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Linking soil microbial community structure to potential carbon mineralization: A continental scale assessment of reduced tillage

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Linking soil microbial community structure to potential carbon mineralization: A continental scale assessment of reduced tillage

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Abbreviations: ASV, amplicon sequence variant; Cmin, 24-h potential carbon mineralization; PERMANOVA, permutational multivariate analysis of variance; NAPESHM, North American Project to Evaluate Soil Health Measurements.

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ABSTRACT

Potential carbon mineralization (Cmin) is a commonly used indicator of soil health, with greater Cmin values interpreted as healthier soil. While Cmin values are typically greater in agricultural soils managed with minimal physical disturbance, the mechanisms driving the increases remain poorly understood. This study assessed bacterial and archaeal community structure and potential microbial drivers of Cmin in soils maintained under various degrees of physical disturbance. Potential carbon mineralization, 16S rRNA sequences, and soil characterization data were collected as part of the North American Project to Evaluate Soil Health Measurements (NAPESHM). Results showed that type of cropping system, intensity of physical disturbance, and soil pH influenced microbial sensitivity to physical disturbance. Furthermore, 28% of amplicon sequence variants (ASVs), which were important in modeling Cmin, were enriched under soils managed with minimal physical

disturbance. Sequences identified as enriched under minimal disturbance and important for modeling Cmin, were linked to organisms which could produce extracellular polymeric substances and contained metabolic strategies suited for tolerating environmental stressors. Understanding how physical disturbance shapes microbial communities across climates and inherent soil properties and drives changes in Cmin provides the context necessary to evaluate management impacts on standardized measures of soil microbial activity.

1. Introduction

Over the past few decades numerous biologically based measurements have been designed to assess how reducing physical disturbance in row-cropping systems impact soil functioning (e.g., cycle nutrients, decompose organic matter) and overall soil health. Current measurements used by the scientific community to evaluate soil heath include microbial biomass, available carbon and nitrogen pools for microbial consumption, and potential carbon and nitrogen mineralization (Acosta-Martinez et al., 2018; Culman et al., 2012; Gonzalez-Quiñones et al., 2011; Li et al., 2020; Norris et al., 2020). Greater values recorded in systems with reduced physical disturbance, when compared to intensively disturbed fields, are commonly interpreted under the assumption, "more is better" (Andrews et al., 2004; Haney et al., 2010, 2018; Moebius-Clune et al., 2016). However, greater values from these measurements are difficult to interpret because the measurements are not directly tied to increases in soil function, such as providing adequate plant nutrition or improved ecosystem health (e.g., increased carbon storage, reduced nitrogen losses) (Fierer et al., 2021). Understanding why these widely use measurements respond positively to adoption of reduced physical disturbance will allow for appropriate interpretations of the measurements and therefore allow stakeholders to understand how management choices affect soil function.

One measure of potential microbial activity related to soil health is potential carbon mineralization (Cmin). Soil microbial community members respire carbon dioxide as a metabolic waste product while degrading organic matter and cycling nutrients. Standardized Cmin assays report carbon dioxide fluxes following rewetting of air-dried, sieved soil under aerobic conditions (Zibilske, 2018), such as from either a 24- or 96-h incubation, among other modifications (Haney Soil Health Test or the Cornell Comprehensive Assessment of Soil Health, respectively) (Haney et al., 2010; Moebius-Clune et al., 2016). Potential carbon mineralization values are generally greater in systems employing reduced tillage across many soil types and climates (Nunes et al., 2020). However, the greater Cmin measurements identified in the standardized laboratory assay conflict with *in situ* carbon mineralization measurements, where soils managed for reduced physical disturbance respire less carbon dioxide than their less disturbed counterparts (Abdalla et al., 2016). Nonetheless, Cmin is often interpreted as *in situ* basal mineralization (Haney et al., 2018). Mineralization resulting from standardized Cmin assays are a combination of the consumption of newly lysed cellular material, fresh metabolic material exuded during rewetting, and newly available organic residues following pretreatment of the soils (Fierer and Schimel, 2003; Kaiser et al., 2015). Identifying the groups of organisms responsible for driving greater Cmin values in soils managed for minimal physical disturbance will help provide a scientifically backed interpretation of this already widely used measurement, rather than relying on the assumption, "more is better."

While Cmin generally increases in soils managed for minimal physical disturbance, the impact of physical disturbance on microbial community structure has varied among site-specific studies. Many studies of physical disturbance and community structure report significant changes in both community structure and community diversity in response to disturbance treatments (Ceja-Navarro et al., 2010; De Quadros et al., 2012; Schmidt et al., 2018; Sengupta and Dick, 2015; Srour et al., 2020; Z. Wang et al., 2016), while just as many others report a significant change in only one of the two metrics (Navarro-Noya et al., 2013; Ng et al., 2012; Schlatter et al., 2019; Schmidt et al., 2019; Smith et al., 2016; Yin et al., 2010). Such variability may be associated with differences in sampling time, tillage equipment, cropping system history, sample processing, statistical analyses, inherent soil properties, and climate factors. Understanding the impact of physical disturbance on soil microbial community structure across a range of climates, cropping systems, and inherent soil properties (e.g., texture, pH) may enhance interpretation of divergent results from site-specific studies.

