### Title: Bacterial, Fungal, and Plant Communities as Indicators of Soil Organic Carbon Content and Dynamics

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Key Words:

Abstract

### Introductionxyz

Soil organic carbon (SOC) is central to soil health (Bradford et al., 2019). Increasing SOC content in soils can improve soil structure, water holding capacity, and fertility (Tisdall and Oades, 1982; Li et al., 2007; Smith, 2018). Additionally, soils hold more carbon than the atmosphere and total terrestrial biomass combined globally, the bulk of which is SOC. SOC is a dynamic pool which receives inputs from plants and releases carbon mainly via microbial respiration (Jobbagy and Jackson, 2000). Imbalances between these SOC inputs and outputs can therefore affect soil health and can cause soil to become a carbon source or sink to the atmosphere, thereby exacerbating or mitigating the problem of greenhouse gas-induced global warming (Schimel, 1995). Therefore, because SOC affects both soil health and the global climate, many recent land management efforts and policy initiatives have focused on maintaining and increasing SOC stocks (Rumpel et al., 2018; Bradford et al., 2019; Vermeulen et al., 2019).

To effectively manage SOC, land managers need to track both the size and the trajectory of the SOC pool. While measuring SOC is relatively simple—and measurement services are widely commercially available—detecting landscape-scale changes in SOC can be difficult. It may take several years for a measurable change in SOC to occur, and extensive sampling may be required to produce confident estimates of SOC stocks (Wiesmeier et al., 2019). Therefore, short-term, direct measurements of changes in SOC (as are often required by SOC policy initiatives) may not adequately capture the effects of management actions on soil (Saby et al., 2008). Furthermore, implementing and adapting SOC management strategies often occurs faster than SOC stocks can be reliably assessed (Harden et al., 2018). This makes it difficult for land managers to evaluate the effectiveness of their actions in time to change course. If reliable indicators of the size and trajectory of SOC stocks were available, land managers could make more informed decisions. Therefore, identifying proxy indicators of SOC change, both in space and time, is a crucial step toward the development of effective soil health management strategies (Bagnall et al., 2020).

There are several attributes that would make an indicator of SOC attractive. SOC indicators useful to land managers indicators should provide information and be sensitive to changes in management and climate on a spatial and temporal scale that matches the scale of management implementation (Powers & Schlesinger, 2002).Although processes that control stabilization and destabilization of SOC vary at micrometer scale, managers typically apply management efforts to larger units of land, such as entire pastures or slopes. (Alexander, 1964; Baveye, 2021; Kuzyakov & Blagodatskaya, 2015). Therefore, good indicators should provide information about average SOC content or trajectories of SOC stocks at this larger scale as well. Additionally, good indicators of SOC must be simpler or easier to measure than directly measuring SOC, or they should provide information that is not captured in direct measurement of SOC (Stott, 2019). For instance, indicators that predict future changes in SOC content or indicate recent changes in SOC content would provide useful information that isn’t apparent from direct measurements.

Because of the complex feedbacks that occur between SOC, biota, and other physiochemical ecosystem properties, many potential indicators do not have clearly resolved causal relationships with SOC (Boyd et al., 2015; Powers et al., 2015; Stott, 2019; Fierer et al., 2021a). While indicators could be directly or indirectly responsible for driving SOC gains or losses, they might also respond to SOC pool sizes. Alternatively, a good indicator may respond to external phenomena that also affect SOC, such as drought or a changing climate. Indeed, different types of relationships between indicators and SOC are not mutually exclusive - many potential indicators both drive and respond to SOC levels, while also responding to external processes that affect SOC. Despite the complexity of the relationships between potential indicators and SOC, indicators are still useful if they can predict SOC stock sizes or dynamics.

Ecological community structure may be a good indicator of SOC, as organisms both drive and respond to key processes in the carbon cycle. Plant communities, the original source of SOC, could be good indicators of SOC stocks or dynamics. Plant traits such as net primary productivity, relative allocation to aboveground and belowground biomass, or root exudate chemical composition can affect SOC formation (de Deyn et al., 2008; Rossi et al., 2020). Because these traits vary between species, the composition of species in the plant community may affect the overall rate of SOC formation at a site. For instance, replacement of perennial grasses with annual grasses has been associated with decreases in SOC (Koteen et al., 2011). Alternatively, plant community diversity could improve SOC storage by affecting ecosystem productivity and microbial activity (Catovsky et al., 2002; Lange et al., 2015; Chen et al., 2018). If this is the case, then land managers may be able to use observations of plant community composition to predict future changes in the SOC stock.

