Soil Biology and Biochemistry 142 (2020) 107701

Contents lists available at ScienceDirect

Soil Biology and Biochemistry

journal homepage: http://www.elsevier.com/locate/soilbio

Do cover crops benefit soil microbiome? A meta-analysis of current research

Nakian Kim [a], María C. Zabaloy [b], Kaiyu Guan [c], María B. Villamil [a,*]

[a] University of Illinois, Department of Crop Sciences, Turner Hall, 1102 S. Goodwin Ave, Urbana, IL, 61801, USA
[b] Centro de Recursos Naturales Renovables de la Zona Semiárida (CERZOS), Universidad Nacional del Sur (UNS)-CONICET, Departamento de Agronomía, Bahía Blanca, Argentina
[c] University of Illinois, Department of Natural Resources and Environmental Sciences, Turner Hall, 1102 S. Goodwin Ave, Urbana, IL, 61801, USA

ARTICLE INFO

Keywords:
Microbial abundance
Microbial activity
Microbial diversity
Agronomy
Climate
Soil order

ABSTRACT

Cover cropping is a promising sustainable agricultural method with the potential to enhance soil health and mitigate consequences of soil degradation. Because cover cropping can form an agroecosystem distinct from that of bare fallow, the soil microbiome is hypothesized to respond to the altered environmental circumstances. Despite the growing number of primary literature sources investigating the relationship between cover cropping and the soil microbiome, there has not been a quantitative research synthesis that is sufficiently comprehensive and specific to this relationship. We conducted a meta-analysis by compiling the results of 60 relevant studies reporting cover cropping effects on soil microbial properties to estimate global effect sizes and explore the current landscape of this topic. Overall, cover cropping significantly increased parameters of soil microbial abundance, activity, and diversity by 27%, 22%, and 2.5% respectively, compared to those of bare fallow. Moreover, cover cropping effect sizes varied by agricultural covariates like cover crop termination or tillage methods. Notably, cover cropping effects were less pronounced under conditions like continental climate, chemical cover crop termination, and conservation tillage. This meta-analysis showed that the soil microbiome can become more robust under cover cropping when properly managed with other agricultural practices. However, more primary research is still needed to control between-study heterogeneity and to more elaborately assess the relationships between cover cropping and the soil microbiome.

1. Introduction

With the global population expected to reach 9 billion by the year 2050, agriculture faces a major predicament of moderating its pressure on the environment while meeting that future food demand (Alexandratos and Bruinsma, 2012). One of the crucial drivers of this impending problem is soil degradation by conventional agriculture (Conacher, 2009; Stavi and Lal, 2015). Much attention has been given to restoring and maintaining soil health, and to exploring and validating alternative practices such as reduced tillage or crop rotations to not only conserve and restore soil health, but also to address other agricultural side-effects like nutrient leaching, water pollution, and soil erosion (Bengtsson et al., 2005; Kessel et al., 2013; Paustian et al., 2016).

Cover cropping is appreciated as a viable sustainable agricultural practice expected to provide many benefits like preventing soil erosion and nutrient leaching, weed suppression, and carbon sequestration (Daryanto et al., 2018; Poeplau and Don, 2015; Sturm et al., 2018; Thapa et al., 2018). These benefits largely develop from the physically, chemically, and biologically distinct agroecosystem that cover crops shape compared to that under bare fallow (Kaye and Quemada, 2017; Marshall et al., 2016; Reicosky and Forcella, 1998). Considering the extent of changes due to cover cropping, the soil microbiome is expected to respond to such modifications especially to those of the soil environment (Abdollahi et al., 2014; Abdollahi and Munkholm, 2014). Cover cropping may impact soil microbial functionality responsible for important soil ecosystem services, especially as the agricultural soil microbiome is sensitive due to its typically low diversity (Tsiafouli et al., 2015). As a crucial component of soil health, the soil microbiome response to cover cropping needs to be assessed to support its viability as a conservation practice.

Many studies have explored the effects of cover cropping on the soil microbiome, finding evidences of benefits like increased microbial

* Corresponding author.
E-mail address: villamil@illinois.edu (M.B. Villamil).

https://doi.org/10.1016/j.soilbio.2019.107701
Received 11 June 2019; Received in revised form 2 December 2019; Accepted 19 December 2019
Available online 2 January 2020

biomass (King and Hofmockel, 2017), microbial enzymatic activities (Surucu et al., 2014), and evenness of relative abundances of bacterial taxa (Li et al., 2012). Yet, recent advancements in genetics and bioinformatics technologies have led to more efficient, precise, and accurate measurements of soil microbial properties (S. Gao et al., 2018; Lienhard et al., 2014). With an increasing number of studies using these contemporary methods, synthesizing their results is necessary to make general claims about the cover cropping effects on the soil microbiome. As a method of quantitative synthesis, meta-analysis can estimate a global effect from studies with heterogeneous conditions (Koricheva et al., 2013). Indeed, many meta-analyses have reported on the relationships between cover cropping and crop yield (Marcillo and Miguez, 2017), greenhouse gas (GHG) emission (Basche et al., 2014), and weed suppression (Osipitan et al., 2018). However, there has not been an extensive meta-analysis dedicated to cover cropping effects on the soil microbial properties.

A few meta-analyses on similar topics exist, but they were either confounded by studies with non-cover cropping practices, limited in microbial taxa, or confined themselves to traditional soil microbial properties (Bowles et al., 2017; Daryanto et al., 2018; McDaniel et al., 2014; Venter et al., 2016). McDaniel et al. (2014) included cover cropping studies in their meta-analysis on the effects of crop rotation and management on soil carbon (C) and nitrogen (N) dynamics. Their results showed that cover cropping increased total soil C and N; however, these properties are not the direct measures of the soil microbiome. More pertinent measures would have been microbial biomass C (MBC) and N (MBN). Venter et al. (2016) used Shannon's diversity index to measure the effects of crop rotation on soil microbial diversity, concluding that microbial density is enhanced with crop diversity; but their results were not specific to cover cropping. The meta-analysis by Bowles et al. (2017) reported positive effects of cover cropping on microbial colonization of plant roots but focused only on arbuscular mycorrhizal fungi (AMF). Overall, there is a critical lack of global perspective on cover cropping effects on the soil microbiome despite the accumulating number of relevant studies.

Our goal was to conduct a comprehensive meta-analysis to fill this gap of knowledge in cover cropping research. Specifically, this meta-analysis assessed whether i) soil microbial abundance, activity, and diversity differ under cover cropping compared to bare fallow, and whether ii) cover cropping effects on soil microbiome are dependent to environmental or managerial factors (see Fig. 8).

2. Materials and methods

2.1. Literature selection and data extraction procedure

From September 2018 to March 2019, we searched for relevant peer reviewed articles in Web of Science, SCOPUS, and Google Scholar. We used search terms generated from combinations of: scientific names of cover crop species, known measures of soil microbial properties, and methodology terms (Table S1). This resulted in an initial collection of 985 studies. This collection was refined for studies that met the criteria for this meta-analysis: i) experimental design allowed pairwise comparison between cover cropping treatments and bare fallow controls, ii) defined cover cropping as crops that are not harvested nor removed, thereby excluding studies with crop residues, iii) field or greenhouse studies, iv) the study reported sample sizes, means, and standard errors; if these statistics were not reported, authors were contacted or the statistics were calculated if possible. After this screening process, 60 studies reporting 48 soil microbial parameters (Table S2) remained. This process is outlined in Fig. 9 modified from PRISMA flow diagram by Moher et al. (2009).

The chosen studies were thoroughly examined to extract necessary information like experimental design, environmental conditions, and the soil microbial properties. The soil microbial properties were categorized into soil microbial abundance, activity, and diversity to represent the response variables (Table S2, S3). Data only presented in figures were extracted using WebPlotDigitizer (Version 3.9; Rohatgi, 2015). Agricultural conditions and practices were recorded to assess their interactions with cover cropping effects. For fertilizer data, rotation average N input by year was recorded if different amounts of N were applied in each year of a rotation. For experimental site information, we recorded the site's Köppen climate classification; if information was missing, we approximated the region of the site using Google Earth, then assigned the climate according to the climate classification entry in Wikipedia (Arnfield, 2019; Beck et al., 2018). Soil order was recorded in USDA soil taxonomy; those without USDA soil taxonomy equivalent were recorded as reported ("Soil Taxonomy | NRCS Soils," n.d.). Spring growth suppression methods of the cover crops were also categorized into mechanical and chemical termination methods. Tillage type was categorized into conservation (reduced tillage or no-till) and conventional tillage (any other tillage methods). If cover cropping planting and termination dates varied by year, dates of the sampling years were used. If a study's soil sampling occurred multiple times a year or in multiple years, results from each sampling event were recorded. If the study only reported averages over multiple sampling events, the last sampling date was recorded. If the exact date of such events were not reported, the 15th of the reported month was recorded as an average.

2.2. Statistical analysis

The statistical method of this meta-analysis follows the procedures described in Koricheva et al. (2013) for mixed-effects model with study weights:

$$T_i = \theta_k + e_i\ ,\ e_i\ \sim\ \mathrm{N}\left(0,\ \sigma_i^2\right) \tag{1}$$

$$\theta_k = \mu + \varepsilon_k\ ,\ \varepsilon_k\ \sim\ \mathrm{N}\left(0,\ \tau^2\right) \tag{2}$$

This model assumes that the observed effect size of a study (T_i) is distributed around the true study effect size (θ_k) with a within-study variance of σ_k^2 (1), which is then distributed around the global true effect size (μ) with a between-study variance of τ^2 (2) (Koricheva et al., 2013).

