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Bacterial community response to environmental change varies with depth in the surface soil

Kristin M. Barbour [a,*], Claudia Weihe [a], Steven D. Allison [a,b], Jennifer B.H. Martiny [a]

[a] Department of Ecology and Evolutionary Biology, University of California-Irvine, Irvine, CA, USA
[b] Department of Earth System Science, University of California-Irvine, Irvine, CA, USA

A B S T R A C T

Bacterial communities in the organic leaf litter layer and bulk (mineral and organic) soil are sensitive to environmental change. However, despite close interactions between these communities, the leaf litter layer has historically been studied in isolation from the bulk soil. Whether bacterial response to environmental change is uniform throughout the surface soil remains unclear. Here, we simultaneously characterized how bacterial community composition in three surface soil layers (the leaf litter layer, 0–2 cm of bulk soil, and 0–10 cm of bulk soil) responded to a wildfire burning through a 13-year drought simulation in two adjacent ecosystems, a grassland and coastal sage scrubland. We found that bacterial communities in all three surface soil layers were distinct in composition and varied with drought, ecosystem type, and temporal variation. Moreover, the impact of these environmental changes on bacterial community composition decreased with depth in the surface soil. Bacterial response to drought was three-fold higher in the leaf litter layer than in the top 10 cm of bulk soil, with the drought treatment explaining 4.8% and 1.6% of the compositional variation, respectively. Wildfire altered bacterial composition in the leaf litter layer but not within the top 10 cm of bulk soil. Further, previous exposure of the bacterial communities in the leaf litter layer to drought did not influence its response to the wildfire. Thus, considering soil depth when assessing the impact of environmental conditions on the surface soil microbiome may improve predictions about the degree to which microbial communities, and therefore soil carbon, will respond to future environmental change.

1. Introduction

As anthropogenic activity changes the frequency of environmental disturbance, there has been considerable effort to characterize how environmental perturbations influence soil microbial communities using global change experiments in the field (Allison et al., 2013; DeAngelis et al., 2015; Gutknecht et al., 2012). While some surveys have been conducted in subsurface soils (below 10 cm) (Engelhardt et al., 2018; Kramer et al., 2013; Taş et al., 2014), most of what is known about microbial response to simulated global change is based on surface soils (above 10 cm) that contain the greatest bacterial diversity and biomass (Eilers et al., 2012; Fierer et al., 2003; Jansson and Hofmockel, 2020). Surface soils are typically treated as a uniform layer, where soil cores are homogenized into a composite sample prior to analysis. Yet, chemical and physical properties driving microbial community structure in soil change with depth (Blume et al., 2002; Eilers et al., 2012; Fierer et al., 2003) such that different layers of the surface soil likely harbor distinct microbial communities. Moreover, soil closer to the surface experiences larger fluctuations in aboveground conditions such as temperature and moisture. Thus, understanding the linkage between microbial community response and resulting changes in soil carbon storage under future climate change may require consideration of soil depth.

One critical layer of the surface soil is the organic leaf litter layer – the topmost layer of soil. The surface leaf litter layer interacts closely with the bulk (mineral or organic) soil below. Senescent plant biomass, or leaf litter, acts as a physical barrier on the soil surface, influencing bulk soil temperature, moisture content, and erosion (Sayer, 2006; Villalobos-Vega et al., 2011). Microbial transformation of leaf litter releases essential nutrients back into the soil (Swift et al., 1979) and contributes to both soil organic matter (SOM) formation and carbon storage (McBride et al., 2020; Prescott and Vesterdal, 2021). Bacteria and fungi are largely responsible for leaf litter decomposition, and the composition of these microbial communities influences decomposition rate (Glassman et al., 2018; Schimel and Schaeffer, 2012). Therefore, changes to the leaf litter microbiome may alter nutrient availability in the underlying soil horizons with potential consequences for bulk soil microbial communities. Given that bulk soil microbes mineralize soil carbon into CO_2 and contribute to stable SOM formation through plant litter processing and necromass accumulation (Gleixner, 2013; Liang et al., 2019), shifts in SOM or soil carbon pools from the leaf litter may alter carbon fluxes in surface soils. Yet, despite the intimate interaction between these layers, the effect of environmental change on leaf litter

* Corresponding author. 321 Steinhaus Hall Department of Ecology and Evolutionary Biology University of California Irvine, CA, 92627, USA.
E-mail address: kbarbou1@uci.edu (K.M. Barbour).

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verses bulk soil microbes is often examined independently. As a result, it remains unclear if microbial communities in the litter layer and bulk soil respond similarly to abiotic change.

Here, we take advantage of a wildfire burning through a decade-long global change experiment to characterize the effects of two interacting disturbances (wildfire and drought) on leaf litter and bulk soil bacterial composition simultaneously. Previous work has demonstrated that microbial communities are sensitive to both drought and wildfire. Drought affects soil microbes directly through desiccation and limits resource connectivity by reducing soil moisture content (Schimel, 2018). Drought also indirectly affects microbial communities by altering plant litter production, thus modifying resource input into the soil (Kimball et al., 2014; Malik et al., 2020). Similarly, wildfires induce changes in microbial community structure both directly, through soil heating, and indirectly, by altering a variety of abiotic and biotic parameters including soil pH, nutrient availability, and plant community composition (Ferrenberg et al., 2013; Xiang et al., 2014; Zhang et al., 2021). While drought and wildfire are known to influence microbes separately, interactions between these disturbances are expected to become more common and may affect microbial communities in yet uncertain ways (Cook et al., 2015; Heidari et al., 2021; IPCC, 2014).