Plant community structure might also reflect the current status or recent history of the SOC stock. For instance, soils with more organic carbon tend to be more fertile (Oldfield et al., 2020). Furthermore, decomposing soil organic matter can supply of plant-available nutrients (Schimel and Bennett, 2004). Because nutrient supply can determine plant community structure, plant communities may respond indirectly to SOC stocks or SOC decomposition rates (Chapin et al., 1986; Wilson and Tilman, 1991a; Harpole et al., 2016). Also, disturbance or environmental changes could simultaneously affect both plant communities and SOC independently, in which case plants might function as useful indicators of SOC stocks (Wilson and Tilman, 1991b; van Miegroet and Olsson, 2011). Therefore, plant community composition could indicate the current status or recent changes in SOC composition.

Plants may be more useful indicators of SOC in surface soils than subsurface soils. Plant inputs to SOC occur largely from roots, which are more abundant closer to the surface (Jackson et al., 1996; Jobbagy and Jackson, 2000; Sokol et al., 2019). Additionally because roots are more abundant near the surface, surface soil SOC stocks may affect plant growth and plant community structure more than subsurface SOC stocks.

Bacterial and fungal communities may also be useful as SOC indicators (Bailey et al., 2002; Fierer et al., 2021; Pec et al., 2021). Microbes can control SOC by influencing the decomposition rates and the fate of carbon during decomposition (Schimel and Schaeffer, 2012). When microbes decompose organic carbon, some carbon is used to build microbial biomass, and some is respired as CO2 (Liang et al., 2017). Because microbial biomass can become stabilized in the soil, the partitioning of organic C between these two fates can affect the size of SOC stocks (Cotrufo et al., 2013). Different taxa of microorganisms may be adapted to different life history strategies that affect the rate of decomposition, or the partitioning of carbon during decomposition (Malik et al., 2020). For instance, some species produce extracellular enzymes to break down polymers while others do not (Allison, 2005). Some species invest more carbon in growth, while others invest more in stress tolerance (Malik et al., 2020). These differences, and therefore the taxonomic composition of the soil microbiome could indicate subsequent changes in the SOC stock.

Additionally, microbial diversity could influence the accumulation or loss of SOC. Higher microbial diversity is linked with faster decomposition, which could accelerate SOC loss (Wagg et al., 2014). Alternatively, faster nutrient cycling associated with more diverse microbial communities could support greater plant productivity, which could increase SOC stocks (van der Heijden et al., 2008; Delgado-Baquerizo et al., 2016a). Therefore, microbial diversity may be a good predictor of SOC dynamics, though its effect on SOC may depend on context.

Despite the hypothesized relationship between microbial community structure and soil carbon, it has been difficult to link microbial communities to important processes that control SOC. This may be because most microbe taxa can carry out important SOC-controlling processes, namely respiration and anabolism (Schimel and Schaeffer, 2012). Additionally, the rate of these processes is largely a function of physical accessibility of SOC to microbes, and not of microbial physiological traits (Dungait et al., 2012). As such, abiotic conditions such as soil moisture or temperature appear to control SOC decomposition and stabilization process rates, even though these processes are carried out by microbes (Orchard and Cook, 1983; Lloyd and Taylor, 1994; Kemmitt et al., 2008). Still, understanding functional traits of the microbial community may help predict SOC changes beyond simple responses to abiotic factor, but it is unclear how useful this approach is in practice (Allison et al., 2010).

Rather than predicting SOC changes, the soil microbial community structure may reflect to the current status or recent changes in SOC. Carbon rich soils may harbor copiotrophic microbes that thrive in the abundance of resources, while soils with less SOC might harbor oligotrophic microbes with more conservative survival strategies (Fierer et al., 2007). If soils recently gained or lost carbon, taxa may have benefited differentially from the processes that drove SOC changes, particularly if conditions that influence SOC-controlling processes. For example, rewetting of dry soil, which causes pulses in soil respiration, differentially affects growth and mortality of bacterial taxa, which could affect community structure (Blazewicz et al., 2020). Another example is the shift in functional composition of the microbial community in response to changes in SOC cycling associated with plant community succession (Shao et al., 2021). In these types of cases, microbial communities can indicate the current status or recent history of SOC at a site.

To assess the utility of ecological communities as SOC indicators at the temporal and spatial scale of land management, we monitored SOC stocks over a six-year period, and characterized plant, bacterial, and fungal communities during the same time period, to see whether ecological communities were able to predict SOC content or dynamics. We hypothesized that: 1) Plant community and microbial community structure can indicate the current size of the SOC pool 2) Plant and microbial community structure can indicate recent changes in the SOC, and 3) Plant and microbial community structure can predict future changes in the SOC pool. We also hypothesized that plant communities are better indicators for surface soils than subsurface soils, but that microbial communities are equally useful indicators in the surface and the subsurface.