2.2.1. Calculating global effect size means and variances

The effect sizes of cover cropping on soil microbial properties were measured as the log response ratio (LRR, T_i), calculated as natural log of the ratio between the mean of a response variable under cover cropping treatment ($\overline{Y}_{CC}$) over that of the control ($\overline{Y}_{NC}$):

$$T_i = LRR = \ln\left(\frac{\overline{Y}_{CC}}{\overline{Y}_{NC}}\right) \tag{3}$$

Cover cropping treatments and controls with comparable conditions, such as sampling depth and sampling year, were paired to calculate the effect size. Therefore, a study can yield multiple effect sizes if it reported each results from multiple treatments of different cover crop species or mixtures, experimental sites, or sampling years.

Estimate of the study variance ($\widehat{\sigma}_k^2$) was calculated from the following formulae:

$$s^2 = \frac{\sum_{i=1}^{n}\left(Y_i - \overline{Y}\right)^2}{n} \tag{4}$$

$$\widehat{\sigma}^2{}_k = \frac{s_{CC}^2}{n_{CC} * \overline{Y}_{CC}^2} + \frac{s_{NC}^2}{n_{NC} * \overline{Y}_{NC}^2} \tag{5}$$

Here, s^2 is the reported variance of the mean of the response variable ($\overline{Y}_i$), and n is the sample size, which is the study's number of replications. The variance s^2 needed to be reported by the literature or be obtained from the authors.

With the study effect sizes and variances calculated, we used R

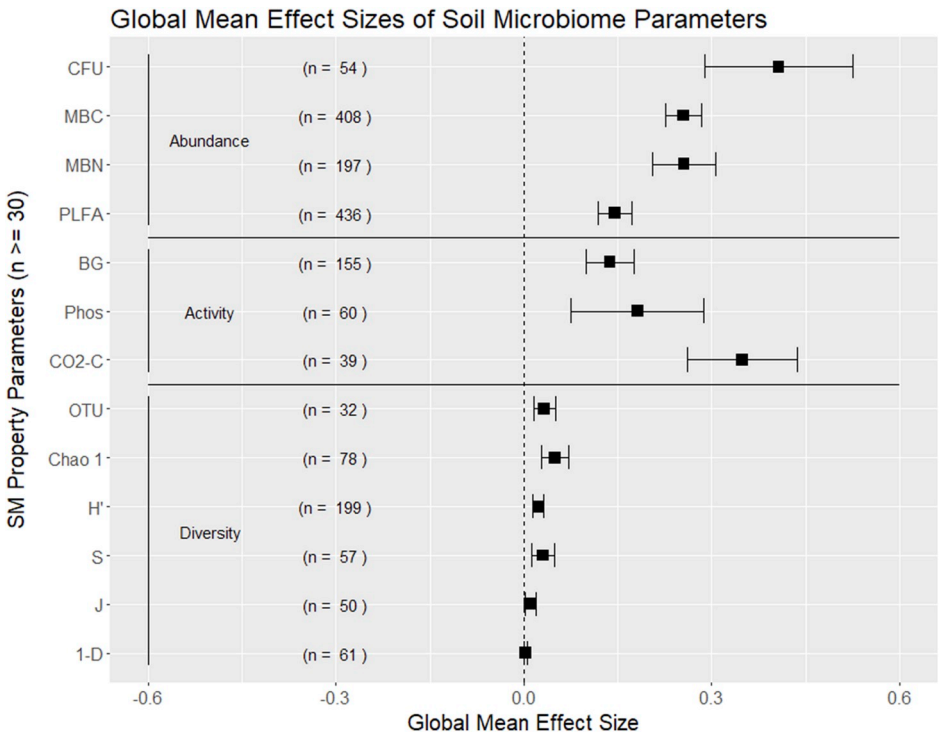

Fig. 1. Forest plot of global effect size means for 13 soil microbial properties with at least 30 observations: colony forming unit (CFU), microbial biomass C (MBC) and N (MBN), phospholipid fatty acid (PLFA), β-glucosidase activity (BG), phosphatase activity (Phos), respiration (CO2–C), operational taxonomic unit (OTU), Chao 1 richness index, Shannon's diversity index (H′), genetic richness (S), Pielou's evenness index (J), and Simpson's diversity index (1-D). Numbers in the parentheses are the number of observations used to calculate the global effect size mean. Whiskers are 95% CIs. Means larger than zero indicate that soil microbiome parameter was larger with cover cropping than bare fallow.

package `metafor` and its function `rma` to calculate the global effect sizes, 95% confidence intervals (CI), and total between-study heterogeneity (I^2) (Viechtbauer, 2010). If the CI of a global effect size mean does not include zero, then the cover cropping effect on a soil microbial parameter is statistically significant. I^2 is the proportion of total between-study heterogeneity in total variability among observations. A large I^2 might imply that studies are too different from each other to perform a meta-analysis. However, identifying significant effects from the covariate factors as the sources of heterogeneity can resolve this issue. Function `funnel` was used to produce the funnel plots for each soil microbial parameters to visually check significant heterogeneity and publication bias (R Core Team, 2019; Viechtbauer, 2010).

2.2.2. Selecting response variables

Of the 48 soil microbial parameters reported, statistical analyses were conducted on those with at least 30 observations. Those with fewer observations came from less than three studies, which is too few for meta-analysis. 13 soil microbial parameters that met the criteria were grouped into three categories: abundance, activity, and diversity. Soil microbial abundance and activity parameters are common metrics recommended by the U. S. Department of Agriculture (USDA) Natural Resources Conservation Service (NRCS) as soil health indicators particular to soil microbial properties (NRCS, 2018). The units of the parameters in this study are listed in Table S2.

The selected soil microbial abundance parameters estimate the overall size of the soil microbial community: colony forming units (CFU), MBC, MBN, and phospholipid fatty acid (PLFA). Soil microbial activity parameters included two enzyme activities, β-glucosidase (BG) and phosphatase (Phos), and laboratory soil respiration (CO2–C). Finally, soil microbial diversity parameters that reflect the richness, diversity, or evenness of a soil microbial population included Operational Taxonomic Units (OTU), Chao 1 richness index, Shannon-Wiener Index (H′), genetic richness (S), Pielou's Evenness Index (J), and Simpson's Diversity Index (1-D).

2.2.3. Assessing the effects of moderators on cover cropping effects on soil microbial properties

We assessed whether cover cropping effect size means varied by agricultural factors to explain the between-study heterogeneity and infer on the importance of these factors on cover cropping management. Agricultural factors will henceforth be referred to as "moderators", to be consistent with how package `metafor` dubs covariate factors (Viechtbauer, 2010). Table S3 summarized the moderators and their levels. These moderators were chosen based on their prevalence in the database, and relevance to cover cropping management and soil microbial properties. In summary, discrete moderators were climate, soil order, cover crop type, cover crop termination method type, tillage type, N fertilization, and soil sampling timing. Continuous moderators were soil pH, annual N fertilizer rate, cover cropping duration, and soil sample depth.

We used the function `rma` for the statistical analysis on the effects of moderators on cover cropping effect sizes. Also, ANOVA provided the overall significance of each moderator effect. For discrete moderators,

Table 1
Global results of cover cropping effects on 13 soil microbial parameters with at least 30 observations, reporting global effect size means, its 95% confidence interval (CI), number of observations (n), estimated total heterogeneity (τ^2), and total between-study heterogeneity (I^2). The 13 soil microbial parameters were: colony forming unit (CFU), microbial biomass C (MBC) and N (MBN), phospholipid fatty acid (PLFA), β-glucosidase activity (BG), phosphatase activity (Phos), respiration (CO2–C), operational taxonomic unit (OTU), Chao 1 richness index, Shannon's diversity index (H′), genetic richness (S), Pielou's evenness index (J), and Simpson's diversity index (1-D).

soil microbiome parameter	Global Mean	n	CI	τ^2	I^2
CFU	0.407	54	0.117	0.167	97.461
MBC	0.254	408	0.029	0.060	85.542
MBN	0.256	197	0.051	0.094	84.620
PLFA	0.145	436	0.026	0.046	82.202
BG	0.138	155	0.038	0.042	99.930
Phos	0.181	60	0.106	0.153	99.920
CO2–C	0.349	39	0.088	0.032	89.396
OTU	0.033	32	0.017	0.000	3.504
Chao 1	0.050	78	0.022	0.003	46.088
H′	0.023	199	0.009	0.002	92.475
S	0.030	57	0.019	0.000	0.311
J	0.010	50	0.008	0.001	72.098
1-D	0.003	61	0.002	0.000	20.116

we calculated an estimate of the effect size means and CIs for each combination of a moderator's levels and soil microbiome parameters, then we visually analyzed the significance with forest plots. Combinations of soil microbial parameters and discrete moderators with at least 30 observations were considered. Combinations were further subset by moderator level if there were at least 5 observations.

For continuous moderators, we used `rma` and included the continuous moderators in the function to calculate the estimate of the coefficients, their associated p-values, and R^2. The relationship was considered significant if its `rma` p-value was significant, therefore the coefficient is likely not zero, and if the R^2 was reasonably high (>10%). Combinations of soil microbial parameters and continuous moderators with less than 30 observations were disregarded.

3. Results

3.1. Overview of cover cropping effects on soil microbial properties

Overall, global cover cropping effect size means were significantly larger than zero for all soil microbial properties, as shown in Fig. 1 and Table 1. Global effect size means of soil microbial abundance parameters (CFU, MBC, MBN, and PLFA) ranged between 0.14 and 0.41, and activity parameters (BG, Phos, and CO2–C) ranged between 0.14 and 0.35. Global effect sizes for diversity parameters (OTU, H', S, J, and 1-D) were also positive but much smaller, ranging from 0.003 to 0.05. As shown in Table 1, total heterogeneity (I^2) for OTU, S, and 1-D were very small, while it was very high for the other ten parameters (46–99.9%), which can be explained by effects from the moderators. Funnel plots also confirmed this result where many observations for parameters except OTU, S, and 1-D were not contained in the funnel, which indicate between-study heterogeneity and possible publication bias (Fig. S6). Indeed, each soil microbial parameters had at least one moderator to explain their between-study heterogeneity (see Tables 2-4).