The primary aim of this study was to test the hypothesis that bacterial response to environmental changes will be attenuated with depth in the surface soil. Bacterial communities in the subsurface soil have been shown to be less affected by climate (temperature and precipitation) than those in the surface soil (Dove et al., 2021; Han et al., 2017). Here, we define bacterial response as the magnitude by which community composition changes, or the degree of compositional variation that can be explained by different environmental variables. To test our main hypothesis, we used the ongoing Loma Ridge Global Change Experiment (LRGCE) in Irvine, CA, which manipulates precipitation in a semi-arid grassland and adjacent coastal sage scrubland (CSS). Understanding how bacterial communities respond to drought and wildfire in these Mediterranean systems is critical as both factors are expected to increase in frequency in southern California and throughout the southwestern US (Cook et al., 2015; Dong et al., 2022; IPCC, 2014).

Extensive work at this site has shown that bacterial and fungal composition in the leaf litter layer differ by ecosystem (grassland versus CSS) and precipitation treatment (simulated drought versus ambient rainfall) (Finks et al., 2021). Whether bulk soil communities exhibit a similar response to these factors and an additional wildfire disturbance is unknown. To investigate this gap, we assessed how environmental drivers (drought, wildfire, ecosystem vegetation, and temporal variation) influence bacterial composition in three surface soil layers (leaf litter, top 2 cm of bulk soil, and top 10 cm of bulk soil) at the LRGCE. Based on our main hypothesis, we expected that the bacterial communities in all surface soil layers would change with both drought and fire, but the changes would be dampened deeper in the soil profile. We further predicted that the influence of wildfire would depend on the precipitation regime as previous work at this site revealed that long-term drought selects for bacterial communities with greater investment in stress tolerance pathways (Malik et al., 2020).

2. Materials and methods

2.1. Field site, experimental design, and fire history

The Loma Ridge Global Change Experiment (LRGCE) is located in a California grassland and adjacent coastal sage scrubland (CSS) in northern Irvine, California, USA (33°44′ N, 117°42′ W, 365 m elevation). Plant communities vary between the grassland and CSS at the LRGCE (Finks et al., 2021). The grassland is dominated by non-native annual grasses (*Bromus diandrus, Avena fatua*) and the native forb *Deindra fasciculata* while native drought-deciduous shrubs (*Artemisia californica, Salvia melifera*) dominate the neighboring CSS (Kimball et al., 2014; Potts et al., 2012). Soils are fine-loamy mixed, thermic *Typic Palexeralfs* sandy loams (California Soil Resource Lab, https://casoilresource.lawr.ucdavis.edu/soilweb-apps/). The climate is Mediterranean (dry summers and wet winters) with a mean annual temperature of 17 °C and a mean annual precipitation of 325 mm.

The LRGCE has manipulated precipitation and nitrogen content in the grassland and neighboring CSS for over a decade. The LRGCE experimental design is described in detail in Allison et al. (2013). Briefly, in 2007, eight treatment blocks were established in the grassland (12.2 m × 6.1 m) and CSS (18.3 m × 12.2 m) in a randomized split-plot design (32 plots total) (Fig. 1A). In both ecosystems, four-replicate treatment plots receive one of four treatments: control, drought, added nitrogen, and drought with added nitrogen (n = 4 plots per treatment per ecosystem). After 10 years of application, the nitrogen treatment displayed a weak impact on microbial community composition in the surface leaf litter (Finks et al., 2021). As a result, we focused this study on the precipitation treatment. Drought plots receive ~50% less rainfall compared to ambient control plots (Fig. S1A). To reduce precipitation, a clear polyethylene film cover is pulled over the drought plots during a subset of large rainfall events each winter. The influence of vegetation composition and precipitation manipulation on surface soil properties at the LRGCE has also been previously described (Khalili et al., 2016). Briefly, total organic C pools are similar between ecosystems while total N is higher in the grassland. Additionally, surface soil C and N pools are generally lower in the drought treatment plots compared to ambient plots, particularly within the CSS. Further, surface soil moisture content is lower in the drought plots throughout the winter (Khalili et al., 2016).

In 2007, all plots at the LRGCE were burned in either an intentional, prescribed fire or the Santiago Fire. Recently, all treatment plots in the grassland and CSS were burned again by the Silverado Fire on October 26, 2020. In the CSS, both fires reduced vegetation cover in all plots. Based on post-fire vegetation traits, the Silverado wildfire was less severe in the CSS drought plots than the ambient plots (Kimball et al. in prep). Fire severity was not quantitatively assessed in the grassland; however, a thin, uniform char layer following the fire suggests the grassland plots burned evenly and at lower severity than in the CSS. In both ecosystems, the fire removed most of the surface litter layer (Fig. 1C–F).

2.2. Soil sampling

Between October 2020 and February 2021, bulk soil cores were collected four times from the ambient and drought plots in both ecosystems (grassland and CSS) (Fig. 1B). Prior to soil core collection, the surface leaf litter was removed from the area to expose the topsoil. During the first collection on October 7, 2020, 20 days prior to the Silverado Fire, a single 10 cm core (3 cm diameter and 10 cm deep) was taken from the 16 experimental plots within the grassland and CSS ecosystems (20 days pre-fire: $n = 16$ samples). On November 18, 2020, 24 days after the fire, a 10 cm core was collected from each of the previously sampled plots. To assess microbial response in different bulk soil layers, shallow soil cores (3 cm diameter and 2 cm deep) were also collected (24 days post-fire: $n = 32$ samples). On January 27, 2021 and February 24, 2021, 94 days and 122 days after the fire respectively, 10 cm and 2 cm soil cores were taken from each of the 16 experimental plots; at these time points, duplicate samples were collected from each plot to capture greater amounts of spatial heterogeneity (94 days post-fire: $n = 64$ samples, 122 days post-fire: $n = 64$ samples). In total, 176 soil samples were collected. On the day of collection, the soil samples were sieved (2 mm) and stored at −70 °C until DNA extraction.