### Methods

#### Site and Sample Design

The study site was located on Tomkat Ranch, a 728 hectare ranch in Pescadero, CA (37.261428, −122.360451). Tomkat Ranch uses a planned grazing approach on this property. The site experiences a Mediterranean climate with mild, relatively dry summers and cool wet winters. Mean annual air temperature is 12.9℃ and mean annual precipitation is 750 mm. Sample sites were located grasslands, which are mostly dominated by exotic annual grasses, with some native and non-native perennial grasses and forbs, as well as some shrubs. Dominant soil series sampled on Tomkat Ranch included Santa Lucia (Pachic, Ultic Haploxerolls, Clayey-skeletal, Mixed, Thermic), Dublin (Typic Pelloxererts, Fine, Montmorillonitic, Thermic), Cayucos (Typic Chromoxererts, Fine, Montmorillonitic Thermic), Pomponio (Typic Palexerolls, Fine, Montmorillonitic, Mesic), and Colma (Fine-loamy, mixed, superactive, mesic Typic Argixerolls).

To choose sample sites, we used a three-step approach. First, we identified a 250 msampling grid, spanning the entire property, based on the Military Grid Reference System, excluding areas of development, and buffered 100m from property boundaries (Porzig et al., 2018). We then used a used a Generalized Random Tesselation Stratification algorithm to select a spatially balanced subset of 30 sample points from this grid. Each sample site then included a 50 m radius circle surrounding the sample point, in which we assessed soil organic carbon, plant communities, and microbial communities.

#### Soil Sampling

We conducted soil sampling in January and February during 2014, 2015, 2018, and 2021. At each sample location, we sampled soil from five randomly chosen points within the 50 m radius circle. Soils were sampled either with a step probe, or by digging a pit and sampling from the face when probes weren’t feasible. We took separate samples from the surface (0-10 cm), and from the subsurface (10-40 cm). Soils from all five sample pits were mixed for each depth at each point, resulting in two composited samples for each plot - one from 0-10 cm and one from 10-40 cm. Samples from 4 sites were taken in 2014, and 26 were taken in 2015. These 30 sites were resampled in 2018, and 15 were resampled in 2021 (Table 1). Upon resampling, the 5 soil pits or probes were taken 1m directly west of the previous sample, in order to avoid sampling soil from sites where previous sampling had disrupted soil structure.

Separate samples were taken for the microbial community in April 2018. In order to produce a sample of the microbial community representative of the whole sample area, at each site we sampled with a sterilized step probe at five locations within the 50-m radius circle. Each sample was split into 0-10cm and 10-40 cm layers, and soils from each depth were combined into a composite sample for a total of 30 samples from each depth. Samples were stored in a whirlpak, and frozen until analysis.

#### Soil Measurements

Soil samples were sent to the University of Idaho Soil Analytical laboratory for texture and SOC analysis. To measure SOC, each sample was pre-treated with acid to remove carbonates, and organic carbon content was determined with an Elemental Analyzer. Soil texture was determined using a hydrometer method to measure relative content of sand, silt, and clay.

#### 16S and ITS Bioinformatics

To quantify bacterial and archaeal communities (henceforth called bacterial communities), we One sample did not produce good quality sequencing data from 0-10 cm, so there were a total of 29 samples from 0-10cm and 30 samples from 10-40 cm.

Explain DNA stuff here

Only forward reads were used for the ITS samples due to low quality reverse reads. Fungal sequences were demultiplexed using QIIME 2 (version 2020.8.0) and filtered using DADA2 (version 1.22.0) with no allowed ‘N’ calls, a maximum of 2 expected errors, and truncated at quality scores of 2 or less for a minimum length of 50bp. After filtering, XX percent of reads were retained for an average of XX reads per sample (min. XX, max XX). We did not rarefy our sequences due to the potential for false positives in differential abundance and maintained ASVs in order to capture the widest diversity of fungi in our samples (McMurdie & Holmes, 2014). Fungal sequence variants were given taxonomic assignments through the UNITE database (Nilsson et al., 2019) (Wright, 2020) and assigned to functional guilds using the FUNGuild database (Nguyen et al., 2016).

#### Plant Community

We assessed plant communities by running two 50 meter transects in opposite directions, from the center to the edge of each sample location. Transects were run at a random direction from the center. Upon resampling, transects were run in the same direction as transects from the first visit. To survey vegetation along the transect, we dropped a steel pin every 1 meter. We recorded every herbaceous species touching the pin. If the pin or the vertical projection of the pin touched woody vegetation, the woody vegetation was recorded as a canopy species (Porzig et al., 2018). We surveyed the same 30 sites that were sampled for soil in the spring of 2018 when most plants were close to maturity and were therefore identifiable. We were only able to return to sample 15 of these sites in 2021, due to pandemic-related complications.