3.2. Moderator effects on the soil microbial abundance

Effects of climate were significant for all abundance parameters except CFU, which only reported one climate category (Fig. 2). For MBC, effect size means by climate varied significantly in the order of tropical (0.87), temperate (0.30), arid/semi-arid (0.19), and continental (0.08), from highest to lowest. For MBN, continental climate had a significantly lower effect size mean (0.05) than arid (0.29) and temperate (0.28)

Table 2
ANOVA results of effects of agricultural moderators on soil microbial abundance parameters: colony forming unit (CFU), microbial biomass C (MBC) and N (MBN), and phospholipid fatty acid (PLFA). Df is the degrees of freedom and p-values less than threshold 0.05 are in bold. Dashes (–) indicate that combination of soil microbiome parameter and moderator had less than two levels, therefore unable to perform ANOVA.

Moderators	CFU			MBC			MBN			PLFA		
	Df	Error Df	p-value	Df	Error Df	p-value	Df	Error Df	p-value	Df	Error Df	p-value
Climate	–	–	–	3	404	**0.000**	2	194	**0.015**	2	433	**0.000**
Soil Order	1	50	0.524	5	261	**0.000**	2	66	**0.030**	3	420	**0.000**
cover cropping Termination	1	34	0.152	1	374	**0.042**	1	177	0.889	1	404	0.256
cover cropping Type	2	51	**0.000**	3	404	0.063	3	193	0.135	3	432	0.290
Tillage Type	1	52	**0.044**	1	335	**0.001**	1	166	**0.004**	–	–	–
Sample Timing	1	20	**0.000**	3	404	**0.000**	2	194	0.644	4	431	**0.000**
N Fertilizer	1	20	**0.003**	1	369	0.584	1	193	0.151	1	350	**0.002**
N Fertilizer Rate	1	20	0.297	1	337	0.326	1	172	**0.027**	1	350	0.143
Soil pH	1	34	0.758	1	294	0.899	1	193	0.351	1	76	0.213
cover cropping Duration	1	34	0.134	1	368	0.252	1	176	0.999	1	404	0.458
Sample Depth	1	52	**0.001**	1	406	**0.000**	1	195	0.342	1	434	0.206

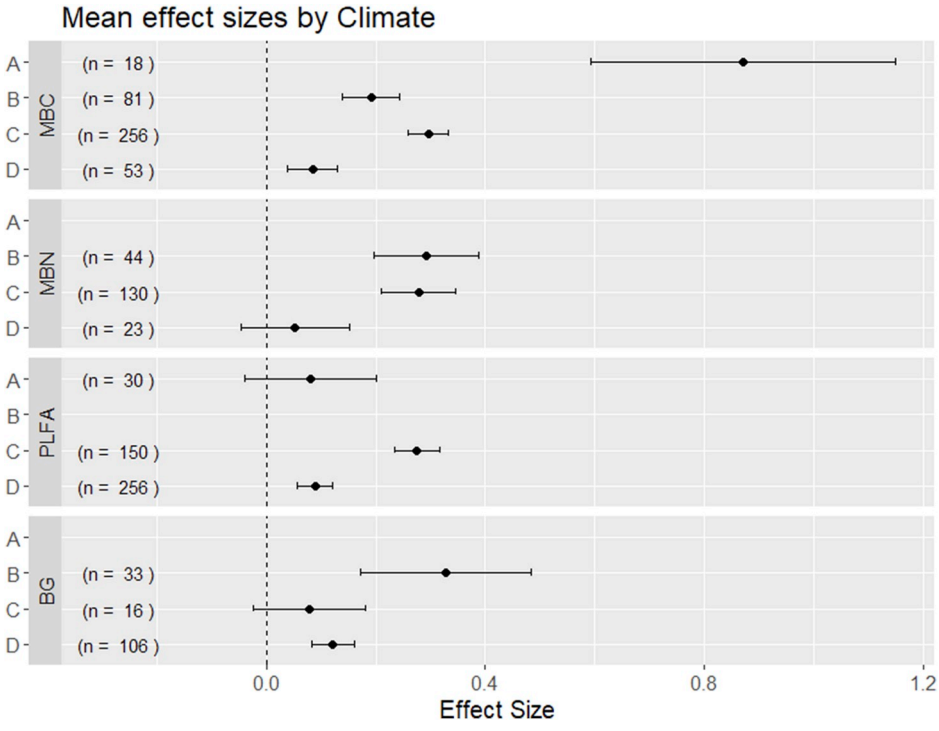

Fig. 2. Forest plots of interactions between soil microbial parameters and climate that had levels with significant differences between effect size means. Number of observations per level is noted in parentheses. Climate is classified by A (tropical), B (arid/semi-arid), C (temperate), and D (continental). Significant soil microbial parameters were microbial biomass C (MBC) and N (MBN), phospholipid fatty acid (PLFA), and β-glucosidase activity (BG). Levels (y-axis) with means larger than zero indicate that cover cropping increased the soil microbiome parameter at those levels, and decreased if the means smaller than zero. Levels with CIs that do not overlap indicate that their effect size means are significantly different.

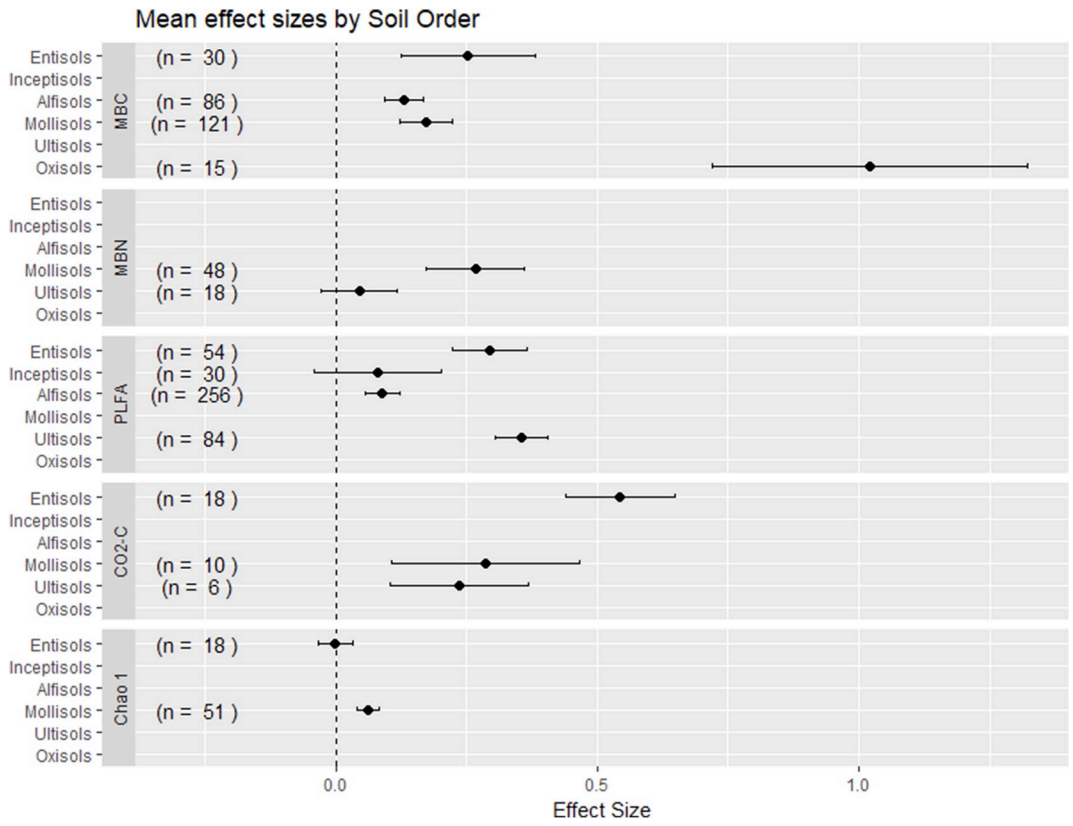

Fig. 3. Forest plots of interactions between soil microbial parameters and soil order that had levels with significant differences between effect size means. Number of observations per level is noted in parentheses. Significant soil microbial parameters were microbial biomass C (MBC) and N (MBN), phospholipid fatty acid (PLFA), respiration (CO_2–C), and Chao 1 richness index. Levels (y-axis) with means larger than zero indicate that cover cropping increased the soil microbiome parameter at those levels, and decreased if the means smaller than zero. Levels with CIs that do not overlap indicate that their effect size means are significantly different.

climates. For PLFA, the temperate climate had a significantly larger effect size mean (0.28) than tropical (0.08) and continental climates (0.09). Overall, the continental climate had lower effect size means than others.