2.3. Surface leaf litter sampling

Surface leaf litter sampling was conducted concurrently with soil sampling on October 7, 2020, November 18, 2020, January 27, 2021, and February 24, 2021 (Fig. 1B). Partially burned leaf litter was

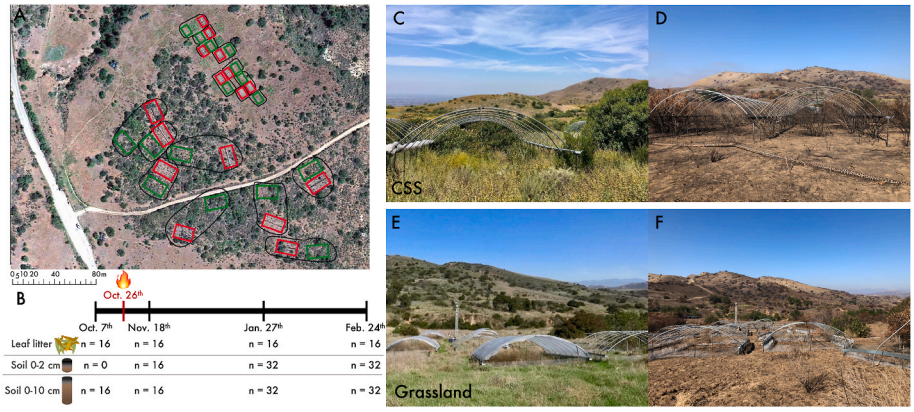

Fig. 1. (A) Satellite image of the Loma Ridge Global Change Experiment site in the Santa Ana Mountains, within the Irvine Ranch National Landmark in Orange County, California, USA. Rectangles indicate the location of the larger coastal sage scrub (CSS) plots and the smaller plots in the adjacent annual grassland. Plots are colored by water treatment, with red indicating water reduction and green for ambient water. The black-outlined polygons indicate blocks containing all treatment combinations. Each plot (rectangle) was divided in half lengthwise, and N treatments (ambient or added) were randomly assigned. Nitrogen addition plots were not sampled in this study. (B) Sample collection timeline and number (n) of leaf litter, 0–2 cm bulk soil, and 0–10 cm bulk soil samples collected at each timepoint. LRGCE treatment plots in the CSS (C) before and (D) after the Silverado fire in October 2020. LRGCE treatment plots in the grassland (E) before and (F) after the Silverado fire in October 2020. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

collected in all three sampling periods following the Silverado wildfire. At each timepoint, litter was collected randomly from three distinct regions within the 16 experimental plots and pooled by plot before being transported back to the lab. Altogether, 16 litter samples were collected at each timepoint producing a total of 64 surface litter samples. On the day of field collection, litter samples were ground, homogenized, and stored at −70 °C until DNA extraction.

2.4. Precipitation

Precipitation data for the LRGCE was collected from rain gauges located at the site (Fig. S1). Precipitation data collected since 2018 is available at http://hydstra.ocpublicworks.com/web.htm.

2.5. DNA extraction and sequencing

Genomic DNA was extracted from 0.1 g of sifted soil and 0.05 g ground litter using ZymoBIOMICS 96 DNA Kits following the manufacturer's protocol, except the maximum centrifuge speed was 2808 g, instead of 3500 g. Bead-beating was conducted for 5 min at 6.5 m/s speed in a FastPrep 24 (MP Biomedicals, Irvine CA, USA). To minimize batch differences, all soil and litter samples were randomized prior to DNA extraction.

To characterize the bacterial community in both the soil and litter samples, we amplified the V4–V5 region of the 16S rRNA gene using the 515F (GTGYCAGCMGCCGCGGTAA) and 926R (CCGTCAATTCCTTTRAGTTT) primers (Caporaso et al., 2012; Lane et al., 1985). For the PCR reactions, 1 μL genomic DNA was combined with 10.5 μL PCR grade water, 12.5 μL AccustartII PCR tough mix (Quanta BioSciences Inc, Beverly, MA, USA), 0.5 μL of the 10 μM barcoded forward primer, and 0.5 μL of the 10 μM reverse primer. An initial denaturation step was performed at 94 °C for 3 min, followed by 30 cycles of denaturing at 94 °C for 45 s, annealing at 55 °C for 30 s, and extension at 72 °C for 60 s, with a final extension at 72 °C for 10 min. The library was created by pooling PCR products based on band brightness in gel pictures (high (1 μL), medium (2 μL), and low (3 μL)). PCR products were not produced for three litter samples (11-18-2020-46RXX, 11-18-2020-32RXX, and 01-27-2021-32RXX) and were, therefore, excluded from the library. The pooled library was cleaned using Sera-Mag SpeedBeads (Jolivet and Foley, 2015). All amplicons were sequenced in one paired-end Illumina Mi-Seq (2 x 300bp) run by the UC Irvine Genomics High Throughput Sequencing Facility (Irvine, CA, USA).

2.6. Amplicon sequence processing

Forward reads from the Illumina amplicon sequences were demultiplexed using QIIME2, version 2020.8 (Bolyen et al., 2019). Single end analysis was performed due to low quality reverse reads. Within the QIIME2 pipeline, forward reads were trimmed to 6–253 bases and DADA2 was used to define 100% exact sequence variants (Callahan et al., 2016). Taxonomic identity was assigned using the q2-feature-classifier plugin and classify-sklearn in QIIME2 to generate a Naive Bayes classifier trained on reference sequences from the SILVA 138 SSU Ref NR99 database filtered at 99% identity trimmed to 253 bp (Bokulich et al., 2018; Quast et al., 2013). Sequences assigned to chloroplast, mitochondria, Archaea, Eukaryota, or unidentified at the phylum level were removed prior to downstream analysis.