#### Statistics

In all models, we used SOC as a dependent variable, and ecological community metrics as independent variables. Even though cause and effect can go both ways when considering SOC and biota, we tested associations this way because we wanted to understand whether ecological community metrics could be used to predict SOC outcomes. Furthermore, because the size of each layer differed, and because we *a priori* expected different SOC content and rates of change in each layer, we did not see surface and subsurface soils as suitable for comparison in the same statistical models. Therefore, for all analyses, surface and subsurface SOC content were treated as separate response variables. Additionally, because 4 points were sampled in 2014 and the remaining 26 were sampled in 2015, we lumped these points together to calculate changes that preceded sampling in 2018. For brevity, these changes are referred to henceforth as SOC content changes for 2015-2018.

Analyses were conducted in R version 4.1.2 using the package *vegan* (Oksanen et al., 2020). For plant, bacterial, and fungal communities, we calculated relative abundance of each species or ASV, and then calculated Bray-Curtis distance and used non-metric multidimensional scaling (NMDS) to ordinate data. For fungal and bacterial data, we used 2 NMDS axes. For plant community data, we ordinated herbaceous and woody community data separately, using 3 NMDS axes for the herbaceous community cover, and 2 for woody cover. For microbial community data, because sample depth was a major driver of community composition, we ordinated data from each layer separately for subsequent analyses, in order to best capture variation in community structure that existed within each layer. We then used NMDS ordination scores for 2018 plant and microbial data along with soil texture data as covariates in variation partitioning analysis to quantify the relative significance of each group of explanatory variables to predict 2018 SOC stocks, 2015-2018 SOC changes, and 2018-2021 SOC changes.

Following variation partitioning analysis, we regressed SOC content and changes against NMDS scores using the function *envfit,* in orderto examine relationships between community composition, SOC stocks, and changes in SOC storage. Because two data points contained much higher SOC content than the rest of points, we ran a second round of analyses excluding these points to check whether they had an outsized influence on statistical associations between community structure and SOC.

For fungal communities, we followed these analyses by using linear regression to test whether specific functional guilds of fungi predicted SOC stocks or dynamics. Because FUNGuild can attribute multiple guilds to a taxon if its function is unknown or if its function varies by context, we calculated relative abundance only from guilds with a known single functional type. By this function, we calculated saprotroph abundance (including plant, leaf, wood, litter, and soil saprotrophs) and mycorrhizal abundance (including arbuscular, ecto-, ericoid, and orchid mycorrhizae).

In bacterial communities, after testing associations between community composition and SOC stocks or change, we sorted taxa into functional groups of copiotrophs and oligotrophs. This sorting was only done for taxa belonging to phyla for which these classifications had been previously published. As such, *Verrucomicrobia* and *Acidobacteria* were classified as oligotrophs while *Proteobacteria*, *Bacteroidetes*, *Actinobacteria*, and *Gemmatimonadates* were classified as copiotrophs (Fierer et al., 2007; Shao et al., 2021). Following this classification, we calculated the ratio of copiotrophs to oligotrophs (C:O) in the bacterial community and used linear regression to test relationships between this ratio and SOC at each depth. Additionally, we calculated species richness of each sample, and used linear regression to test associations between richness and SOC stocks.

For vegetation, we used *envfit* to test associations between species composition NMDS scores and SOC at each depth. When we found significant associations, we followed by using regression to examine relationships between the relative cover of functional groups and SOC changes. Additionally, we calculated Shannon-Weaver diversity for the herbaceous community at each site from 2018 and 2021 and used linear regression to test associations between diversity and SOC stocks. Furthermore, because vegetation data was taken in multiple years, to characterize changes across years, we simply took the difference between the standardized herbaceous community composition at the same sites in different years. We then calculated Euclidean distance for the matrix of community composition change and used NMDS to ordinate these data. We then used linear regression between NMDS scores for community composition change and changes in SOC over the same time period. When we found significant associations, we followed by examining associations between changes in specific functional groups and changes in SOC.

### Results

Mean SOC content was lower in 2018 than in 2014 and 2015, and was lower in 2021 than in 2018 for both 0-10 cm and 10-40 cm. However, because only half of the points were measured in 2021, the measured points actually showed a mean increase in SOC from 2018 to 2021 (Table 2).