Soil order also had significant relationships with MBC, MBN, and PLFA (Fig. 3). For MBC, Oxisols had a significantly larger effect size mean (1.02) than Entisols (0.25), Alfisols (0.13), and Mollisols (0.17); however, Oxisols had much fewer observations (n = 15) than Mollisols

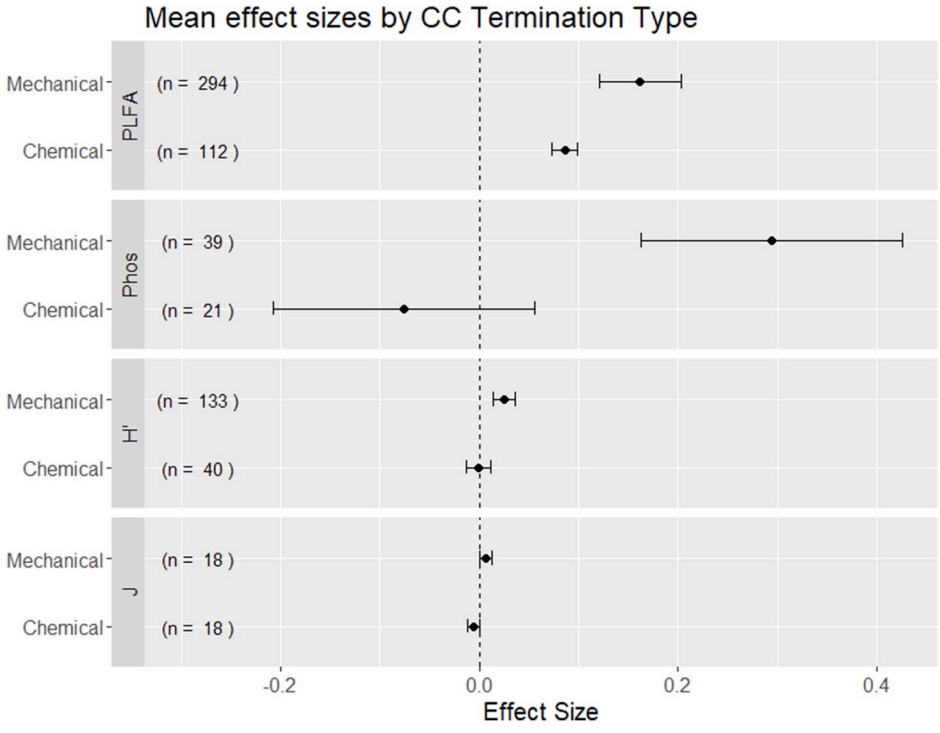

Fig. 4. Forest plots of interactions between soil microbial parameters and cover cropping termination method type that had levels with significant differences between effect size means. Number of observations per level is noted in parentheses. Significant soil microbial parameters were phospholipid fatty acid (PLFA), phosphatase activity (Phos), Shannon's diversity index (H′), and Pielou's evenness index (J). Levels (y-axis) with means larger than zero indicate that cover cropping increased the soil microbiome parameter at those levels, and decreased if the means smaller than zero. Levels with CIs that do not overlap indicate that their effect size means are significantly different.

(n = 121) and Alfisols (n = 86). For MBN, Mollisols had significantly larger effect size mean (0.27) than Ultisols (0.05). For PLFA, effect size means for Entisols (0.29) and Ultisols (0.36) were significantly larger than those of Alfisols (0.09) and Inceptisols (0.08). Except for MBN, less fertile soils like Oxisols, Ultisols, and Entisols had larger effect size means than those of more fertile soils.

Cover crop termination method had significant effects only on PLFA, where mechanical termination effect size mean (0.16) was significantly larger than that of chemical termination (0.09) (Fig. 4). Cover crop type had significant but inconsistent effects on CFU and MBC. Grass cover crops had the highest effect size mean (0.82), followed by Others (0.23) and Mixed (0.02) for CFU. Conversely, Mixed (0.34) was significantly larger than Grass (0.17) for MBC. Nitrogen fertilizer input demonstrated no significant effects for PLFA.

Soil sampling timing had significant effects on MBC and PLFA (Fig. 7). For MBC, sampling after the cash crop harvest (0.30) and during the cover crop (0.38) had larger effect size means than that of sampling during the cash crop (0.18). For PLFA, the opposite was observed where sampling during the cash crop (0.24) had the highest effect size mean than compared to those of sampling during cover crop (0.12), after cover crop termination (0.04) and before cash crop planting (0.05). Overall, while sampling timing had a significant influence on effect size means, the influence was inconsistent. Finally, tillage types were significant for CFU and MBC. Conventional tillage methods had larger effect sizes for CFU (0.67) and MBC (0.38) than no-till and reduced tillage (CFU: 0.27; MBC: 0.21). For continuous moderators, soil sample depth had significant negative correlation with CFU ($\beta_1 = -0.05$; p-value < 0.001; $R^2 = 0.35$; Fig. S2; Table S4).

3.3. Moderator effects on the soil microbial activity

Effects of climate was significant for BG, where arid climates had a larger effect size (0.33) than that of continental (0.12); temperate climates also had a lower effect size mean (0.08) but the CI slightly overlapped with arid climates (Fig. 2).

Soil order was significant for CO2–C where the Entisols effect size mean (0.54) was significantly larger than that of Ultisols (0.24) (Fig. 3). Cover crop termination method was only significant for Phos where mechanical termination had a larger effect size mean (0.29) than that of chemical termination (−0.08) (Fig. 4). Cover crop type was significant for CO2–C only, where effect size mean of Other cover crops (0.62) was significantly larger than that of Legume (0.21) (Fig. 5). N fertilizer input was not significant for soil microbial activity (Fig. S1).

Soil sampling timing was significant for Phos and CO2–C (Fig. 7). For Phos, effect size mean of sampling during cover crop (0.37) was significantly larger than that of sampling after cash crop harvest (−0.11). For CO2–C, sampling during cover crop (0.52) was larger than that during cash crop (0.28). Tillage type was not significant for soil microbial activity (Fig. 6).

Only BG had a significantly positive yet very weak linear relationship with annual N fertilizer amount ($\beta_1 = 0.00154$; p-value < 0.001; $R^2 = 0.11$; Table S4). Visually (Fig. S3), however, these results seem dubious, as effect sizes at higher N input were not significantly larger than that at lower N fertilizer rate, which confirmed that the association is very weak. This was also supported by the overlapping CI for MBC effect sizes between N fertilized and non-fertilized observations (Fig. S1) (see Table 3).

3.4. Soil microbial diversity

The soil microbial diversity parameters OTU, Chao 1, H′, S, J, and 1-D had a wide range of between-study heterogeneity from 0.3% to 92.5%. Despite the high heterogeneity for H' (92.5%) and Chao 1 (46.1%), none of the ANOVA results were significant (Table 4). Soil order was significant for Chao 1, where the effect size mean of Mollisols (0.06) was larger than that of Entisols (<0.001) (Fig. 3). Cover crop termination method had a significant effect on H′ and J (Fig. 4). In both cases, mechanical termination had larger effect size mean (H: 0.025; J: 0.007) than that of chemical termination (H': 0.001; J: 0.006), similar to results of soil microbial abundance and activity. Tillage type was significant for S and J (Fig. 6). Like soil microbial abundance and activity, conventional tillage had larger effect size mean (S: 0.044; J: 0.021) than that of conservation practice (S: 0.016; J: 0.006). For Chao 1, effect size means from sampling during cash crop (0.056) and before cash crop planting (0.081) was significantly larger than that of sampling after cash crop harvest (−0.046) (Fig. 7).

OTU had statistically significant negative correlations with soil pH ($\beta_1 = -0.04$; p-value = 0.003; $R^2 = 0.65$; Fig. S8) and soil sample depth ($\beta_1 = -0.003$; p-value = 0.021; $R^2 = 0.38$; Fig. S2). Soil pH ranged from 6.28 to 8.3, and the negative correlation between OUT and pH was expected, as the soil microbiome generally thrives under neutral pH condition (Fierer and Jackson, 2006; Lauber et al., 2009). However, this relationship had small number of observations and much skewed distribution, requiring careful interpretation of this result. Chao 1 also demonstrated significant negative correlation with N fertilizer rate ($\beta_1 = -0.0007$; p-value = 0.0096; $R^2 = 0.36$; Fig. S3).

4. Discussion

4.1. Overall positive effects of cover cropping on soil microbial properties

Past meta-analyses have generally suggested positive effects of cover cropping on soil microbial properties (Daryanto et al., 2018; McDaniel et al., 2014; Venter et al., 2016). Indeed, cover cropping increased all 13 soil microbial parameters in this meta-analysis as well. However, heterogeneity between studies was high for most of the soil microbial parameters with the exception of those with fewer observations: OTU, S, and 1-D. According to the significant differences between effect size

Table 3
ANOVA results of effects of agricultural moderators on soil microbial activity parameters: β-glucosidase activity (BG), phosphatase activity (Phos), and respiration (CO2–C). Df is the degrees of freedom and p-values less than threshold 0.05 are in bold.