Assessment of microbial community structure is capable of identifying changes in community composition due to agricultural management, but it does not provide context as to how the change affects soil functioning. Measuring change in microbial community structure and function, in unison, provides context as to whether changes in agricultural management alter microbial function as well as the potential drivers responsible for changes in function. To date, a number of studies have attempted to link management driven changes in soil microbial community composition to changes in carbon mineralization (Guo et al., 2019; Khanghahi et al., 2019; Liu et al., 2018; Malik et al., 2018; Mbuthia et al., 2015). These studies indicate that analyzing soil microbial community composition in addition to inherent soil properties and other biological measurements enhances the predictability of carbon mineralization. However, the goal of these studies was to uncover drivers of basal soil mineralization, which may differ from the organisms responsible for driving the burst of mineralization recorded in standardized Cmin incubations. Uncovering the microbial community members responsible for driving greater Cmin measurements in systems with reduced physical disturbance may provide much needed context to the measure, which in turn will allow stakeholders to appropriately synthesize their results in the context of building soil health.

The goal of the present study was to evaluate the impact of reduced physical disturbance on soil bacterial and archaeal community members and their potential influence on greater Cmin measurements recorded in long-term reduced disturbance systems across major agricultural areas in North America. We hypothesized that bacterial and archaeal communities that were enriched under minimum physical disturbance would be important predictors of Cmin. We first explored relationships between disturbance intensity and changes in bacterial and archaeal community structures. We identified a subset of ASVs which were enhanced in systems employing minimum disturbance management across a range of inherent soil properties and climates. Finally, we identified a suite of bacteria and archaeal taxa, which were enriched under minimum disturbance and important predictors of Cmin models.

2. Methods

2.1. Sample collection

Data used in these analyses were collected as part of the North American Project to Evaluate Soil Health Measurements (NAPESHM). NAPESHM sites were chosen based on the presence of treatments to test the management effects of tillage, cover crops, crop rotation, nutrient amendments, irrigation, and livestock stocking rate and intensity. A full description of the project can be found in Norris et al. (2020). The project consisted of 2032 experimental units from 688 replicated treatments located at 124 long term experimental agricultural research sites across North America (Fig. 1). Out of the 688 replicated treatments, 568 treatments contained at least ten years of consistent crop rotations and agricultural management practices (e.g. tillage, cover cropping), while 120 treatments contained between six and ten years of consistent

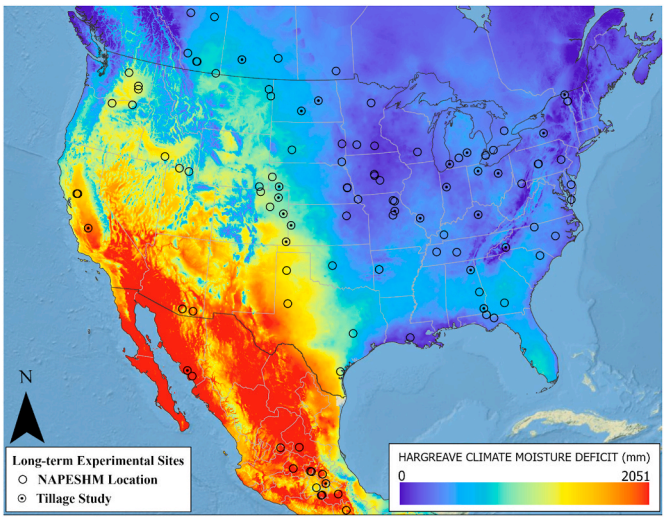

Fig. 1. Experimental unit sampling locations included in the North American Project to Evaluate Soil Health Measurements (NAPESHM). Concentric circles indicate sites containing at least 12 experimental units with paired tillage treatments. The map is colored by Hargreaves Climate Moisture Deficit.

practices. Detailed treatment and site information is located in Table 1, Supplemental Table 1, and in Norris et al. (2020).

Sites were predominantly sampled in spring of 2019 prior to fertilization, spring tillage, and planting. Five-year detailed management histories were collected for each treatment. Soil sampling for each experimental unit was performed using a sharpshooter shovel and soil knife. A total of 18 knife slices (15- by 4-cm) were collected uniformly to a depth of 15 cm from six locations across each experimental unit in a zig-zag pattern and placed on ice. Samples were composited in a bucket prior to bagging and shipping. Sampling equipment was cleaned and sterilized with isopropyl alcohol between experimental units. Additionally, sterile nitrile gloves were worn during sampling and sample processing.

2.2. Site climate data

The Hargreaves Climate Moisture Deficit was calculated to capture the combined effect of precipitation and temperature (Hargreaves and Allen, 2003). The moisture deficit calculations included a monthly estimate of precipitation deficit averaged from 1991 to 2020 (T. Wang et al., 2016). The monthly deficit for a given location represented the difference between reference evapotranspiration and precipitation, and the deficit is considered zero for any month where precipitation is greater than reference evapotranspiration.

2.3. Laboratory measurements

For each experimental unit, composite soil samples were sent to the Soil Water and Environmental Lab[1] at Ohio State University for measurement of particle size distribution, pH, total nitrogen, total carbon, inorganic carbon, and Cmin. Particle size analyses were performed using the pipette method and sands were wet sieved (Gee and Or, 2018). Soil pH measurements were made using a 1:2 soil:water slurry with a pH electrode (Campbell et al., 2018). Total nitrogen and carbon were measured by dry combustion (Nelson and Sommers, 2015). Inorganic carbon was measured using Chittick gasometric calcimeter[a] (St. Louis, MO, USA). Soil organic carbon was calculated as the difference between

[1] Name is given to provide specific information and does not constitute endorsement by the authors over other entities that may be equally suitable.

Table 1
Primary tillage implements used in disturbance category analyses.