2.7. Statistical analysis

To account for uneven sequencing depth, the ESV table produced in QIIME2 was rarefied to 5439 sequences per sample with 200 resamplings using the EcolUtilis package in R version 4.0.3 (R Core Team, 2020; Salazar, 2021). Bacterial community composition did not vary significantly between soil core replicates collected in the last two sampling periods (PERMANOVA: $P > 0.05$ for both timepoints). Therefore, following rarefaction, ESV abundance was averaged between soil core duplicates from the same plot and used for all downstream analyses. We compared community composition across samples using Bray-Curtis dissimilarity matrices generated from square root transformed rarefied ESV tables. To test the effects of environmental (ecosystem and sampling date) and global change (drought and wildfire) factors on soil and leaf litter bacterial composition, permutational multivariate analysis of variance (PERMANOVA) and post-hoc tests were performed using PERMANOVA + on PRIMER v6 (Anderson et al., 2010; Clarke and Gorley, 2006). Block was included as a random effect factor nested within ecosystem for all PERMANOVA models. When testing the effects of wildfire on bacterial community composition, we only considered samples collected from 20 days before the fire and the samples collected 24 days after the fire. All PERMANOVA analyses were conducted using type III partial sum of squares under a reduced model with 999 permutations. To assess the sensitivity of bacterial communities to each experimental factor, we calculated the proportion of variance attributable to each factor. Variance explained by experimental variables was determined by dividing the estimated components of variation from each statistically significant term by the sum of all significant terms plus the residuals. To assess whether variation in dispersion between groups could be contributing to significant compositional differences identified in a PERMANOVA test, homogeneity of multivariate dispersion tests were performed using PERMDISP on PERMANOVA+ (Anderson et al., 2010; Clarke and Gorley, 2006). PERMDISP was performed for all main effects in the overall PERMANOVA as well as main effects in

PERMANOVAs conducted by soil layer and by ecosystem to investigate potential drivers of significant interactions between main effects. A SIMPER analysis was also performed in PRIMER v6 (Clarke and Gorley, 2006) to determine which particular genera and ESVs contributed most to compositional differences between ecosystems as well as bulk soil and leaf litter communities. To visualize the effect of soil depth, environmental factors, and disturbance on bacterial community composition, nonmetric multidimensional scaling (NMDS) ordination plots were created from Bray-Curtis dissimilarity matrices.

To analyze alpha diversity, ESV richness and Shannon diversity were calculated from the rarefied ESV table using the "specnumber()" and "diversity()" functions respectively from the vegan package in R (Oksanen et al., 2020). To test for alpha diversity differences among experimental variables, mixed model analysis of variance (ANOVA) was performed using the "lmer" function from the lme4 package in R (Bates et al., 2015). The block factor nested within ecosystem was included as a repeated-measure, random effect. The repeated measures mixed model ANOVAs took the general form of (alpha diversity metric) ~ (fixed effect$_1$)*(fixed effect$_2$)* … *(fixed effect$_n$) + (1| Ecosystem:Block). This model design accounts for non-independence within blocks and repeated measures across time. Significant pairwise comparisons were determined using post hoc Tukey's HSD test. Figures were made using ggplot2 in R (Wickham, 2016) and formatted using Adobe® Illustrator 2021.

3. Results

3.1. Bacterial community composition and alpha diversity throughout the surface soil profile

We characterized community composition within all three surface soil layers: the leaf litter layer, 0–2 cm of bulk soil, and 0–10 cm of bulk soil. Bacterial composition differed across all surface soil layers in both the grassland and CSS (Fig. 2A, Tables S1 and S2; PERMANOVA: $P \leq 0.001$ in both ecosystems, all post-hoc pairwise comparisons significant: $P \leq 0.001$). Surface soil layer explained approximately 23% of the total variation in community composition across all samples (Table S1). Significant variance in dispersion was found across soil layers which may also contribute to the compositional differences found between layers (PERMDISP: $P < 0.05$) The phylum Proteobacteria displayed high relative abundance across all surface soil layers but was most dominant in the leaf litter layer (Fig. S2). Actinobacteria were also highly abundant throughout the surface soil, displaying similarly high abundance in the leaf litter and bulk soil. In contrast, the phyla Firmicutes and Acidobacteria comprised greater fractions in the bulk soil layers while Bacteroidetes exhibited higher relative abundance in the leaf litter. Compositional differences between the leaf litter and bulk soil communities were also apparent at the genus and ESV level (Figs. 2B and 3A, Tables S3 and S4). Although the majority (66%) of the 845 identified genera were shared between the leaf litter and bulk soil, 66 and 222 genera were unique to leaf litter and bulk soil respectively (Fig. 2B). Further, ESVs belonging to the genera *Massilia, Curtobacterium,* and *Pseudomonas* were characteristic of leaf litter communities while ESVs from *Bacillus* were characteristic of the bulk soil (Fig. 2B, Tables S3 and S4; SIMPER analysis).

Similar to community composition, bacterial richness and Shannon diversity also varied significantly between soil layers (Fig. 4; ANOVA: $P \leq 0.001$ for both metrics). The leaf litter layer contained lower observed richness and Shannon diversity than either bulk soil layer within each ecosystem (Fig. 4). Further, alpha diversity varied across soil layers in an ecosystem-dependent manner (Table S6; ANOVA: ecosystem by soil layer interaction, $P < 0.05$ for both richness and Shannon diversity). Specifically, alpha diversity varied significantly across all three soil layers in the CSS (post-hoc TukeyHSD: $P < 0.05$ for both metrics), but not between the 0–2 cm and 0–10 cm bulk soil layers in the grassland (Fig. 4).