Moderators	BG			Phos			CO2–C		
	Df	Error Df	p-value	Df	Error Df	p-value	Df	Error Df	p-value
Climate	2	152	**0.000**	2	57	0.144	2	36	**0.044**
Soil Order	1	118	**0.001**	3	50	**0.001**	4	34	0.088
cover cropping Termination	1	153	0.646	1	58	**0.001**	1	31	0.999
cover cropping Type	3	151	**0.007**	3	56	0.267	3	35	0.052
Tillage Type	1	130	0.876	1	34	**0.033**	1	8	0.464
Sample Timing	2	152	**0.047**	2	57	**0.002**	2	36	0.384
N Fertilizer	1	153	**0.003**	1	50	0.462	1	32	**0.021**
N Fertilizer Rate	1	126	**0.001**	1	22	0.522	1	32	0.467
Soil pH	1	107	**0.001**	1	33	0.484	1	14	0.608
cover cropping Duration	1	153	**0.000**	1	51	0.278	1	26	0.541
Sample Depth	1	153	0.905	1	58	0.092	1	37	0.191

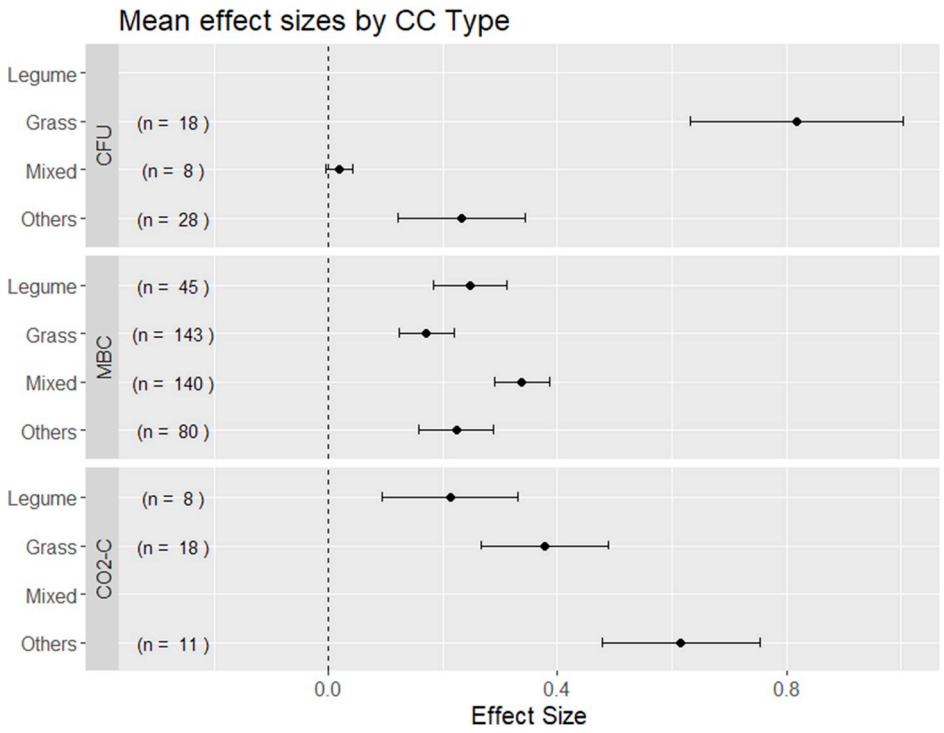

Fig. 5. Forest plots of interactions between soil microbial parameters and cover cropping type that had levels with significant differences between effect size means. Number of observations per level is noted in parentheses. Significant soil microbial parameters were colony forming unit (CFU), microbial biomass C (MBC), and respiration (CO2–C). Levels (y-axis) with means larger than zero indicate that cover cropping increased the soil microbiome parameter at those levels, and decreased if the means smaller than zero. Levels with CIs that do not overlap indicate that their effect size means are significantly different.

means by moderator levels, most of the high heterogeneity could be attributed to the effects of agricultural moderators on the soil microbial parameters.

All four soil microbial abundance parameters increased with cover cropping treatments by large ratios (14.5–40.7%). Considering that cover cropping provides above- and belowground plant biomass and root exudates known to boost soil microbial growth and prevent rich topsoil from eroding, the significant cover cropping benefits on soil microbial abundance were indeed expected (Vukicevich et al., 2016). Meta-analysis by Daryanto et al. (2018) reported similar increases in MBC, MBN, and microbial biomass P (MBP), and significantly decreased soil loss under cover cropping treatments. Based on the consistency with past meta-analyses and significant mean global effect sizes, these results suggest that cover cropping can be expected to increase soil microbial abundance.

BG and Phos are two of the four enzymes accepted by the USDA NRCS as indicators of general microbial activity for soil health assessment along with N-acetyl-β-D-glucosaminidase and arylsulfatase (NRCS, 2018). The positive global effect size means for these enzymes and CO2 respiration rate suggest positive cover cropping effects on soil microbial activity. Since BG reflects the last step in cellulose decomposition, an increase in BG activity is expected with increased cellulose input from cover crop decomposition; likewise, increases in other enzymes responsible for previous processes in cellulose decomposition would be expected (Shewale, 1982). As for Phos, the presence of organic P substrates can promote phosphatase production. Cover crops return the biomass P to the soil during decomposition which could have resulted in increased Phos (Almeida et al., 2018; Hallama et al., 2019; Nannipieri et al., 2011; Sharma et al., 2018). Moreover, a meta-analysis by Hallama et al. (2019) suggested that cover cropping indirectly enhances soil P availability. For example, cover cropping may enhance AMF colonization which improves access to P pool, or change soil pH to levels more favorable for Phos and other enzyme activities. Meanwhile, since some plants are known to produce phosphatase themselves, this result requires careful interpretation to account for plant-originated Phos (Tarafdar and Claassen, 1988).

This meta-analysis is the first to exclusively assess the effects of cover cropping on soil microbial diversity. The most closely related meta-analysis focused on soil microbial diversity and richness, and reported positive weighted mean differences of 3.36% for diversity and 15.11% for richness (Venter et al., 2016). However, their analysis focused on the effects of crop rotations which happened to include cover cropping studies. Compared to those of soil microbial abundance and activity, our global effect size means for diversity parameters were also positive but almost ten-fold smaller on average. In fact, the global effect size mean for Simpson's diversity index was negative (−0.009) until 6 outliers with relatively extreme variances (>0.4) or effect sizes (<-0.5) were removed. Nonetheless, such sensitivity may be limited to parameters with smaller number of observations like 1-D. However, without historical references for comparison and with effect sizes small enough to raise doubt on the significance of cover cropping effects on the soil microbial diversity, making a solid and generalized statement on this relationship will require more primary research and meta-analyses.

4.2. *Significance of agricultural moderators*

Statistical results suggested that agricultural moderators can determine how responsive soil microbial properties are to cover cropping effects. The environmental moderators, climate and soil order, had significant effects on soil microbial abundance and activity. Results varied by parameters for observations on tropical, arid, and temperate climates, but continental climates consistently had the smallest effect size means. Interestingly, 46% of the studies on continental climates were on productive soils like Alfisols and Mollisols, primarily from the fertile agricultural regions like the Midwest, USA (NRCS, 2005). Consistently lower effect size means for continental climates may be attributed to the high fertility of these soils on which cover cropping benefits experience diminishing return on already productive soils. Overall, climate results indicate that cover cropping can improve the soil microbiome especially in regions expected to have less robust soil microbiome. However, previous studies warn that cover cropping may put more pressure on dry agroecosystems, highlighting the need for careful irrigation and management decisions (Calderon et al., 2016).

Meanwhile, the main effects from soil order exhibited conflicting

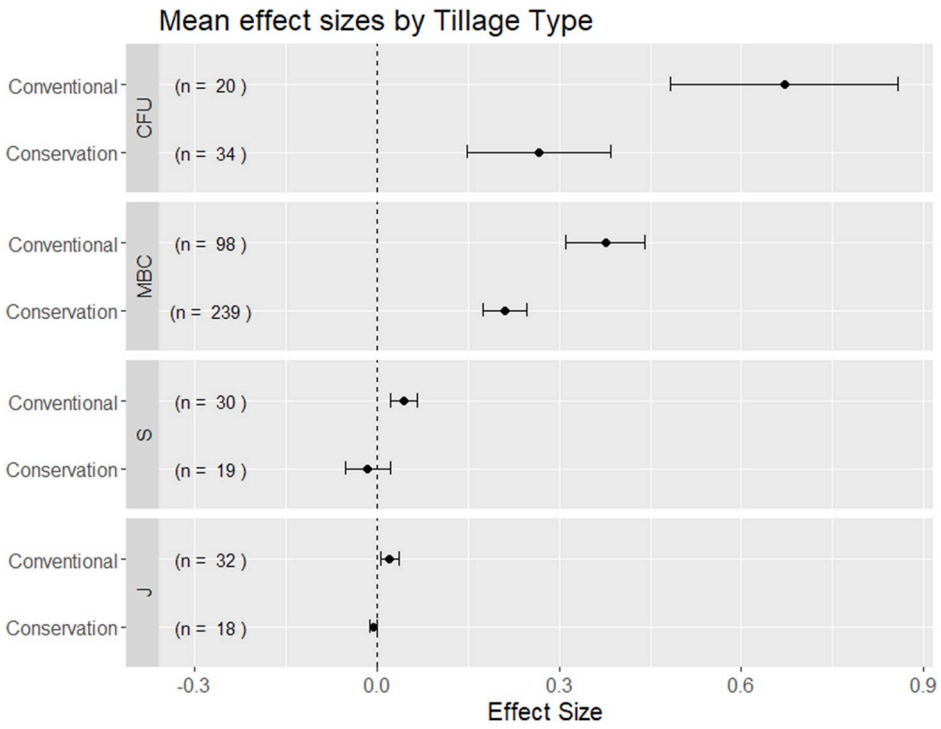

Fig. 6. Forest plots of interactions between soil microbial parameters and tillage type that had levels with significant differences between effect size means. Number of observations per level is noted in parentheses. Significant soil microbial parameters were colony forming unit (CFU), microbial biomass C (MBC), genetic richness (S), and Pielou's evenness index (J). Levels (y-axis) with means larger than zero indicate that cover cropping increased the soil microbiome parameter at those levels, and decreased if the means smaller than zero. Levels with CIs that do not overlap indicate that their effect size means are significantly different.