Site ID	Disturbance Category			Crop Rotation
	Minimum	Moderate	Intense	
CASK01	Planting only	N/A	Cultivate	Spring wheat-fallow; wheat-pea, chickpea, lentil pulse
MXEM01	Planting only	N/A	Disk harrow, chisel plow	Continuous corn; continuous wheat; wheat-corn
MXSO03	Planting only	N/A	Disk harrow, chisel plow	Continuous spring wheat; wheat-corn
USAL01	Planting only	N/A	Rototill, disk	Corn-soybean
USAL03	N/A[a]	Strip-till	Moldboard	bahiagrass-bahiagrass-peanut-cotton; peanut-cotton
USCA03	Planting with fertilizer shank	N/A	Subsoiler, disk harrow, bedder	Garbanzo bean-sorghum
USIL02	Planting only	Chisel plow, disk harrow, row cultivate	Moldboard, disk harrow, cultivate	Corn-soybean
USIN01	Planting only	Chisel plow, disk harrow, row cultivate	Moldboard, disk harrow, cultivate	Continuous corn; continuous soybean; corn-soybean
USKY03	Planting only	N/A	Moldboard, disk harrow	Continuous corn
USMI01	N/A	Strip-till, row cultivate, disc harrow	Disk harrow, rototill, row cultivate	Specialty vegetables
USMI02	N/A	Spring strip-till, fall disc harrow	Moldboard, disk harrow	Specialty vegetables
USMO01	Planting only	Biennial spring chisel and fall disc harrow	N/A	Corn-soybean
USNC01	Planting only	N/A	Chisel plow and rotary hoe	Corn-soybean-sorghum
USND01	Planting only	Spring cultivate	N/A	Spring wheat-fallow; spring wheat-corn; spring wheat-corn-soybean
USND02	Planting only	Fall disk harrow and chisel plow; Spring cultivate every four year	Chisel plow, disk harrow, cultivate	Spring wheat-field pea- corn-soybean
USNY01	Planting with double disk fertilizer opening	N/A	Moldboard, cultivate	Continuous corn
USNY04	Planting with double disk fertilizer opening	N/A	Moldboard, cultivate	Continuous corn
USOH02	Planting only	Chisel and rototill	Moldboard, rototill	Corn; corn-soybean; corn-alfalfa-alfalfa
USOH03	Planting only	Chisel and cultivate	Moldboard, disk harrow, cultivate	Corn; corn-soybean; corn-red clover-red clover

[a] Treatment was not present at study location.

total carbon and inorganic carbon (Dreimanis, 1962). Soil samples used in Cmin measurements were air dried and passed through a 2-mm sieve prior to incubation. Potential carbon mineralization was measured as accumulation of CO_2–C following rewetting by capillary action and a 24-h incubation period (Zibilske, 2018).

2.4. DNA extraction and sequencing

Composite moist soil samples from each experimental unit were passed through a sterile 8-mm sieve and shipped overnight on ice to the Center for Genome Research and Biocomputing at Oregon State University for DNA extraction and subsequent sequencing. From each experimental unit, 0.25 g of soil was weighed for DNA extraction. DNA extractions were performed using a Thermo KingFisher Flex robotic magnetic bead system[a] (Swindon, UK) with Qiagen MagAttract Power Soil DNA kits[a] (Germantown, MD, USA). A Zymbiotics microbial community standard was included on each DNA extraction plate. DNA concentrations were quantified fluorometrically using the Invitrogen Quant-iT dsDNA High Sensitivity Assay Kit[a] (Waltham, Massachusetts, USA) and read on a BioTek Synergy HT microplate reader[a] (Winooski, VT, USA).

Following Earth Microbiome Project protocols (Caporaso et al., 2018), the V4 region of 16S rRNA was amplified and sequenced using the Illumina MiSeq platform[a]. The QIIME 2 platform was used for classification of reads to taxa counts (v. 2019.4). Adapters were trimmed with the qiime cutadapt trim-paired tool. Read pairs were merged with qiime vsearch join-pairs with a maximum merge length of 256 base pairs and removing any reads with any Ns present. Reads were filtered for a minimum PHRED score of 20. QIIME deblur denoise-16S was used to denoise the reads by removing reads that did not have a sequence similarity of 60% to the 85% OTU GreenGenes database and reads were trimmed to 250 base pairs or discarded if shorter. Results were tabulated with the qiime feature-table tabulate-seqs. Taxonomy were assigned with the QIIME feature-classifer classify-sklearn using the silva database classifier version 132. Data was exported from QIIME2 with QIIME tools export. Amplicon sequence variants that were observed less than three times in 5% of samples were removed. Remaining samples were rarified to 8000 sequences using the function rarify_even_depth in the R package phyloseq (McMurdie and Holmes, 2013). Rarified samples were used in all downstream analyses. Demultiplexed sequences were deposited in the National Center for Biotechnology Information Sequence Read Archive with the following accession number: PRJNA762046.

2.5. Statistical analysis

In addition to treatments that represented management changes, sites included in the study cover a broad range of climates, inherent soil properties, and organic matter. To identify significant differences in community structure as a result of differences in inherent soil properties and climate, permutational multivariate analysis of variance (PERMANOVA) with distance matrices was performed using the Adonis function in the R package vegan (Dixon, 2003). Canonical correspondence analysis was also performed to visualize how inherent soil properties and climate were related to community structure using the ordinate function. Alpha diversity was assessed by calculating Shannon Diversity Index values for all experimental units. Shannon Diversity and richness were calculated using the estimate_richness function in the R package phyloseq (McMurdie and Holmes, 2013) Experimental units with extreme Shannon Diversity and richness outliers were removed from the dataset.