#### Variation Partitioning

The variation partitioning model of 2018 SOC content, which included ordinations of plant communities, bacterial communities, and fungal communities, predicted 73% of variation for 0-10cm (Fig. 2A) and 71% of variation for 10-40cm (Fig. 2B). Fungal communities were the strongest predictors of SOC content in surface soil, explaining 28% of variation individually, though plant and bacterial communities also explained 6% and 19% of variation respectively (Figure 2A.). Bacterial communities were the strongest individual predictors of SOC content in the subsurface, explaining 25% of variation individually, while plant community structure explained 1% of variation and fungal communities explained 7% (Figure 2B). Variation partitioning models did not effectively explain past changes in SOC content between 2014 and 2015-2018 in surface soils, or in subsurface soils (Fig 2C-D). Variation partitioning models predicted 58% of variability SOC content changes between 2018 and 2021 in surface soils (Fig 2E). For these models, plants communities individually explained 6% of variation, bacterial communities explained 18%, and fungal communities explained 14% of variability, with 52% of explained variability shared between plant and fungal communities (Fig 2E). Variation partitioning models did not explain any of the variance in SOC content changes 2015-2018 from subsurface soils over the same time period, though fungi and bacteria individually explained 35% and 17% of variability respectively (Fig 2F).

#### Microbial Community

Bacterial communities were dominated by ASVs from the phyla *Verrucomicrobia*, *Acidobacteria*, and *Proteobacteria*. Bacterial community NMDS scores in the 0-10cm layer predicted SOC content (r^2 = 0.3392, p = 0.006) (Figure3A). However, 2018 bacterial community NMDS scores did not predict recent changes in SOC content from 0-10 cm (r^2 = 0.0385, p = 0.606) (Figure 3A). Similarly, the bacterial community NMDS scores in the 10-40cm layer predicted current SOC content (r^2 = 0.5590, p = 0.001) but did not predict recent changes in SOC content (r^2 = 0.0508, p = 0.531). These associations held even when outlier points were excluded from analyses (Figure S3). Bacterial community NMDS scores did not predict future changes in SOC content in either the 0-10 cm layer (r^2 = 0.209, p = 0.277) or the 10-40 cm layer (r^2 = 0.048, p = 0.72).

The six phyla that were classified into functional groups represented an average of 85.9% of sequences (range 72.4 - 91.5%). The mean C:O was 0.79±0.25 for the 0-10 cm layer and 0.44±0.10 for the 10-40 cm layer. The C:O ratio and depth predicted SOC content in the surface (effect = 2.617, r^2 = 0.249,p = 0.0058), and in the subsurface (effect = 3.829, r^2 = 0.1989, p = 0.0135) (Figure 4). The association between C:O and SOC remained significant even when outlier points were excluded in surface soils but not in subsurface soils. C:O in 2018 did not predict changes between 2015 and 2018 in the surface (p = 0.886) or in the subsurface (p= 0.244). However, higher C:O in 2018 predicted greater losses or smaller increases in SOC between 2018 and 2021 in both the surface (effect = -0.6096, r^2 = 0.31, p = 0.0386) and in the subsurface (effect = -1.1871, r^2 = 0.31, p = 0.0310) (Figure 5).

The mean bacterial ASV richness for bacteria was 1443.1±218.2 in the surface and 1146.72±190.0 in the subsurface. Bacterial ASV richness did not predict SOC stock size in surface soils (p = 0.238) or in subsurface soils (p = 0.590). Bacterial richness in 2018 did not predict changes in SOC between 2015 and 2018 in the surface (p = 0.267) or subsurface (p = 0.590). However, 2018 richness weakly predicted changes between 2018 and 2021 in the subsurface (effect = -0.00047, r^2 = 0.195, p = 0.09965), but not in the surface (effect = -0.00052, r^2 = 0.1498, p = 0.172) (Figure 6).

#### Fungal Community

Mean fungal ASV richness was 958.3 ± 205.0 in the surface and 627.5 ± 198.7 in the subsurface. Higher fungal ASV richness predicted higher SOC content in surface soils (effect = 0.003, r^2 = 0.2973, p = 0.00222) (Figure 7). This effect remained even when outlier points were removed from analysis. Fungal ASV richness did not predict SOC content in subsurface soils (p = 0.571). Furthermore, 2018 fungal ASV richness failed to predict SOC content changes between 2015 and 2018 in surface soils (p = 0.944) and in subsurface soils (p = 0.654). Fungal ASV richness in 2018 also did not predict changes in SOC content between 2018 and 2021 in surface soils (p = 0.604) or subsurface soils (p = 0.360).

Fungal community NMDS scores predicted SOC content in surface soils (r^2 = 0.4483, p = 0.004) and in subsurface soils (r^2 = 0.6037, p = 0.001) (Figure 7). This relationship remained significant even when we excluded outlier points from analysis (Figure S4). Fungal community NMDS scores from 2018 did not predict changes in SOC content between 2015 and 2018 in surface (p = 0.578) or subsurface soils (p = 0.894) (Figure 7). Fungal community NMDS scores in 2018 also did not predict SOC content changes between 2018 and 2021 in surface (p = 0.29) and subsurface soils (p = 0.732).