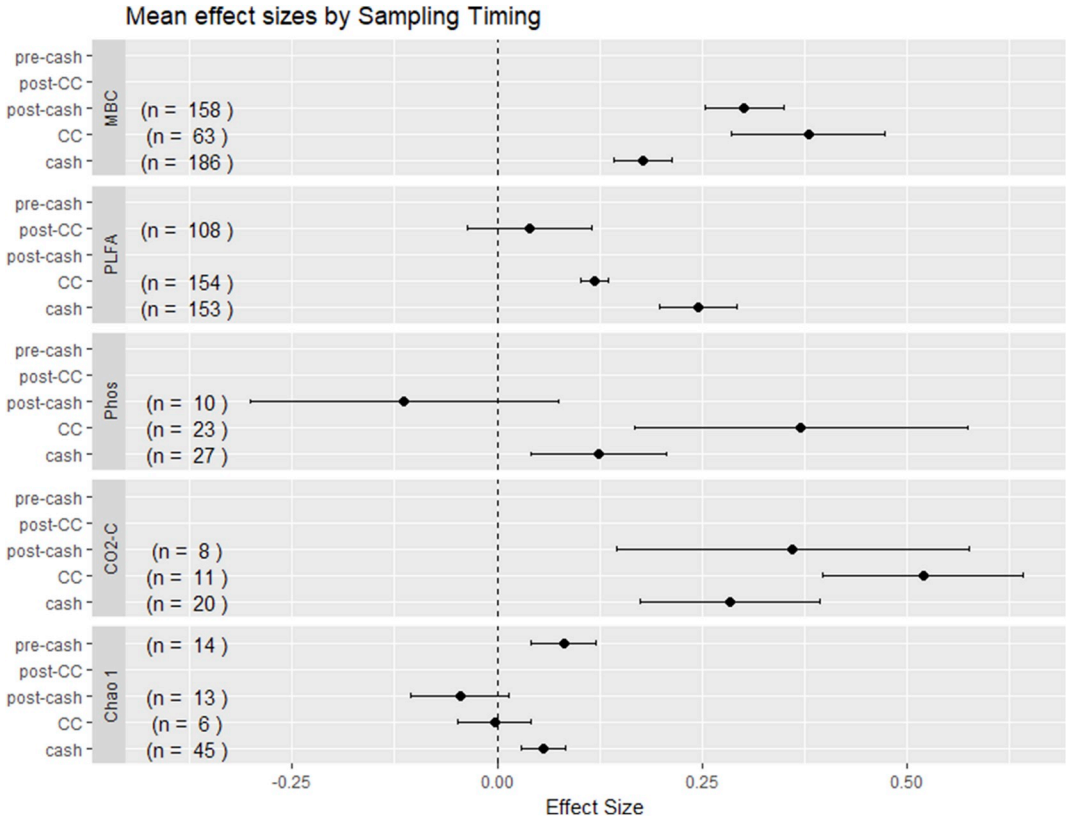

Fig. 7. Forest plots of interactions between soil microbial parameters and soil sampling timing that had levels with significant differences between effect size means. Number of observations per level is noted in parentheses. Significant soil microbial parameters were microbial biomass C (MBC), phospholipid fatty acid (PLFA), phosphatase activity (Phos), respiration (CO2–C), and Chao 1 richness index. Levels (y-axis) with means larger than zero indicate that cover cropping increased the soil microbiome parameter at those levels, and decreased if the means smaller than zero. Levels with CIs that do not overlap indicate that their effect size means are significantly different.

Table 4
ANOVA results of effects of agricultural moderators on soil microbial diversity parameters: operational taxonomic unit (OTU), Chao 1 richness index, Shannon's diversity index (H′), genetic richness (S), Pielou's evenness index (J), and Simpson's diversity index (1-D). Df is the degrees of freedom and p-values less than threshold 0.05 are in bold. Dashes (–) indicate that combination of soil microbiome parameter and moderator had less than two levels, therefore unable to perform ANOVA, or the combination had no observations.

Moderators	OTU			Chao 1			H′			S			J			1-D		
	Df	Error Df	p-value	Df	Error Df	p-value	Df	Error Df	p-value	Df	Error Df	p-value	Df	Error Df	p-value	Df	Error Df	p-value
Climate	2	29	**0.032**	2	75	0.610	2	196	0.366	2	54	0.658	1	48	0.077	2	58	0.084
Soil Order	1	26	**0.000**	2	70	0.463	4	153	0.261	1	16	0.430	–	–	–	1	52	0.073
cover cropping Termination	1	28	0.433	1	73	0.331	1	171	0.520	1	41	0.183	1	34	**0.021**	1	54	0.235
cover cropping Type	2	29	**0.004**	3	74	0.077	3	195	0.667	2	54	0.423	1	48	0.077	3	57	**0.009**
Tillage Type	1	26	**0.010**	1	30	0.938	1	155	0.254	1	47	0.062	1	48	**0.047**	1	29	**0.000**
Sample Timing	1	30	**0.008**	3	74	0.420	3	195	0.293	2	54	0.844	2	47	**0.038**	2	58	**0.008**
N Fertilizer	1	30	0.188	1	76	0.379	1	194	0.969	1	55	0.786	1	48	0.598	1	59	0.485
N Fertilizer Rate	1	30	0.564	1	47	0.247	1	147	0.943	1	12	**0.000**	1	12	**0.009**	1	34	0.253
Soil pH	1	30	**0.001**	1	75	0.412	1	137	0.286	1	5	0.130	–	–	–	1	56	0.656
cover cropping Duration	1	28	**0.000**	1	73	0.286	1	135	0.634	1	5	0.130	–	–	–	1	54	**0.005**
Sample Depth	1	30	**0.028**	1	76	0.367	1	197	0.334	1	55	0.952	1	48	0.650	1	59	0.826

results, with less productive soil orders showing larger effect size means for MBC and PLFA and smaller effect size means for MBN and Chao 1. This discrepancy should be further explored with an emphasis on interactions between climates and soil orders. However, the current database has too few observations to make reliable inference on interactions. Together, climate and soil order should be considered when managing cover cropping to maximize the benefits.

Management factors also had significant influences on the cover cropping effects sizes. Tillage type consistently affected cover cropping effects where conservation tillage had smaller effect size means than those of conventional tillage. This result initially seemed contradictory to previous findings which reported the benefits of reduced tillage or no-till on various soil properties (Blanco-Canqui and Ruis, 2018; Bowles et al., 2017; Hussain et al., 1999; Zuber and Villamil, 2016). For example, a meta-analysis on the effects of tillage on soil microbiome by Zuber and Villamil (2016) reported negative effect sizes for soil microbial properties with conventional tillage. Another meta-analysis by Bowles et al. (2017) on the effects of cover cropping and tillage on AMF colonization reported benefits of alternative tillage methods, although they did not find evidence for benefits from interactions between cover cropping and tillage. Considering these past findings, negative effects of conventional tillage on the soil microbial properties may have been mitigated by cover cropping, thereby pronouncing the cover cropping effects. Another potential explanation is that bare fallow under conservation tillage often allows weed covers that can mimic some cover cropping effects, thereby leading to smaller cover crop effect size compared to that under conventional tillage.

Chemical cover crop termination methods that used herbicide showed smaller cover crop effect size means than mechanical termination methods. This result may be relevant to herbicide effects on plants and soil microbiome. Past studies have found that herbicides may directly impact soil properties and the microbial community. For example, herbicides may decrease soil denitrification (Tenuta and Beauchamp, 1996), promote plants to exudate ammonium, thus stimulating growth of specific microbial functional groups (Damin et al., 2010, 2008; Mijangos et al., 2010; Nyerges et al., 2010; Zabaloy et al., 2017), and temporarily change microbial respiration and biomass (Nguyen et al., 2016). Because both termination method categories included studies with tillage and those without, tillage or other mechanical methods are unlikely to have contributed to the differences. Although further investigation is necessary to verify this result, it suggests that mechanical termination will maximize cover crop benefits.

As expected, soil sampling timing had significant effects on soil microbial properties, where either observations during the cover crop or cash crop phases had larger effect size means. This result emphasizes that soil sampling timing must be accounted for in the analysis of soil microbial properties, as they are time dependent. More than half of the observations were during cash crop phase ($n > 600$), followed by the cover cropping phase with just under 300 observations. For consistent research synthesis without a timing bias, primary research should report the crop phase of soil measurements.

4.3. Limitations of this study

While the cover cropping effects on soil microbial activity are clearly positive, this relationship must be interpreted carefully because microbial activity correlates with both abundance and diversity. First, the increase in microbial activity could be attributed to an overall increase in microbial abundance, and their significant positive correlation has been observed by others (Acosta-Martinez et al., 2011). More work is needed to discern whether activity increased because of changes in abundance of active microbes or via an increase in per-capita enzyme production rate. Of course, both may be responsible. Indeed, effect sizes on BG and Phos had positive linear relationships with MBC, although the number of observations was small for Phos (Fig. 8). This result also suggests other correlations between enzymes and microbial abundance parameters, such as Phos and PLFA or MBP, are likely. However, more studies reporting both soil microbial activity and abundance are needed perform multivariate analysis and to confirm our results.

Second, soil microbial activity closely intertwine with microbial diversity because extracellular enzyme production varies by soil microbial group and is not universal, especially for soil microbial activities responsible for ecosystem services like nutrient cycling (Wang et al., 2017; Zang et al., 2018). To assess cover cropping effects on these specific soil microbial processes, using soil microbial genes and their products involved in those processes are potentially more informative than the parameters assessed in this study. For example, to understand cover cropping effects on N fixation, abundance changes in genes like *nifH* and their products should be analyzed. Some studies in our databases included this type of information but the studies were too sparse. Moreover, if the identities of soil microbial groups harboring specific genes are known, assessing cover cropping effects on their relative abundance may strengthen the argument that cover cropping enhances soil microbial processes beneficial for agriculture. However, studies reporting both soil microbial activity and diversity are lacking, and information linking soil microbial groups with specific enzyme

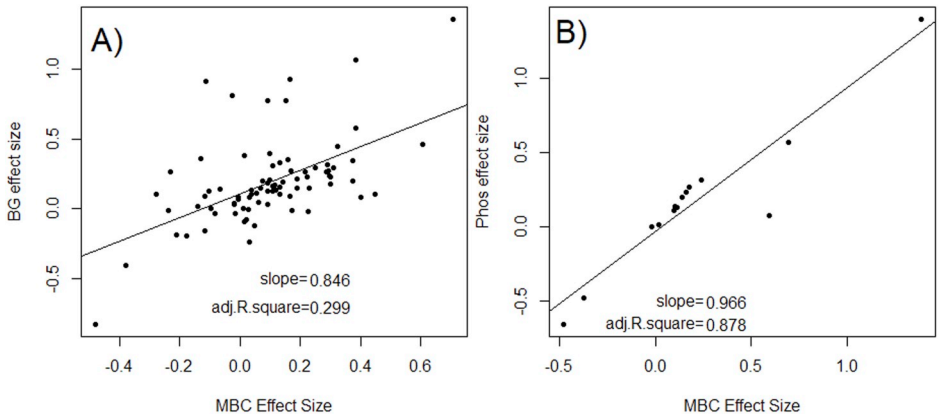

Fig. 8. Scatter plot and linear regression of cover cropping effect sizes of β-glucosidase (BG; A) and those of phosphatase activity (Phos; B) on those of microbial biomass C (MBC). The linear coefficient of the model (slope) and R^2 are noted. Both linear coefficients had significant (p-values). These relationships signify the unit change in soil microbial activity by abundance.