A subset of replicated, paired tillage treatments was selected from nineteen sites for specific disturbance-based analysis (Fig. 1, Table 1). For this analysis, only sites which contained at least twelve experimental units evenly distributed across two or more tillage regimes were included in disturbance analyses. Furthermore, treatments were only included in disturbance analyses if a paired treatment existed, that is the only difference in management was physical disturbance through tillage. Treatments were classified into minimum, moderate, or intense disturbance categories. Minimum disturbance included experimental units whose only physical soil disturbance occurred during planting, commonly referred to as "no-till". Moderate disturbance encompassed a wide range of reduced or conservation tillage practices, including strip tillage, row cultivation, and chisel plow. Intense disturbance included experimental units from treatments commonly described as "conventional tillage" where practices are among the most disruptive tillage practices for a given cropping system and climate. Sites included in tillage analyses were assigned a six-digit unique identifier (Supplementary Table 1). Additionally, treatments that only differed by tillage were assigned a two-digit unique identifier to ensure direct comparison of the treatments in downstream analyses. To visualize differences in community structure among disturbance categories, detrended correspondence analyses (DCAs) were performed with bray-curtis distance matrices to account for non-linear relationships. Significant differences in community structure as a function of physical disturbance at individual sites were assessed using adonis function in the vegan package (Dixon, 2003). If a site contained a factorial design (e.g. tillage and cover cropping), the non-tillage factor was accounted for using the strata argument to ensure the direct comparison of treatments that only differed by tillage regimes. Permutational analysis of multivariate dispersions were assessed prior to implementing PERMANOVA using the betadisp function in the vegan package (Dixon, 2003). Non-significant values ($p > 0.05$) confirmed that the paired treatments contained similar within treatment variances, indicating significant differences in beta diversity were due to differences in physical disturbance treatments.

Experimental units from sites with significant differences in community structure due to physical disturbance, were used to identify ASVs whose abundances were significantly enriched in reduced disturbance treatments across all sites. Enrichment of specific ASVs was determined by differential expression analyses based on the negative binomial distribution (Gamma-Poisson), performed using the function Deseq from the R package DESeq2 (Love et al., 2018) with Wald tests as the test argument. Amplicon sequence variants were considered differentially expressed when $p < 0.05$. Three separate analyses were performed to identify: 1) ASVs that were in enriched in minimum disturbance treatments in relation to intense disturbance treatments, 2) ASVs that were enriched in minimum disturbance treatments in relation to moderate disturbances treatments, and 3) ASVs that were enriched in moderate disturbance treatments in relation to intense disturbance treatments. The analysis was performed on rarefied experimental units due to large differences among experimental unit library sizes (~10x) (Weiss et al., 2017). Lastly, differences in alpha diversity were assessed separately between the three disturbance comparisons described above using the lm function contained within the base R package. In each analysis, disturbance category was set as a fixed effect and tillage treatment comparison as random effect using the assigned two-digit unique identifiers, therefore permitting comparison of treatments which only differed by physical disturbance. Model outputs were assessed using the anova function, contained within the base R package, to identify significant differences between disturbance categories.

Random forest regression models were employed to identify microbial drivers of Cmin measurements. Thirty random forest regressor models were fit to the full set of 689 experimental treatments to help sort and filter ASVs that were most highly associated with Cmin. In each model run, Cmin was the response variable, with ASVs as predictor variables. The ASVs included in the final set models were pruned by average abundance until total model permutation importance began to decline, resulting in 328 ASVs contained in each model. Training and testing datasets were built at random for each model iteration, with experimental units from 586 to 608 treatments randomly selected for inclusion in the training dataset, resulting experimental units from 80 to 102 treatments placed in the testing dataset. The set of fitted models had

an average R^2 of 0.58 predicting on testing data sets, which were held out from model training. The average ASV importance across models was used to estimate the relative utility of each ASV for predicting on testing data sets. Here, ASV importance is the difference between the initial prediction fit and the prediction fit after randomly permuting the respective ASV data. These analyses were performed in the Scikit-learn Python module ((Pedregosa et al., 2011); version 0.23.1, https://scikit-learn.org/stable/). The maximum number of ASVs allowed in any regression tree was 18 ($328^{½}$), with minimization of the mean squared residual error as the model criteria. The relationships between individual ASVs contained in the top decile of importance and Cmin were explored using linear regression. Code for analyses is located at https://github.com/erieke/NAPESHM-tillage-mineralization.

3. Results

3.1. Continental community and cmin assessment

Experimental units covered a wide range of inherent soil properties and climates (Table 2). Following rarefaction, 1924 experimental units remained in the dataset, consisting of 5322 unique ASVs. Twenty-seven phyla were identified in the dataset, with major contributions from *Acidobacteria, Actinobacteria, Bacteroidetes, Proteobacteria,* and *Verrocomicrobia*. Shannon's diversity index ranged from 4.36 to 6.70, while observed ASV richness ranged from 342 to 1580. Greatest diversity and richness were observed at moderate pH values (5.5–7.5) and humid climates (Fig. 2). The PERMANOVA among communities across the continent indicated pH and climate moisture deficit explained more variation than clay, sand, soil organic carbon and total nitrogen (Table 2). Furthermore, the canonical correspondence analysis results suggest that climate and inherent soil properties predict only a small fraction of microbial community structure (Supplementary Fig. 1).

An in-depth analysis of Cmin in relation to climate, inherent soil properties, carbon-based soil health indicators, and agricultural management can be found in Liptzin et al. (Liptzin et al., n.d.). Briefly, measures of Cmin ranged from 4.7 to 126.7 mg C $kg^{-1}d^{-1}$, with a median of 49.0 mg C $kg^{-1}d^{-1}$. Potential carbon mineralization and soil organic carbon were moderately related ($r = 0.58$). Prediction of Cmin with inherent soil properties and climatic variables using multiple linear regression resulted in a R^2 value of 0.27. Clay, pH and precipitation were positively correlated with the measurement, while temperature was negatively correlated. Response ratios of paired treatments indicated significantly greater Cmin in systems employing reduced tillage, cover cropping, application of organic nutrients, or residue retention.