3.2. Effect of ecosystem and temporal variation on bacterial composition and diversity across soil layers

At this site, ecosystem and temporal (seasonal and interannual) variability have been previously shown to affect leaf litter microbial community composition (Finks et al., 2021; Matulich et al., 2015). Here, ecosystem also significantly affected bacterial composition within all three surface soil layers (Fig. 2A, Table 1; PERMANOVA: $P < 0.05$ in all cases). The main effect of ecosystem explained approximately 13% of the observed variation in community composition within the leaf litter (18% when including ecosystem by sampling date interaction), and similar variation in 0–2 cm (15%) and 0–10 cm (12%) of bulk soil (Fig. 5, Table 1).

In both ecosystems, community composition also varied significantly across sampling dates, which encompassed both the wildfire and transition from the dry to wet season (Fig. S1B, Table S2; $P \leq 0.001$ in all cases). This temporal variation had the greatest impact in the leaf litter where it explained approximately 10% of the compositional variation. In contrast, bacterial communities in the bulk soil varied over time to a lesser extent, with sampling date explaining only 2.1% of the compositional variation in the top 0–2 cm and 1.4% in 0–10 cm (Fig. 5, Table 1). These temporal changes were visible at the genus level; most notably, the genus *Massilia* generally increased in relative abundance across the sampling period in all surface soil layers (Figs. 3B and S3). Temporal changes in bacterial diversity were also not uniform across soil layers nor ecosystems (Fig. S4). For instance, bacterial richness and Shannon diversity varied temporally in the CSS leaf litter (ANOVA: $P < 0.05$ in both cases) while remaining stable across time in all soil layers in the grassland (Table S7).

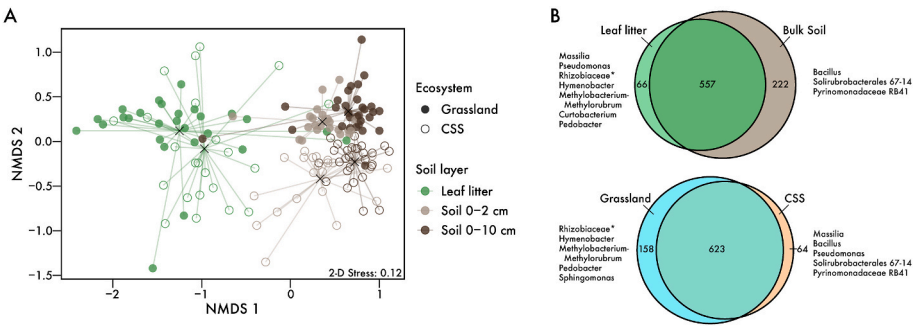

Fig. 2. (A) Non-metric multidimensional scaling (NMDS) ordination of surface soil and leaf litter bacterial community composition. Ecosystem type is distinguished by symbol shape. Symbol color represents soil layer: leaf litter (green), top 2 cm of soil (light brown), and top 10 cm of soil (dark brown). Centroids for each ecosystem by soil layer combination are included for clarity. (B) Number of bacterial genera unique to or shared between (intersections of circles) the leaf litter and bulk soil (top panel) and grassland and CSS (bottom panel). Top 10 bacterial genera or *families contributing to differences between the leaf litter and bulk soil communities (top panel) and ecosystems (bottom panel) (Tables S4 and S5; SIMPER analysis). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

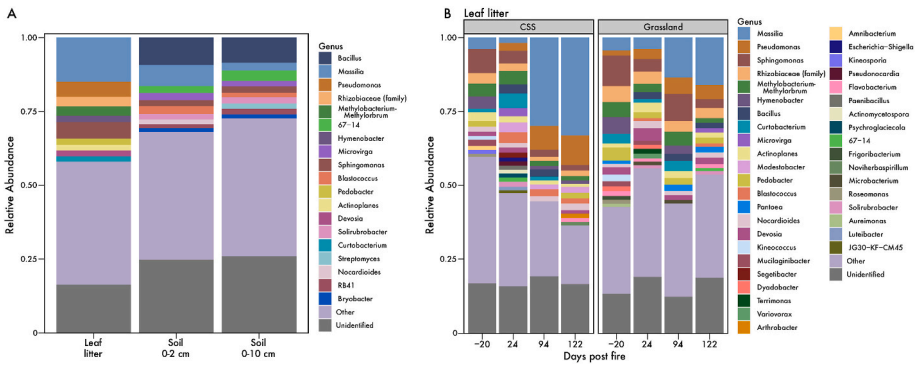

Fig. 3. Relative abundance of bacterial genera within (A) all three surface soil layers and (B) CSS and grassland leaf litter across the sampling period. "Other" genera represent (A) all classified genera outside the top 10 most abundant genera within each surface soil layer and (B) all classified genera below 1% relative abundance. (B) Days post fire indicates the passage of time between the sampling dates and Silverado fire (−20 = 20 days pre-fire).