Fungal taxa that could be identified as mycorrhizal or saprotrophic comprised and average of 56.2±11.9% of reads in the surface, and 54.9±13.7% of reads in the subsurface. For both functional groups relative abundance failed to predict current SOC content or changes in SOC content between 2015 in 2018 at either depth. However higher relative abundance of saprotrophic fungi predicted greater increases in SOC between 2018 and 2021 in surface soils (effect = 1.1882, r^2 = 0.3102, p = 0.0385), though not in subsurface soils (p = 0.484). Relative abundance of mycorrhizal fungi in 2018 did not predict changes in SOC between 2018 and 2021.

#### Plant Community

Herbaceous plant communities were dominated by annual grasses, mainly *Brachypodium distachyon*, *Festuca bromoides*, *Festuca perennis*, and *Bromus hordeaceus*. Annual forbs were the next most common growth form, with *Plantago lanceolata*, *Geranium dissectum*, *Linum bienne*, and *Conium maculatum*. Common perennial grasses included *Phalaris aquatica*, *Danthonia californica*, and *Stipa pulchra*.

Herbaceous community NMDS scores predicted current SOC content in the 0-10 cm layer (r^2 = 0.3847, p = 0.006) and for the 10-40 cm layer (r^2 = 0.4370, p = 0.001) (Figure 10). However, there was no functional group of plants for which relative cover predicted differences in SOC. Herbaceous community NMDS scores from 2018 did not explain recent changes in SOC content from 2015 to 2018 in the surface (p = 0.775) or the subsurface (p = 0.739) (Figure 10). However, 2018 herbaceous community NMDS scores explained changes in SOC content from 2018 to 2021 in the surface (r^2 = 0.5987, p = 0.007), but not from the 10-40 cm layer (r^2 = 0.17, p = 029724) (Figure 11).

There was no functional group measured in 2018 for which relative cover predicted current SOC content or SOC changes between 2015 and 2018. Sites with a greater perennial grass cover in 2018 gained less or lost more SOC in the surface (effect = -0.98, r^2 = 0.3568, p = 0.0187) and in the subsurface (effect = -0.6655, r^2 = 0.3637, p = 0.0173) (Figure 12). However, sites that had larger increases in perennial grass relative to annual grass between 2018 and 2021 had greater gains in carbon in the 0-10cm layer (effect = 0.36, r^2 = 0.24, p = 0.0621), though not in the 10-40cm layer.

Plant community Shannon-Weaver diversity in 2018 did not effectively predict SOC stock size in surface (p = 0.7050) or subsurface soils (p = 0.567). 2018 Shannon-Weaver diversity also did not not explain changes in SOC stocks between 2015 and 2018 in surface soils (p = 0.569) or in subsurface soils (p= 0.798). Similarly, Shannon-Weaver diversity didn’t predict future changes in SOC stocks in the surface (p = 0.865) or the subsurface (p = 0.466). Changes in Shannon-Weaver diversity between 2018 and 2021 also did not predict changes in SOC over the same time period in the surface (p = 0.4614) or the subsurface (p = 0.4705).

Cover of woody vegetation in 2018 did not predict current SOC stock, recent changes, or future changes. However, changes in woody cover between 2018 and 2021 predicted changes in SOC in the 0-10cm layer, with plots where woody cover increased more tending to gain less SOC (effect = -0.82105, r^2 = 0.2394, p = 0.0642) .

### Discussion

Developing indicators of SOC will help land managers make decisions about how to manage land for soil health. In this study, we found that both plant communities and microbial communities can indicate either the size or the trajectory of the SOC pool in rangeland ecosystems, but that different indicators may serve different purposes.

#### Bacterial Communities as Indicators

Prokaryote communities were moderately effective predictors of SOC content both in surface and subsurface soils. However, they seemed to be ineffective indicators of the trajectory of the SOC stock, they were unable to predict recent changes or future changes in SOC content. Classifying microbial phyla into copiotrophs and oligotrophs improved the effectiveness of the microbial community as an indicator of SOC stocks.

Fundamentally, it is unsurprising that prokaryote communities would reflect the content of SOC at the time of sampling. Microorganism populations can grow quickly under favorable conditions and undergo rapid mortality when conditions change. Therefore, microbial communities would be expected to equilibrate rapidly to new conditions. This explains why prokaryote communities would only reflect current SOC content, and not past or future changes in SOC, at least on the three year resample schedule that we followed.