3.2. Microbial response to tillage intensity

Out of the 14 sites that contained at least 12 experimental units with minimum and intense disturbance comparisons, 11 contained significantly different microbial community structures ($p < 0.01$) as a result of differences in disturbance, which were identified using the adonis function (Fig. 3, Supplementary Table 2). The three sites with non-significant differences ($p > 0.01$) all contained wheat-centric rotations (Table 1). Differential abundance testing of the 214 experimental units from the 11 sites identified 717 ASVs whose abundances were significantly greater in minimum disturbance experimental units ($p < 0.05$). The associated ASVs represent 119 of 242 families identified in both minimum and intense disturbance experimental units. On average, the ASVs accounted for 16% of sequences associated with intense disturbance experimental units, and 33% of sequences were associated with minimum disturbance. The 717 ASVs were confined within 14 phyla, with most sequences associated with *Acidobacteria*, *Actinobacteria*, *Bacteroidetes*, *Gemmatimondetes*, *Proteobacteria*, *Rokubacteria*, and *Verrocomicrobia* (Fig. 4). Alpha diversity, represented by the Shannon Diversity Index, and richness were not significantly different ($p > 0.10$) between minimum and intense disturbance categories (Supplementary Fig. 2).

While most minimum and intense disturbance comparisons returned significant differences in community structure at the site level, comparisons between minimum and moderate disturbance returned mixed results. Among the minimum and moderate disturbance comparisons, four of seven sites had significant differences ($p < 0.01$) in bacterial and archaeal community structures which were identified using the adonis function (Supplementary Table 3). The four sites with significant differences in community structure all contained a site average pH ≤ 5.7 or pH > 6.5 (Supplementary Table 3). Differential abundance testing of the 76 experimental units from the four sites returned 242 ASVs whose abundances were enriched ($p < 0.05$) in minimum compared to moderate disturbance. In general, the resulting ASVs accounted for 14% of ASV relative abundance in minimum disturbance and 4% of ASV relative abundance in moderate disturbance. Of the 75 bacterial and archaeal families enriched under minimum disturbance compared to moderate disturbance, 73 were also enriched in minimum compared to intense disturbance. Lastly, alpha diversity and richness were not significantly different ($p > 0.10$) between minimum and moderate disturbance (Supplementary Fig. 3).

Sites with moderate and intense physical disturbance comparisons returned a similar percentage of site level differences to minimum-moderate disturbance comparisons, with four of eight sites containing significant differences due to disturbance ($p < 0.01$) (Supplementary Table 4) identified using the adonis function. The four sites with significant differences in community structure all contained a site average pH ≤ 5.7 or pH > 6.5 (Supplementary Table 4). Additionally, differential abundance testing of the 74 experimental units from the four sites identified a similar number of enriched ASVs. However, the 282 ASVs, comprised of 77 unique families, enriched under moderate disturbance compared to intense disturbance accounted for similar relative abundances in the two treatments. Like minimum-intense and minimum-moderate comparisons, alpha diversity and richness did not significantly differ ($p > 0.10$) between moderate and intense treatments (Supplementary Fig. 4).

3.3. Modeling respiration with bacterial and archaeal community members

Three hundred and twenty-eight ASVs remained in the respiration model training dataset, post pruning, and on average, accounted for 44% of sequences in rarified experimental units. The respiration model had substantial predictive power ($R^2 = 0.58$) between predicted and actual respiration values. Amplicon sequence variants belonging to *Proteobacteria* contributed the most to variable importance, followed by *Acidobacteria*, and *Verrocomicrobia*, (Supplementary Fig. 5, Supplementary Table 5). Of the 328 ASVs included in the respiration model, 90 were significantly enriched in minimum disturbance systems compared to intensive disturbance systems (Supplementary Table 6). Additionally, 44% of the ASVs with model importance in the top decile were enriched in minimum disturbance systems compared to intensive disturbance systems (Fig. 5). Furthermore, all but one ASV contained in the top decile of important sequences contained weak, but significant relationships with Cmin ($p < 0.01$), which were identified through individual

Table 2
16S rRNA permutational multivariate analysis of laboratory soil measurements and climate. All measurement analyses were significant ($p < 0.01$).

Measurement	r^2	n[a]	Minimum	Maximum	Median
Clay (%)	0.04	1909	2	63	21
Sand (%)	0.01	1909	3	91	32
pH	0.12	1909	4.0	9.0	6.3
Soil Organic Carbon (%)	0.02	1909	0.20	10.42	1.49
Hargreave Climate Moisture Deficit (mm)	0.07	1909	93	1773	259
Total Nitrogen (%)	0.02	1903	0.02	1.07	0.14

[a] Number of samples included in the analysis.

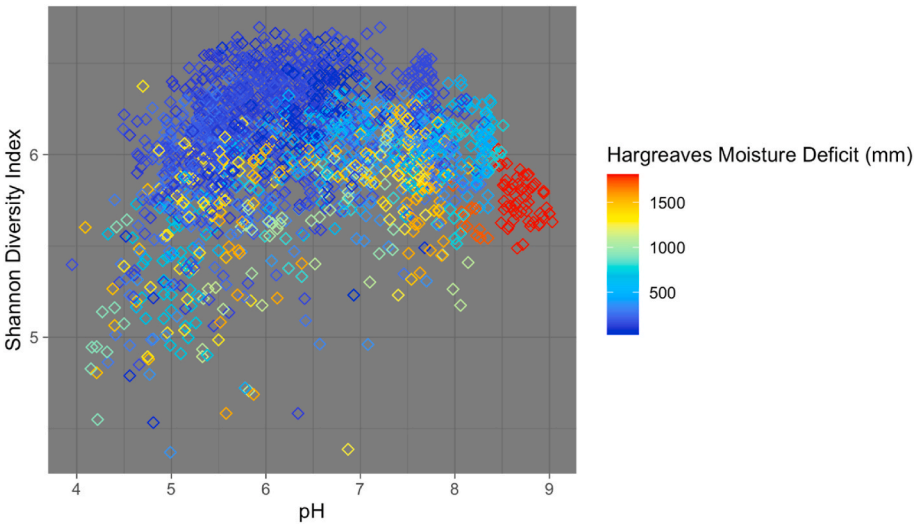

Fig. 2. 16S rRNA Shannon Diversity Index values for North American Project to Evaluate Soil Health Measurements experimental units plotted against pH. Colors represent Hargreaves Moisture Deficit values for each experimental unit. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