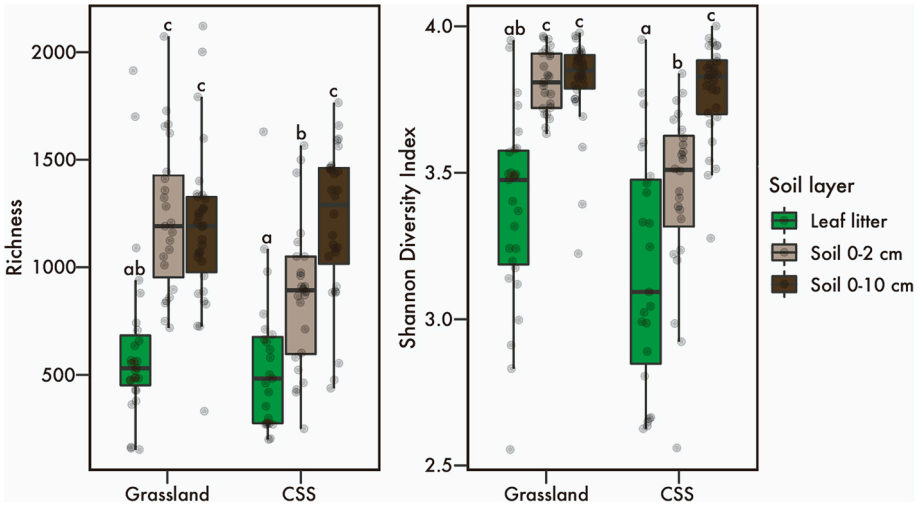

Fig. 4. (A) Bacterial richness and (B) Shannon diversity index across all three surface soil layers within the grassland and CSS. Letters indicate significant (Tukey's HSD, $p < 0.05$) differences between soil layers across ecosystems.

3.3. Influence of drought and wildfire on bacterial community composition and diversity across soil layers

Both drought and wildfire affected bacterial composition throughout the surface soil. Specifically, drought altered bacterial composition in all three surface soil layers (Table 1; PERMANOVA: $P < 0.01$ in all cases). The influence of drought decreased with depth, supporting our hypothesis. Drought treatment explained approximately 4.8% of the compositional variation within the leaf litter, 3.6% in the top 2 cm of bulk soil, and 1.6% in the top 10 cm of bulk soil (Fig. 5, Table 1). Consistent with previous studies at this site (Finks et al., 2021), drought altered bacterial composition in an ecosystem-dependent manner (Table S1; ecosystem-by-precipitation treatment interaction, $P < 0.01$). To tease apart the ecosystem-drought interaction, we reanalyzed the composition data within each ecosystem separately. Drought significantly altered bacterial communities in all three surface soil layers in the grassland ($P < 0.05$ in all cases). In contrast, drought only influenced 0–2 cm bulk soil bacterial composition in the CSS ($P < 0.05$) and did not affect leaf litter nor 0–10 cm bulk soil composition. Notably, drought did not alter bacterial richness nor Shannon diversity at any depth in either the grassland or CSS (Tables S6 and S7; ANOVA: $P > 0.05$ in all cases).

In addition to the drought treatment, we examined how a compounding wildfire disturbance influenced the bacterial communities. To assess the impact of wildfire, we compared bacterial composition and diversity between the first two sampling periods which occurred 20 days before the fire and 24 days after. The 0–2 cm bulk soil cores were not collected before the fire and were, therefore, excluded from this assessment. There was a significant timepoint by soil layer interaction when assessing bacterial composition across all leaf litter and 0–10 cm bulk soil samples collected in the first two sampling periods (PERMANOVA: $P < 0.01$). To investigate this interaction further, we re-analyzed community composition separately for the bulk soil and leaf litter samples. Post-fire community composition in the bulk soil did not differ significantly from pre-fire composition (Table S8; $P > 0.05$). However, the wildfire did alter leaf litter bacterial composition (Table S8; $P < 0.05$). In contrast to our predictions, the effect of the wildfire on bacterial communities was not influenced by historical precipitation regime (Table S8; timepoint-by-precipitation interaction, $P > 0.05$). Further, the wildfire did not influence bacterial alpha diversity (richness and Shannon diversity) in the leaf litter or top 10 cm of bulk soil layer in either ecosystem (Fig. S4; Welch *t*-test, $P > 0.05$ in all cases).

Although there was not a significant change in overall composition, there was a notable increase in the relative abundance of the genus *Massilia* (phylum *Firmicutes*) in both the leaf litter and bulk soil 94 days after the fire (Figs. 3B and S3) that persisted until at least 122 days post-fire. At 122 days post-fire, relative abundance of *Massilia* increased 8-fold from 3.9% pre-fire to 33% in the CSS and 3-fold from 4.4% to 16% in the grassland.

Table 1
PERMANOVA analysis of bacterial communities from surface leaf litter, top 2 cm of bulk soil, and top 10 cm of bulk soil separately. Significant factors and p-values are bolded. Asterisks indicate factors with a significant PERMDISP analysis ($P \leq 0.05$).

PERMANOVA						
Leaf litter samples						
Factor(s)	df	SS	MS	Pseudo-F	P	% Variance Explained
Ecosystem	1	8102.4	8102	3.31	**0.014**	12.97
Ecosystem X Precipitation treatment	1	2798.5	2799	1.46	0.076	–
Ecosystem X Sampling date	3	8514	2838	1.48	**0.018**	5.55
Precipitation treatment	1	4780.5	4781	2.50	**0.001***	4.77
Precipitation treatment X Sampling date	3	6053.1	2018	1.05	0.342	–
Sampling date	3	16008	5336	2.79	**0.001**	10.21
Block	8	21809	2726	1.43	**0.006**	6.10
Residuals	29	55475	1913			60.40
Total	49	131450				
Soil (0–2 cm) samples						
Factor(s)	df	SS	MS	Pseudo-F	P	% Variance Explained
Ecosystem	1	11330	11330	4.12	**0.030***	14.74
Ecosystem X Precipitation treatment	1	2517.5	2518	1.37	0.066	–
Ecosystem X Sampling date	2	3306.5	1653	0.90	0.707	–
Precipitation treatment	1	3912.3	3912	2.13	**0.003**	3.57
Precipitation treatment X Sampling date	2	3544.1	1772	0.97	0.551	–
Sampling date	2	5267.4	2634	1.44	**0.009**	2.06
Block	6	16539	2757	1.50	**0.001**	6.32
Residuals	31	56820	1833			73.30
Total	46	103330				
Soil (0–10 cm) samples						
Factor(s)	df	SS	MS	Pseudo-F	P	% Variance Explained
Ecosystem	1	10795	10795	4.04	**0.024**	12.24
Ecosystem X Precipitation treatment	1	2212.1	2212	1.18	0.166	–
Ecosystem X Sampling date	3	6203.9	2068	1.11	0.157	–
Precipitation treatment	1	2880.8	2881	1.54	**0.006**	1.55
Precipitation treatment X Sampling date	3	5514.4	1838	0.98	0.535	–
Sampling date	3	7040.5	2347	1.25	**0.021**	1.44
Block	6	15934	2656	1.42	**0.001**	4.76
Residuals	39	72949	1871			80.01
Total	57	124580				