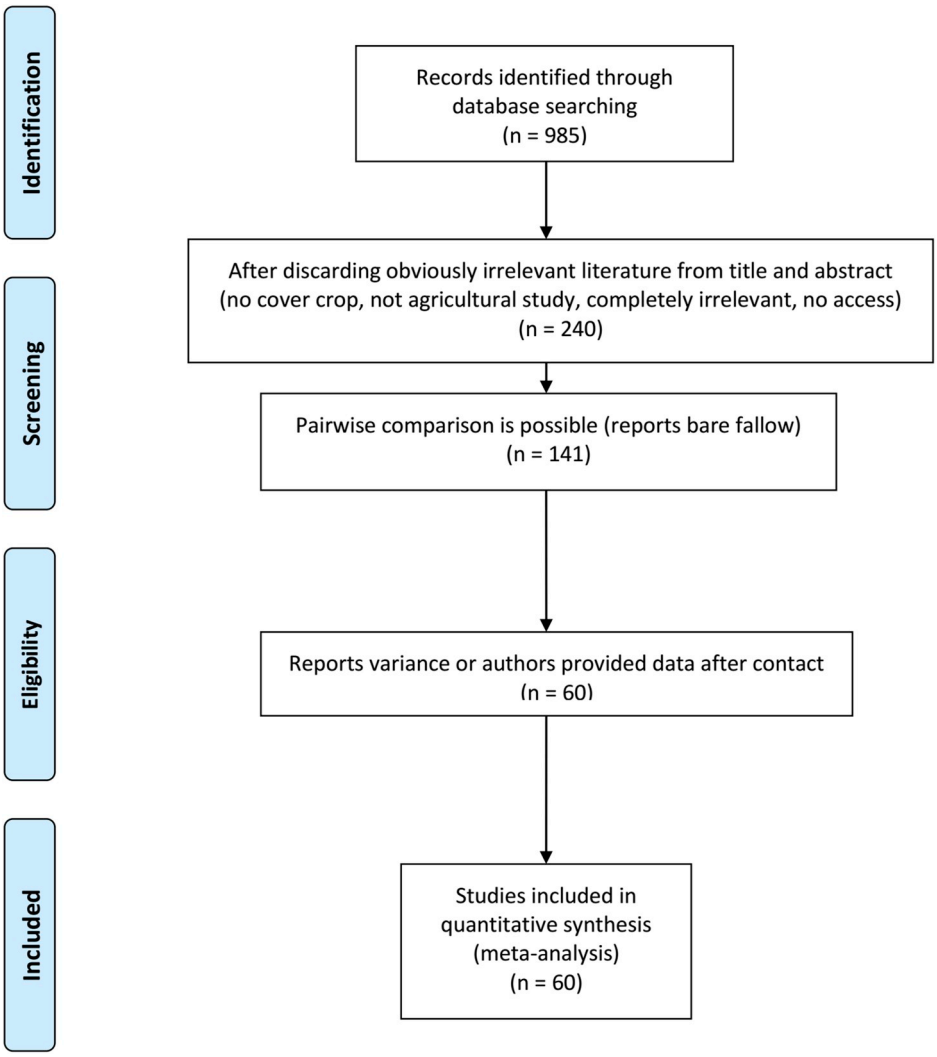

Fig. 9. PRISMA flow diagram modified from that by Moher et al. (2009). The chart shows what criteria was applied and how many literature remained at each stage (n =).

productions and genomic data is largely unavailable (Hai et al., 2009; Wang et al., 2017). Therefore, more future cover cropping studies connecting soil microbial diversity and activity are needed.

As a meta-analysis, this study will inevitably share the methodological limitations of its compiled primary research. For example, current enzyme activity assays are optimized for laboratory conditions and may not accurately distinguish soil enzymes that were segregated physically and biologically, therefore overestimating the *in*

situ activity. Laboratory enzyme assays require disturbing the soil aggregates, which may release stabilized enzymes that would have been inactive *in situ* (Burns, 1982; Wallenstein and Weintraub, 2008). Also, enzyme activity assays may not accurately demonstrate *in situ* activity because of the *in vitro* conditions of the assays. Current enzyme assay methods are done under ideal conditions for enzyme activity, which can overestimate the actual enzyme activities *in situ* (Tabatabai, 2003). The similar is also true for some microbial abundance parameters like CFU that cultures and counts the microbes in the laboratory condition. In general, our understanding of the role of management practices on the soil microbial community will be limited by the best available methods, and research will be required to reevaluate the state of knowledge as better methodologies develop.

4.4. Current state of cover cropping research on soil microbiome and future needs

Out of 48 soil microbial parameters reported by a total of 60 studies, only 13 had a statistically significant number of observations ($n \geq 30$). MBC was the parameter with the greatest number of observations (403 observations). The most studied soil microbiome property was microbial abundance, and further research seems unnecessary with the clear cover cropping benefits that this study has demonstrated. Soil microbial activity had the second most studies, primarily represented by two enzyme activities. These enzymes alone are insufficient considering the vast complexity of soil microbial activity crucial for agriculture. Therefore, more enzymes and the genes coding them need to be studied to better understand the still largely unknown complexity of soil microbial activity. As for soil microbial diversity, most studies reported diversity indices derived from changes in relative abundances of soil microbial phyla or genera; some derived from a broader classification such as PLFA data (gram +/−, fungi, and eukaryote). Some studies used community catabolic profiles like average well color development (AWCD) which can capture both activity and diversity. However, the number of such studies was small and they are subject to limitations on data integration arising from various methodological considerations like cell culture conditions (Konopka et al., 1998; Preston-Mafham et al., 2002; Weber et al., 2007).

The current landscape of cover cropping research and its effects on soil microbial properties is still unable to answer more complex questions. Making meaningful inferences on such questions like "how much do changes in soil microbial abundance contribute to changes in activity" requires more studies that address comprehensive sets of soil microbial parameters. Nevertheless this meta-analysis marks a meaningful start in this effort, and the trend seems hopeful as half of the studies in our database were conducted in the last four years (2016–2019), thanks to developing technology, lowering costs, increased interest in sustainable agriculture, and accumulating experience. Meaningful updates on this meta-analysis could be possible with a larger database in the near future that would include analyses that this study could not perform due to insufficient number of observations.

5. Conclusion

As the first meta-analysis dedicated to evaluating the cover cropping effects on soil microbial properties, this study concludes that cover cropping generally enhances soil microbial abundance, activity, and, to a lesser degree, diversity. With proper implementation considering termination methods, climate, soil order, and tillage, cover cropping will build a more robust soil microbiome. Other than these significant moderators, this study found no strong evidence for dependence on other agricultural factors. This meta-analysis showed that cover cropping still needs more research but also demonstrated that this need is being met with an increasing number of recent relevant studies. Nonetheless, this study urges more researchers to investigate the interactions between microbial properties and cover cropping practices as more important answers surrounding the complex interactions still lie unveiled. With a database large enough to perform more complex analysis, a future meta-analyses may reveal specific cover cropping effects on the soil microbiome that are relevant to both agricultural and environmental interests.

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.

Acknowledgements

Support for this project was provided by USDA-NIFA, Award No. AG 2018-67019-27807 "Understanding shifts in the microbial N cycle with inclusion of cover crops into long-term agricultural experiments and their links to soil health and productivity", and Award No. AG 2018-68002-27961 "An Integrated approach to assessing cover crops as an adaptation to improve resilience of the U.S. Midwest agroecosystems".

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.soilbio.2019.107701.

References

Reicosky, D.C., Forcella, F., 1998. Cover crop and soil quality interactions in agroecosystems. Journal of Soil and Water Conservation 53, 224–229.

Tarafdar, J.C., Claassen, N., 1988. Organic phosphorus compounds as a phosphorus source for higher plants through the activity of phosphatases produced by plant roots and microorganisms. Biology and Fertility of Soils 5, 308–312. https://doi.org/10.1007/BF00262137.

Abdollahi, L., Munkholm, L.J., 2014. Tillage system and cover crop effects on soil quality:I. Chemical, mechanical, and biological properties. Soil Science Society of America Journal 78, 262–270. https://doi.org/10.2136/sssaj2013.07.0301.

Abdollahi, L., Munkholm, L.J., Garbout, A., 2014. Tillage system and cover crop effects on soil quality: II. Pore characteristics. Soil Science Society of America Journal 78, 271–279. https://doi.org/10.2136/sssaj2013.07.0302.