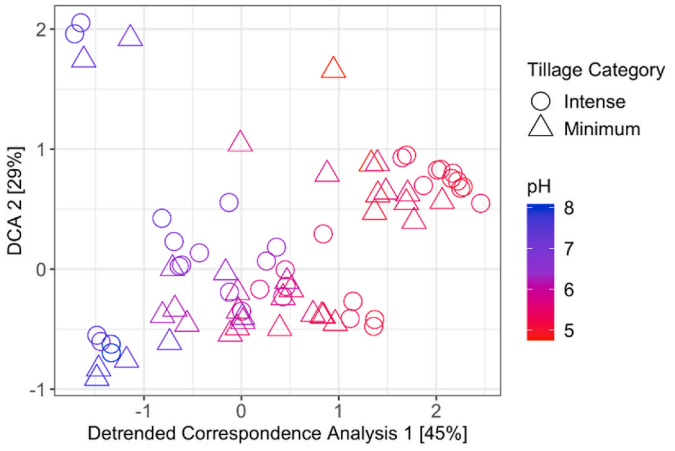

Fig. 3. Detrended correspondence analysis (DCA) of treatments from sites with significant differences in bacterial and archaeal community structure between minimum and intense disturbance comparisons.

linear regressions, with r^2 values ranging from 0.01 to 0.15. The vast majority of ASVS that were enriched in minimum disturbance and contained within the top decile of model importance contained significant ($p < 0.01$), positive relationships with Cmin (Fig. 5).

4. Discussion

The majority of sites analyzed for shifts in community structure in relation to minimal and intensive disturbance comparisons exhibited significantly different shifts in community structures. The three locations with non-significant differences in community structure had predominantly wheat-based rotations. Previous site-specific studies consistently reported significant differences in community structure because of physical disturbance in corn-based rotations (De Quadros et al., 2012; Sengupta and Dick, 2015; Smith et al., 2016; Srour et al., 2020). However, prior results from wheat-based rotations are less definitive, with differences in community structure varying by location (Essel et al., 2019; Ng et al., 2012; Schlatter et al., 2019; Yin et al., 2010). Insignificant differences in microbial community structure due to disturbance in wheat-based rotations may stem from greater root density and/or composition associated with wheat plant roots compared to

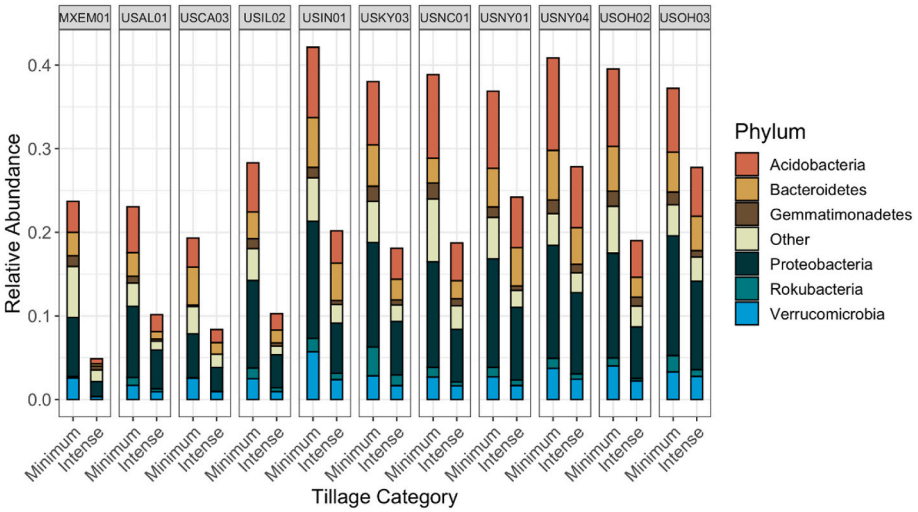

Fig. 4. Average relative abundances of 717 amplicon sequence variants enriched under minimum tillage when compared to intensive tillage, grouped by site.