4. Discussion

We investigated whether surface soil microbes respond differently to environmental change throughout three layers in the surface soil. In support of our main hypothesis, bacterial communities in all layers responded to drought, ecosystem type, and temporal variation, and the impact of these factors decreased with depth in the surface soil.

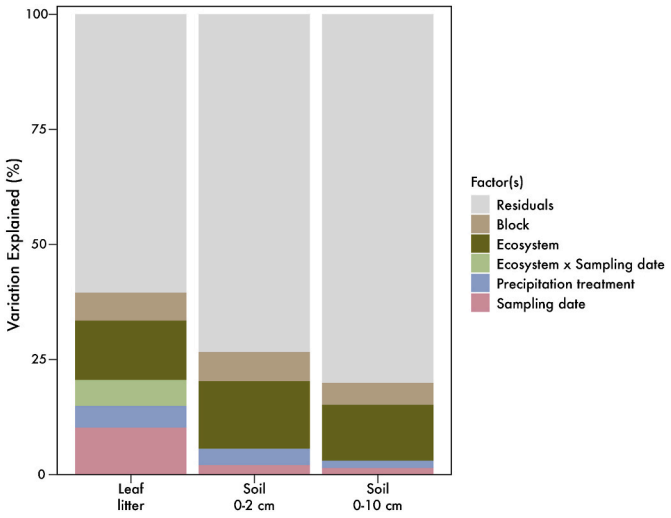

Fig. 5. Estimated percent variation explained for significant factors from mixed-effects PERMANOVAs (999 permutations) for bacterial communities within the leaf litter layer, 0–2 cm of bulk soil, and 0–10 cm of bulk soil.

However, contrary to our expectation, we found little evidence that historical precipitation regime influenced the initial bacterial response to a compounding wildfire disturbance.

4.1. Bacterial community composition and diversity vary between surface soil layers

Bacterial composition differed among depths within the top 10 cm of bulk soil, indicating that environmental conditions (e.g., moisture and temperature) and edaphic factors (e.g., pH and carbon availability) that drive bacterial composition in bulk soil vary throughout the top 10 cm, just as they do throughout the larger soil profile (Eilers et al., 2012; Stone et al., 2014; Zhang et al., 2017). Further, the leaf litter layer harbored a distinct bacterial community from the surface bulk soil in both the grassland and CSS. Leaf litter and bulk soil differ widely in physical and chemical properties. It is, therefore, unsurprising that microbial community composition and diversity varies between these surface soil layers. However, bacterial composition along the continuum from surface leaf litter into bulk soil is not well described, because leaf litter and bulk soil are often not sampled together from the same location (but see, e.g., Chemidlin Prevost-Boure et al., 2011; Urbanová et al., 2015). The leaf litter community also had lower average alpha diversity compared to the bulk soil communities. This pattern may reflect differences in nutrient availability, habitat heterogeneity, and differential exposure to more hostile aboveground conditions (i.e. UV intensity and temperature fluctuations) (Curd et al., 2018; Delgado-Baquerizo et al., 2017).

4.2. Surface soil bacteria respond to environmental change in a depth-dependent manner

Ecosystem type had the strongest impact on bacterial composition in all three surface soil layers. At this field site, the grassland and adjacent CSS experience similar climactic conditions. Thus, we attribute these differences in bacterial composition to plant community identity which varies between the CSS and grassland (Finks et al., 2021). Plant community structure is known to influence surface soil microbial communities. Plant species differences in litter quality and quantity alter microbial identity on leaf litter (Chapman et al., 2013; Malik et al., 2020). Plants also have species-specific effects on chemical and physical properties of soil (Bardgett et al., 2014; Waring et al., 2015). For instance, different plant species, such as grasses and forbs, release

unique types of root exudates into the surrounding soil, which can alter microbial composition and functioning (Haichar et al., 2008) even in bulk soil (Dassen et al., 2017; Eisenhauer et al., 2010).

Notably, the effect of ecosystem was relatively uniform across surface soil layers. In contrast, the bacterial response to other environmental conditions decreased with soil depth. For instance, the effect of temporal variation on leaf litter composition was approximately 5–10 times higher than that in bulk soil communities. This high degree of temporal variation in the leaf litter communities is consistent with previous studies in this system which found that seasonal variation has a greater influence on microbial composition than the drought treatment (Finks et al., 2021; Matulich et al., 2015). However, unlike previous surveys, partially burned leaf litter and charred soil samples were collected following the wildfire. Therefore, we cannot disentangle how much of the temporal change in community composition is due to the wildfire or temporal variability in the environment.