The copiotroph:oligotroph ratio was a good predictor of SOC content. Within each depth layer, sites with a greater relative proportion of copiotrophs had more SOC. This pattern tracked across depths too, as soils from 10-40cm had a greater proportion of oligotrophs, which corresponds with their lower SOC content. Copiotrophic microbes have higher demands for resources, and exhibit faster growth rates when resources are abundant, whereas oligotrophic microbes have lower resource demands, and are expected to compete well when resources are scarce. Therefore, the pattern in our data provides additional evidence for the ecological coherence of the six phyla that were categorized into functional groups.

Higher bacterial ASV richness was associated with greater SOC stock size in the surface but was unrelated to SOC stock size in the subsurface. This result concurs with other results that associate higher SOC content has been associated with greater microbial diversity (Delgado-Baquerizo et al., 2016b; Yang et al., 2018). It is not clear from our data why this pattern only holds in the surface, but one reason might be the physical status of carbon in the subsurface. A greater fraction of carbon in subsurface soils tends to be stabilized, mineral-associated organic matter (Kögel-Knabner et al., 2008). Although we did not measure physical fraction of SOC, this is likely the case for the soils in this study as well. If more subsurface carbon is not accessible to microbes, SOC stock may not have as direct an effect on bacterial diversity community structure in the subsurface.

In contrast, higher bacterial ASV richness in 2018 was weakly associated greater losses or lower gains in SOC between 2018 and 2021 in the subsurface but was not strongly related to SOC changes in the surface. This relationship in subsurface soils may be because more diverse communities can exploit resources more effectively. Because the bacteria are responsible for returning carbon to the atmosphere via respiration (Liang et al., 2017), bacterial communities that more efficiently exploit soil carbon may drive losses in SOC over time. The differing results in the subsurface and subsurface may be related to the relative importance of bacteria in each area. Bacterial communities tend to be more dominant in subsurface soils, whereas surface soils are often more influenced by roots and by fungal communities (Fierer et al., 2003). This may explain why bacteria are less effective as predictors of SOC changes in the surface than in the subsurface.

Although prokaryotic communities predicted current SOC content, their utility as an indicator for SOC is probably limited. Characterizing prokaryotic communities takes far more time, resources, and expertise than just measuring SOC directly. However, the fact that plot-level measurements of bacterial communities corresponded with plot-level SOC measurements is notable. This suggests that larger-scale aggregate measurements of bacterial communities may have some power to explain other ecosystem measurements at the same scale, despite the small scale heterogeneity exhibited by soil bacterial communities. Bacterial diversity also weakly predicted future changes in SOC in subsurface soil. Measurements of bacterial diversity therefore might be useful for predicting changes in SOC, particularly in areas of soil that are less dominated by plant and fungal biomass.

#### Fungal communities as indicators

Fungal community composition was a strong predictor of SOC content both in surface and subsurface soils. However, neither saprotroph nor mycorrhizae relative abundance predicted SOC content. This apparent contradiction suggests that perhaps specific taxa rather than entire functional groups were associated with SOC content. Functional groups are classified in FUNGuild by the method that they use to acquire resources, but this result suggests that this method of classification may not reflect how fungal communities respond to SOC. Fungal functional classification by trophic mode differs from our method of bacterial functional classification, which was related to rates of resource use. For instance, even though all fungi within the saprotroph guild decompose organic matter to acquire resources, different taxa may have different resource demands, and so may become more or less dominant as organic matter becomes more or less available. Therefore, classification of fungi by trophic mode may not be an effective strategy for indicating SOC content.

However, even though total community composition did not predict future changes in SOC stocks, saprotroph abundance was a good predictor of future changes, as sites with more saprotrophs in 2018 gained more carbon between 2018 and 2021. It is not immediately clear why this would be the case, as saprotrophs survive by decomposing organic matter, and thus should be responsible for SOC losses. Perhaps saprotrophs use carbon more efficiently, leading to stabilization of more SOM than other fungal guilds. Saprotrophs may also contribute to accelerated nutrient cycling, boosting primary productivity and subsequent SOC inputs. Alternatively, the presence of saprotrophs may reflect litter or root carbon input rates to soil, with sites that receive greater inputs supporting more saprotrophs. This could also explain why sites with a greater share of saprotrophs gained more carbon.

Fungal community diversity positively predicted SOC content in surface soils but not in the subsurface. Overall, fungal diversity was higher in the surface, where SOC content was also higher. Higher SOC content may act as a greater resource pool for fungal communities reducing competition so that more species may coexist.

These results suggest that fungal communities have some capacity to act as SOC indicators. However, it is unclear whether existing functional classification schemes are appropriate for relating fungi to SOC. Finding classification schemes based on resource use rather than trophic mode may make fungal communities more effective as SOC indicators.