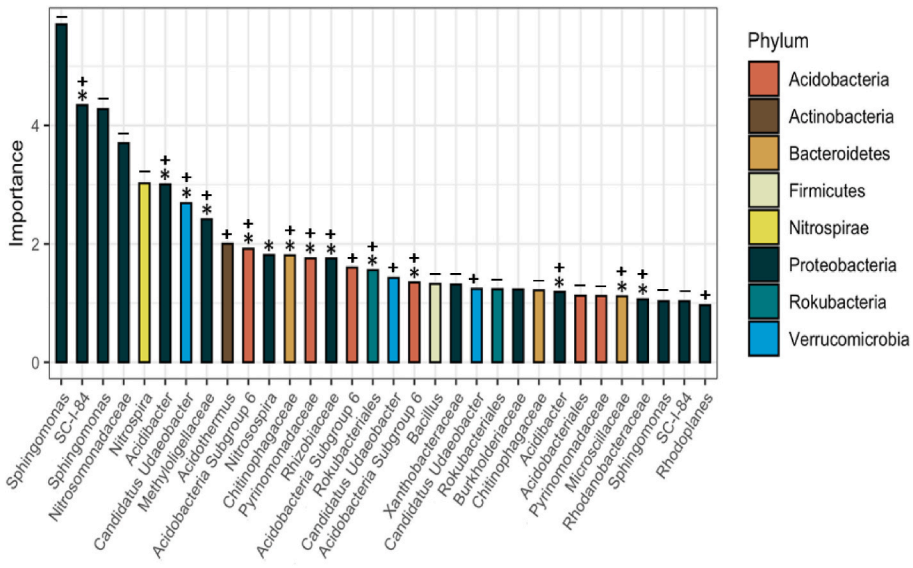

Fig. 5. Top 10% of most important amplicon sequence variants included in the random forest regression potential carbon mineralization model. Sequences are labeled by finest level of available taxonomic classification. Importance was calculated as the average reduction in mean square error across thirty model simulations. Asterisks above a given sequence importance indicates the sequence was enriched under minimum disturbance when compared to intensively disturbed systems. Plus symbols above a given sequence indicate the sequence had a significant ($p < 0.01$), positive relationship with potential carbon mineralization. Negative symbols above a given sequence indicate the sequence had a significant ($p < 0.01$), negative relationship with potential carbon mineralization. Relationships were identified using linear regression.

other crop rooting systems included in the study (Yamaguchi and Tanaka, 1990). Increasing below ground biomass decay may enhance microbial access to nutrient rich organics in a similar fashion to residue incorporation following tillage operations.

Significant differences in minimum-moderate and moderate-intense disturbance comparisons were less consistent in this study, with just over half containing significant differences in community structure due to differences in disturbance treatments. Differences in physical soil disturbance between minimum-moderate disturbance and moderate-intense disturbance treatment comparisons were not as extreme as minimum-intense comparisons. However, trends in significance between these treatments were identified in relation to pH. Minimum-moderate and moderate-intense site level disturbance comparisons did not contain significantly different ($p > 0.01$) microbial community structures at locations where site average pH ranged from 5.7 to 6.5, while locations with site average pH $\leq$ 5.7 or pH $>$ 6.5 contained significantly different community compositions ($p < 0.01$). Average alpha diversity, measured as Shannon's Diversity Index, and richness were slightly greater at tillage sites with pH ranges from 5.7 to 6.5. Increasing diversity has shown to enhance resilience in some microbial systems, but not in others (Shade et al., 2012). Resiliency in microbial communities is defined as "the rate at which a microbial community returns to its original composition after being disturbed" (Allison and Martiny, 2008). The insignificant differences between less disruptive comparisons are indicative of microbial resilience to physical disruption in slightly acidic soils. This differential response to moderate changes in disturbance when grouped by pH, may be indicative of a link between archaeal and bacterial diversity and resilience driven by inherent features and part of the reason why some soils are less susceptible to changes in function as a result of changes in management (i.e., soils below pH 5.7 or above 6.5). However, this resilience to changes in management may be less evident in soil fungal communities, which are less dependent on soil pH when compared to bacterial communities (Lauber et al., 2008).

The sampling strategy employed allowed us to identify management conditions capable of creating divergent soil microbial community structures. Significant differences in bacterial and archaeal community structure among non-wheat based, minimum-intense tillage comparisons demonstrate community divergence as a result of repeated tillage over multiple years. Differential abundance testing of minimum-intense tillage treatments with significant differences allowed us to identify ASVs responsible for the change in community structure across locations. ASVs identified as *Pedosphaerales,* contained within the phylum *Verrucomicrobia*, were highly abundant and enriched under minimum tillage conditions when compared to intensive tillage. While *Verrucomicrobia* is a dominant phylum in soil (Bergmann et al., 2011), accounting for over 50% of bacterial 16S rRNA gene sequences in native tall grass prairie soils in the USA (Fierer et al., 2013), their functioning in soil remains poorly understood. Although much remains to be uncovered regarding *Pedosphaerales* functional potential, the order has been identified as an indicator of large macroaggregates (Bach et al., 2018), as well as enriched in permanent raised beds when compared to tilled raised beds (Jiménez-Bueno et al., 2016). Coupling indicators of soil health and relative abundance of microbial community members can shed light on the mechanisms behind why practices enhance soils' ability to function. Work has shown that minimum tillage systems compared to intensive tillage generally: 1) increase macroaggregate stability (Al-Kaisi et al., 2014; Zhang et al., 2018), 2) increase soil organic carbon (Nunes et al., 2020), and 3) enhance relative abundance of *Pedosphaerales*. Furthermore, tall grass prairies and other minimally managed perennials contain greater measures of aggregate stability and soil organic carbon than row cropping systems that utilize soil health promoting practices (i.e., reduced tillage, cover crops, organic amendments) (Grandy and Robertson, 2007). Together this indicates that in the top 15 cm of soil the repeated pulse events of tillage shift the microbial community and soil structure away from organisms known to exist in unmanaged, natural systems. Conversely a major reduction in physical disturbance can redirect the community structure, back toward a naturally functioning soil.