The bacterial community response to drought was also dampened deeper in the surface soil. The effect of drought on the bacterial communities in the leaf litter was approximately three times greater than that in the top 0–10 cm of bulk soil. Bacterial communities near the soil surface likely endure greater fluctuations in moisture than deeper layers, experiencing more rapid increases in moisture during a precipitation event and faster desiccation afterwards (Xu et al., 2012). Further, rainfall infiltration depth depends on rainfall intensity such that the low intensity rainfall events common to Southern California may not penetrate deep into the surface soil (Huang et al., 2013). These fluctuations potentially explain why the leaf litter layer displayed greater sensitivity to shifts in precipitation regime than either of the bulk soil communities. Even within the bulk soil itself, bacterial communities closer to the surface (0–2 cm) displayed a stronger response to the drought treatment than homogenized communities from the top 10 cm. This result suggests that using 10 cm soil cores to assess microbial response to environmental change may underestimate the effect of environmental conditions on microbes at the soil surface. Indeed, the overall amount of compositional variation that could be not explained by the above-ground treatments (the residual variation) increased with depth, indicating that other, unmeasured factors and/or the role of stochastic processes are more important to bacterial composition below 2 cm than at the surface.

The bacterial response to drought also occurred in an ecosystem-dependent manner. This ecosystem-dependent response may reflect trait differences between the grassland and CSS plant communities (i.e. canopy cover, transpiration rate, or water use efficiency). These factors can influence drought intensity by altering evaporation rate and rainfall infiltration at the soil surface (Becllot et al., 1999; Huxman et al., 2005). In both ecosystems at the LRGCE, drought has also been shown to alter plant composition and thus, litter quality and quantity (Finks et al., 2021). Therefore, drought may also affect leaf litter communities indirectly by altering litter type and amount. These drought-induced shifts in leaf litter bacterial composition can change litter decomposition rates, potentially altering C and N content in the underlying surface soil (Allison et al., 2013). Leaf litter manipulations have demonstrated that changing carbon substrate availability in the soil can alter microbial composition and community functioning, including respiration rate, C storage, and belowground decomposition of residual plant matter (Bowden et al., 2014; Chapman et al., 2013; Nottingham et al., 2009).

4.3. Bulk soil communities display an initial resistance to wildfire

To minimize confounding effects from intra-annual variation, we assessed the impact of the fire in the leaf litter and 0–10 cm of bulk soil by comparing community composition between samples collected 20 days before the fire and those collected 24 days post-fire. Bacterial composition in the leaf litter was significantly different between pre-fire and post-fire samples. Following the fire, we collected fully or partially burned leaf litter from the soil surface. Therefore, post-fire shifts in leaf litter composition may be due to chemical differences between unburned and pyrolyzed litter (Lammers et al., 2009). In contrast, bacterial composition in the bulk surface soil was not affected by the fire. Wildfire effects on soil bacterial communities have been found to persist for months (Ferrenberg et al., 2013; Yang et al., 2020) to years (Taş et al., 2014; Xiang et al., 2014) post-fire. This variation in the post-fire recovery of bacterial communities may be due to differences in ecosystem type, sampling period, sampling depth, and fire severity across studies (Pressler et al., 2019). However, our results are consistent with previous studies examining lower severity wildfires or prescribed burns which report little to no change in soil microbial composition (Kranz and Whitman, 2019; Sáenz de Miera et al., 2020). Thus, low severity fires may not increase soil temperature enough to elicit a measurable response from soil communities. However, we cannot exclude the possibility that bulk soil bacterial communities rapidly recovered from the perturbation in the 3 weeks between the wildfire and our first post-fire sampling period. Furthermore, we were unable to assess the short-term response of communities exclusively in the 0–2 cm of bulk soil which likely experienced a more intense heat during the fire than those throughout the top 10 cm (Raison, 1979).

Despite the lack of a significant change in overall bulk soil composition between the first two sampling periods, substantial increases in the relative abundance of the genus *Massilia* seen several months post-fire suggests that there may have been a delayed response to the fire. *Massilia* has been previously shown to respond positively to fire (Whitman et al., 2019) and was an early colonizer of freshly disturbed leaf litter at this field site (Albright and Martiny, 2018). When reprocessing 16S sequences from a previous leaf litter survey conducted from August 2016 to March 2018 at the LRGCE (Finks et al., 2021) through the same taxonomic classifier used in this analysis, we found that relative abundance of *Massilia* on leaf litter increased less than 2-fold between the dry and wet season in both the CSS and grassland. In contrast, in this study the relative abundance of *Massilia* increased over 8-fold in the CSS and over 3-fold the grassland between the pre-fire samples taken at the end of the dry season and those taken 122 days post fire in the middle of the wet season. This substantial relative increase in *Massilia* suggests that some temporal changes in community composition were likely related to the wildfire rather than temporal variation in the environment. However, our assessment of the wildfire effects on bulk surface soil bacterial communities is limited by our lack of unburned control samples at the field site and lack of historical soil samples from the LRGCE plots. Thus, further work is needed to assess the short- and long-term impacts of low-severity wildfires on bulk surface soil microbes.

5. Conclusions

The influence of environmental change on bacterial communities in surface soil has historically been studied independently from the surface leaf litter layer using 0–10 cm composite samples. Here, we show that bacterial communities at all depths in the surface soil respond to above-ground environmental change but do so in a depth-dependent manner. Microbial communities in both the leaf litter and surface bulk soil engage in carbon substrate transformation, storage, and respiration. Given that nutrients and metabolites diffuse throughout the soil matrix, changes to microbial communities in one soil layer can have cascading effects on those in surrounding layers. Thus, predicting how environmental change will alter microbially mediated carbon processing in surface soil requires consideration of interactions between the leaf litter and bulk soil.

Data statement

The raw amplicon reads are available through the NCBI Sequence Read Archive under BioProject accession number PRJNA816090.

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. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.soilbio.2022.108761.

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