can. J. For. Res. 42 (3), 593–604.
Rodman, K.C., et al., 2022. Rocky Mountain forests are poised to recover following bark beetle outbreaks but with altered composition. J. Ecol. 110 (12), 2929–2949.
Rother, M.T., Veblen, T.T., Furman, L.G., 2015. A field experiment informs expected patterns of conifer regeneration after disturbance under changing climate conditions. Can. J. For. Res. 45 (11), 1607–1616.
Roy, M.-H., Larocque, D., 2012. Robustness of random forests for regression. J. Nonparametr. Stat. 24 (4), 993–1006.
Salsac, L., Chaillou, S.S., Morot-Gaudry, J., Lesaint, C., Jolivet, E., 1987. Nitrate and ammonium nutrition in plants. Plant Physiol. Biochem. 25 (6), 805–812.
Santana, V.M., Alday, J.G., Baeza, M.J., 2014. Mulch application as post-fire rehabilitation treatment does not affect vegetation recovery in ecosystems dominated by obligate seeders. Ecol. Eng. 71, 80–86.
Santín, C., Doerr, S.H., Otero, X.L., Chafer, C.J., 2015. Quantity, composition and water contamination potential of ash produced under different wildfire severities. Environ. Res. 142, 297–308.
Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. Nat. Methods 9 (7), 671–675.
Schuler, S.M., 2021. Fire Effects on Soil Properties: Amending Post-Fire Soils with Native Microbial Communities and Biochar to Improve Sagebrush Performance. Boise State University.
Siefert, A., Lesser, M.R., Fridley, J.D., 2015. How do climate and dispersal traits limit ranges of tree species along latitudinal and elevational gradients? Glob. Ecol. Biogeogr. 24 (5), 581–593.
Stanke, H., Finley, A.O., Domke, G.M., Weed, A.S., MacFarlane, D.W., 2021. Over half of western United States' most abundant tree species in decline. Nat. Commun. 12 (1), 451.
Stevens-Rumann, C., Morgan, P., Hoffman, C., 2015. Bark beetles and wildfires: How does forest recovery change with repeated disturbances in mixed conifer forests? Ecosphere 6 (6), 1–17.
Stevens-Rumann, C.S., Morgan, P., 2019. Tree regeneration following wildfires in the western US: a review. Fire Ecol. 15 (1), 1–17.
Suding, K.N., 2011. Toward an era of restoration in ecology: successes, failures, and opportunities ahead. Annu. Rev. Ecol. Evol. Syst. 42 (1), 465–487.
Team, R.C., 2024. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Thomas, S.C., 2021. Post-processing of biochars to enhance plant growth responses: a review and meta-analysis. Biochar 3 (4), 437–455.
USFS, 2010. Church's Park Fire - Burned Area Emergency Rehabilitation Burn Severity Estimate - Technical Report.
Vitousek, P.M., 2004. Nutrient cycling and limitation: Hawai'i as a model system. Princeton University Press.
Vitousek, P.M., Howarth, R.W., 1991. Nitrogen limitation on land and in the sea: how can it occur? Biogeochemistry 13, 87–115.
de Vries, F.T., et al., 2018. Soil bacterial networks are less stable under drought than fungal networks. Nat. Commun. 9 (1), 3033.
de Vries, F., Lau, J., Hawkes, C., Semchenko, M., 2023. Plant-soil feedback under drought: does history shape the future? Trends Ecol. Evol. 38 (8), 708–718.
Wan, S., Hui, D., Luo, Y., 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. Ecol. Appl. 11 (5), 1349–1365.
Wang, G.G., Kemball, K.J., 2005. Effects of fire severity on early development of understory vegetation. Can. J. For. Res. 35 (2), 254–262.
Wang, L., Macko, S.A., 2011. Constrained preferences in nitrogen uptake across plant species and environments. Plant Cell Environ. 34 (3), 525–534.
Weigelt, A., et al., 2021. An integrated framework of plant form and function: the belowground perspective. N. Phytol. 232 (1), 42–59.
Westoby, M., Wright, I.J., 2006. Land-plant ecology on the basis of functional traits. Trends Ecol. Evol. 21 (5), 261–268.
White, T.J., Bruns, T., Lee, S., Taylor, J., 1990. Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. PCR Protoc. a Guide Methods Appl. 18(1 315–322.
Wolkovich, E.M., Cleland, E.E., 2014. Phenological niches and the future of invaded ecosystems with climate change. AoB Plants 6 plu013.
Wright, I.J., et al., 2004. The worldwide leaf economics spectrum. nature 428 (6985), 821–827.
Xu, J., et al., 2021. Preferential ammonium: nitrate ratio of blueberry is regulated by nitrogen transport and reduction systems. Sci. Hortic. 288, 110345.
Yu, M., et al., 2021. Plant material and its biochar differ in their effects on nitrogen mineralization and nitrification in a subtropical forest soil. Sci. Total Environ. 763, 143048.
Zhang, Q., et al., 2013. Effects of biochar amendment on soil thermal conductivity, reflectance, and temperature. Soil Sci. Soc. Am. J. 77 (5), 1478–1487.
Zou, H., Hastie, T., 2005. Regularization and variable selection via the elastic net. J. R. Stat. Soc. Ser. B Stat. Methodol. 67 (2), 301–320.