Reducing tillage often leads to increases in stable aggregates (Al-Kaisi et al., 2014; Zhang et al., 2018). Stable aggregates form niche microbial communities, capable of supporting oligotrophic lifestyles (Bach et al., 2018). ASVs matching *Acidobacteria Subgroup 6* were highly abundant, enriched under minimum disturbance, and important sequences in modeling Cmin. *Acidobacteria* are present in a wide range of habitats across the globe and constitute on average 20% of bacteria in soils (Janssen, 2006). Although *Acidobacteria* are present across a variety of environments, relatively little is known about the phylum due to difficulties related to culturing individual isolates. The first *Subgroup 6* isolates were cultivated in 2011 and characterized as slow growing, adaptive to very low nutrient concentrations, and produced uncharacterized extracellular polymeric substances (George et al., 2011). Sequencing efforts of *Acidobacteria Subgroup 6* have revealed the presence of cellulose synthesis genes and a multitude of high molecular weight proteins with excretion pathway motifs, which are postulated to be involved in extracellular polymeric substance production (Kielak

et al., 2016). Extracellular polymeric substances are largely responsible for building biofilm structure and function (Wingender et al., 1999) and are highly correlated with aggregate stability (Redmile-Gordon et al., 2020). Additionally, extracellular polymeric substance production helps regulate osmotic pressure faced by bacteria under changing moisture regimes (Roberson and Firestone, 1992). Bacteria and archaea capable of producing extracellular polymeric substances have demonstrated higher survival rates when subjected to desiccation (Anderson et al., 2012; Tamaru et al., 2005), which may indicate they are better equipped to resume activity following the drying and rewetting in Cmin measurements.

Candidatus Udaeobacter, contained in the phylum *Verrucomicrobia,* was also enriched under minimum disturbance conditions and was an important contributor to the Cmin regression model. *Candidatus Udaeobacter* is widespread in soils, but has not yet been successfully grown in the laboratory (Poehlein and Schöning, 2020). However, a recently published metagenome-assembled genome revealed enriched amino acid transporter and protease gene concentrations in *Candidatus Udaeobacter* compared to other soil bacteria with larger genomes (Brewer et al., 2016). The authors speculated the bacteria is able to prosper in resource limiting conditions through acquisition of amino acids and vitamins contained in the soil environment, rather than internal biosynthesis (Brewer et al., 2016). One proposed mechanism for Cmin bursts measured following drying and rewetting of soil is consumption of cytoplasmic substances exuded by bacteria to regulate changing osmotic pressure upon rewetting (Fierer and Schimel, 2003). *Candidatus Udaeobacter* and other bacteria capable of utilizing expelled cytoplasmic substances may contribute to greater standardized Cmin measurements in minimum tillage systems when compared to an intensively tilled soil.

Results from NAPESHM indicated Cmin was significantly greater in systems managed for minimal physical disturbance when compared to systems with greater physical disturbance (Liptzin et al., n.d.). However, these results are not indicative of *in situ* carbon mineralization in similar cropping systems where mineralization is lower in systems managed for minimal disturbance (Abdalla et al., 2016). Potential carbon mineralization measured in the laboratory rewetting incubation is a result of the consumption of cells lysed during drying, fresh metabolic waste, and newly available organic residues resulting from physical disruption (Fierer and Schimel, 2003; Kaiser et al., 2015). Soils managed for minimal physical disturbance generally contain greater amounts of organic carbon in the top 15 cm than highly disturbed counterparts (Nunes et al., 2020). Increases in organic carbon may be partially attributed to increases in aggregation, which can lead to organic residues becoming physically unavailable for microbial consumption (Paustian et al., 2019). Disruption of aggregates through sieving prior to the incubation releases an unknown fraction of organic residues previously unavailable for microbial consumption. The diverse set of bacterial and archaeal taxa whose abundances were important in predicting Cmin are indicative of the broad range of newly available organic compounds available for microbial consumption. Furthermore, within the top 15 cm of soil, many bacterial and archaeal community members reside in aggregates containing unique sets of organisms, which adapt to organic matter resources, pore-space networks, and water and oxygen availability (Bach et al., 2018). Disruption of these habitats during the sieving and drying process may alter access to water, oxygen, and organic matter resources, depending on the soil in question. Understanding which bacteria and archaea are capable of thriving post drying and sieving and the mechanisms they employ (e.g., biofilm formation, alternative nutrient consumption) will provide further context as to why soils managed for minimum disturbance report greater Cmin than their disturbed counterparts. Sequences deemed important when modeling Cmin and enriched under minimum disturbance provide a starting point for understanding the microbial community members which influence Cmin.

4.1. Conclusions

The unique sampling design incorporated in this study elucidated a set of ASVs that were enriched in soils under minimum tillage management across soil types and climates. Results from this study indicate that type of cropping system, intensity of physical disruption, and soil pH all influence the degree of archaeal and bacterial sensitivity to tillage. The multiple factors capable of affecting bacterial and archaeal community structure may explain divergent results among site specific studies and underscore the importance of limiting interpolation of individual studies to a broad scale. These results indicate a benefit to performing analyses across a range of agricultural soils to capture how core microbial members respond to changes in agricultural management.

The subset of ASVs enriched under minimum disturbance management and identified as important variables in random forest regression modeling, provide insight into the bacterial and archaeal community members who may be responsible for increases in Cmin measurements in systems with reduced tillage. While many biologically based soil health measurements are sensitive to management, few are tied to changes in soil function. Better understanding the microbial drivers of widely used soil health indicators, such as Cmin, rather than interpreting increases in measurements as an indication of increasing soil health, provides stakeholders context as to why the measures increase in soils managed for minimal disturbance. Soils with reduced disturbance foster bacterial and archaeal organisms with diverse lifestyles as a function of niche diversity developed within stable aggregates. Stable microbial communities formed in aggregates in soils managed for minimal physical disturbance represent communities capable of functioning in the absence of nutrient rich amendments. Understanding how soil microorganisms adapt and function in agricultural systems managed for minimal physical disturbance may provide the appropriate context for stakeholders to interpret Cmin results and help guide adoption of the practice.

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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

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