#### Plant Communities as Indicators

Like prokaryotic communities, herbaceous plant community composition predicted SOC stock size, for both the surface and subsurface layers. However, no specific functional group of plants was associated with SOC content. Herbaceous community composition was not useful for predicting recent SOC changes, but was useful for predicting future SOC changes in the 0-10cm depth. Sites with greater relative cover of perennial grass in 2018 had lower increases in SOC from 2018 to 2021. However, sites where perennial grass cover decreased between 2018 and 2021 also had lower increases in SOC over the same time period.

Plant community composition would be expected to be associated with SOC content. Plants are the source of SOC, so species that are more productive or that produce more roots might be expected to contribute to greater SOC stocks. Additionally, SOC content affects soil conditions, which could affect plant community assembly. Indeed, prior work in California grasslands has found that perennial grass cover is generally associated with greater SOC content. While we did find that overall plant species composition was associated with SOC content, we did not find relationships between SOC content and perennial grass cover, or any other functional group. This makes it difficult to establish plants as an indicator for SOC content. Particular combinations of species may be common in our sample points that have more SOC, but it is not obvious that it would be appropriate to use these species as indicators at locations beyond our study site.

Herbaceous plants also were associated with changes in SOC from 0-10cm depth, but not from 10-40cm. Sites with a higher ratio of perennial grass to annual grass cover in 2018 subsequently gained less or lost more SOC between 2018 and 2021. This result is in contrast with previous work from this region showing that replacement of native perennial grass species with non-native annual grasses has led to losses in SOC (Koteen et al., 2011). This difference may be because in our study, a perennial grass cover was largely driven by *Phalaris aquatica*, a non-native perennial grass. This suggests that the growth form of grass is not necessarily as important. Rather, it may be the case that differences in SOC content between native and non-native dominated grasslands are due to site history – disturbance events that facilitated the establishment of non-native species may have also led to losses in SOC. As such, cover of perennial grass may be problematic as an indicator of SOC if the specific species aren’t accounted for.

Herbaceous diversity was not related to SOC stock size, or future changes, but did indicate recent changes in SOC in surface soils, with higher diversity reflecting greater SOC losses. This contrasts with previous work that suggests a positive relationship between plant diversity and SOC (Fornara and Tilman, 2008; Lange et al., 2015; Yang et al., 2019).

Increasing woody vegetation between 2018 and 2021 had a negative relationship with SOC accumulation over the same time period. Gains in woody vegetation in our site are mostly caused by encroachment of the native shrub *Baccharis pilularis*. Thus, our results conflict with previous work that suggests that invasion of *B. pilularis* in California grasslandsleads to increases in soil carbon (Zavaleta). This difference might be caused by the different time periods of the study - Zavaleta et. al observed linear increases in soil carbon over a 25 year period. Perhaps, encroachment is initially associated with processes that cause SOC losses, but these losses may be regained in the long term as ecosystems become shrub-dominated. Either way, these conflicting results make woody encroachment an ambiguous indicator of changes in SOC. Still, invasion of shrubs into grasslands is easy to observe and is already a management concern in rangeland ecosystems, so relationships between woody encroachment and SOC are worthy of more direct investigation.

#### Plants as Static or Dynamic Indicators

When identifying indicators of SOC or other soil health metrics, it is important to consider whether the status of an indicator at a single time point or the dynamics of an indicator through time are more important. This distinction is illustrated by the relationship between woody vegetation cover and SOC in our study. If we considered woody vegetation cover as a static indicator at a single time point in 2018, we would be left with the conclusion that it is unrelated to changes in SOC. However, when we consider woody vegetation as a dynamic indicator, and look for changes in woody cover through time, we can see that sites that gain woody vegetation tend to lose carbon as well. Therefore, considering woody cover as a dynamic or static indicator could lead to differing conclusions.

This result shows the importance of considering the distinction between dynamic and static indicators when identifying indicators of SOC. Measuring a static indicator at a single time point would be informative about the status or trajectory of the SOC pool. Measurements of dynamic indicators, however, are only informative if taken over time. Assessing changes in a dynamic indicator over time can be informative about changes in the SOC pool over the same time period. However, if a dynamic indicator is only measured at a single time point, it may not give any information about SOC, or it might even be misleading.

#### Conclusions

Biological communities can indicate SOC, but different measurements indicate different things. Both plant and microbial communities worked as static indicators of SOC stock size. However, given the cost and expertise required to characterize microbial communities, they are unlikely to be very useful as an indicator. Plant communities may be more useful as dynamic indicators of changes in SOC stocks, at least for surface soils. Observing changes in plant communities through time may be more useful to indicate changes in SOC than assessing plant communities at any single time point. Researchers should consider the distinction between dynamic and static indicators when trying to identify indicators of SOC or other soil health metrics.

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