Acosta-Martinez, V., Lascano, R., Calderon, F., Booker, J.D., Zobeck, T.M., Upchurch, D. R., 2011. Dryland cropping systems influence the microbial biomass and enzyme activities in a semiarid sandy soil. Biology and Fertility of Soils 47, 655–667. https://doi.org/10.1007/s00374-011-0565-1.

Alexandratos, N., Bruinsma, J., 2012. World Agriculture towards 2030/2050: the 2012 Revision, vol. 12, p. 154.

Almeida, D.S., Menezes-Blackburn, D., Rocha, K.F., de Souza, M., Zhang, H., Haygarth, P. M., Rosolem, C.A., 2018. Can tropical grasses grown as cover crops improve soil phosphorus availability? Soil Use & Management 34, 316–325. https://doi.org/10.1111/sum.12439.

Arnfield, J., 2019. Koppen climate classification [WWW Document]. Encyclopedia Britannica. URL. https://www.britannica.com/science/Koppen-climate-classification. accessed 4.21.19.

Basche, A.D., Miguez, F.E., Kaspar, T.C., Castellano, M.J., 2014. Do cover crops increase or decrease nitrous oxide emissions? A meta-analysis. Journal of Soil and Water Conservation 69, 471–482. https://doi.org/10.2489/jswc.69.6.471.

Beck, H.E., Zimmermann, N.E., McVicar, T.R., Vergopolan, N., Berg, A., Wood, E.F., 2018. Present and future Köppen-Geiger climate classification maps at 1-km resolution. Sci. Data 5, 180214.

Bengtsson, J., Ahnström, J., Weibull, A.-C., 2005. The effects of organic agriculture on biodiversity and abundance: a meta-analysis. Journal of Applied Ecology 42, 261–269. https://doi.org/10.1111/j.1365-2664.2005.01005.x.

Blanco-Canqui, H., Ruis, S.J., 2018. No-tillage and soil physical environment. Geoderma 326, 164–200. https://doi.org/10.1016/j.geoderma.2018.03.011.

Bowles, T.M., Jackson, L.E., Loeher, M., Cavagnaro, T.R., 2017. Ecological intensification and arbuscular mycorrhizas: a meta-analysis of tillage and cover crop effects. Journal of Applied Ecology 54, 1785–1793. https://doi.org/10.1111/1365-2664.12815.

Burns, R.G., 1982. Enzyme activity in soil: Location and a possible role in microbial ecology. Soil Biol. Biochem. 14, 423–427. https://doi.org/10.1016/0038-0717(82)90099-2. A. D. McLaren Memorial Issue.

Calderon, F.J., Nielsen, D., Acosta-Martinez, V., Vigil, M.F., Lyons, D., 2016. Cover crop and irrigation effects on soil microbial communities and enzymes in semiarid agroecosystems of the central great plains of north America. Pedosphere 26, 192–205. https://doi.org/10.1016/S1002-0160(15)60034-0.

Conacher, A., 2009. Land degradation: a global perspective. New Zealand Geographer 65, 91–94. https://doi.org/10.1111/j.1745-7939.2009.01151.x.

Damin, V., Trivelin, P.C.O., Carvalho, S.J.P., Moraes, M.F., Barbosa, T.G., 2010. Herbicide application increases nitrogen (15N) exudation and root detachment of Brachiaria decumbens Stapf. Plant and Soil 334, 511–519. https://doi.org/10.1007/s11104-010-0402-6.

Daryanto, S., Fu, B., Wang, L., Jacinthe, P.-A., Zhao, W., 2018. Quantitative synthesis on the ecosystem services of cover crops. Earth-Science Reviews 185, 357–373. https://doi.org/10.1016/j.earscirev.2018.06.013.

Fierer, N., Jackson, R.B., 2006. The diversity and biogeography of soil bacterial communities. Proceedings of the National Academy of Sciences 103, 626–631. https://doi.org/10.1073/pnas.0507535103.

Gao, S.-J., Chang, D.-N., Zou, C.-Q., Cao, W.-D., Gao, J.-S., Huang, J., Bai, J.-S., Zeng, N.-H., Rees, R.M., Thorup-Kristensen, K., 2018. Archaea are the predominant and responsive ammonia oxidizing prokaryotes in a red paddy soil receiving green manures. European Journal of Soil Biology 88, 27–35. https://doi.org/10.1016/j.ejsobi.2018.05.008.

Google Earth [WWW Document], n.d. URL https://earth.google.com/web (accessed 4.21.19).

Hai, B., Diallo, N.H., Sall, S., Haesler, F., Schauss, K., Bonzi, M., Assigbetse, K., Chotte, J.-L., Munch, J.C., Schloter, M., 2009. Quantification of key genes steering the microbial nitrogen cycle in the rhizosphere of sorghum cultivars in tropical agroecosystems. Applied and Environmental Microbiology 75, 4993–5000. https://doi.org/10.1128/AEM.02917-08.

Hallama, M., Pekrun, C., Lambers, H., Kandeler, E., 2019. Hidden miners - the roles of cover crops and soil microorganisms in phosphorus cycling through agroecosystems. Plant and Soil 434, 7–45. https://doi.org/10.1007/s11104-018-3810-7.

Hussain, I., Olson, K.R., Ebelhar, S.A., 1999. Long-term tillage effects on soil chemical properties and organic matter fractions. Soil Science Society of America Journal 63, 1335–1341. https://doi.org/10.2136/sssaj1999.6351335x.

Kaye, J.P., Quemada, M., 2017. Using cover crops to mitigate and adapt to climate change. Agronomy for Sustainable Development 37, 4. https://doi.org/10.1007/s13593-016-0410-x.

van Kessel, C., Venterea, R., Six, J., Adviento-Borbe, M.A., Linquist, B., van Groenigen, K. J., 2013. Climate, duration, and N placement determine N2O emissions in reduced tillage systems: a meta-analysis. Global Change Biology 19, 33–44. https://doi.org/10.1111/j.1365-2486.2012.02779.x.

King, A.E., Hofmockel, K.S., 2017. Diversified cropping systems support greater microbial cycling and retention of carbon and nitrogen. Agriculture, Ecosystems & Environment 240, 66–76. https://doi.org/10.1016/j.agee.2017.01.040.

Konopka, A., Oliver, L., Turco Jr., R.F., 1998. The use of carbon substrate utilization patterns in environmental and ecological microbiology. Microbial Ecology 35, 103–115. https://doi.org/10.1007/s002489900065.

Köppen climate classification, 2019. Wikipedia, the Free Encyclopedia.

Koricheva, J., Gurevitch, J., Mengersen, K., 2013. Handbook of Meta-Analysis in Ecology and Evolution. Princeton University Press.

Lauber, C.L., Hamady, M., Knight, R., Fierer, N., 2009. Pyrosequencing-based assessment of soil pH as a predictor of soil bacterial community structure at the continental scale. Applied and Environmental Microbiology 75, 5111–5120. https://doi.org/10.1128/AEM.00335-09.

Li, J.H., Jiao, S.M., Gao, R.Q., Bardgett, R.D., 2012. Differential effects of legume species on the recovery of soil microbial communities, and carbon and nitrogen contents, in abandoned fields of the Loess Plateau, China. Environmental Management 50, 1193–1203. https://doi.org/10.1007/s00267-012-9958-7.

Lienhard, P., Terrat, S., Prévost-Bouré, N.C., Nowak, V., Régnier, T., Sayphoummie, S., Panyasiri, K., Tivet, F., Mathieu, O., Levêque, J., 2014. Pyrosequencing evidences the impact of cropping on soil bacterial and fungal diversity in Laos tropical grassland. Agronomy for Sustainable Development 34, 525–533.

Marcillo, G.S., Miguez, F.E., 2017. Corn yield response to winter cover crops: an updated meta-analysis. Journal of Soil and Water Conservation 72, 226–239. https://doi.org/10.2489/jswc.72.3.226.

Marshall, M.W., Williams, P., Nafchi, A.M., Maja, J.M., Payero, J., Mueller, J., Khalilian, A., 2016. Influence of tillage and deep rooted cool season cover crops on soil properties, pests, and yield responses in cotton. Open Journal of Soil Science 6, 149–158. https://doi.org/10.4236/ojss.2016.610015.

McDaniel, M.D., Tiemann, L.K., Grandy, A.S., 2014. Does agricultural crop diversity enhance soil microbial biomass and organic matter dynamics? A meta-analysis. Ecological Applications 24, 560–570. https://doi.org/10.1890/13-0616.1.

Mijangos, I., Albizu, I., Garbisu, C., 2010. Beneficial effects of organic fertilization and no-tillage on fine-textured soil properties under two different forage crop rotations. Soil Science 175, 173–185. https://doi.org/10.1097/SS.0b013e3181dd51ba.

Moher, D., Liberati, A., Tetzlaff, J., Altman, D.G., The PRISMA Group, 2009. Preferred reporting items for systematic reviews and meta-analyses: the PRISMA statement. PLoS Medicine 6 (7), e1000097. https://doi.org/10.1371/journal.pmed1000097.

Nannipieri, P., Giagnoni, L., Landi, L., Renella, G., 2011. Role of phosphatase enzymes in soil. In: Bünemann, E., Oberson, A., Frossard, E. (Eds.), Phosphorus in Action: Biological Processes in Soil Phosphorus Cycling, Soil Biology. Springer Berlin Heidelberg, Berlin, Heidelberg, pp. 215–243. https://doi.org/10.1007/978-3-642-15271-9_9.

Nguyen, D.B., Rose, M.T., Rose, T.J., Morris, S.G., van Zwieten, L., 2016. Impact of glyphosate on soil microbial biomass and respiration: a meta-analysis. Soil Biology and Biochemistry 92, 50–57. https://doi.org/10.1016/j.soilbio.2015.09.014.

NRCS, 2005. Distribution Maps of Dominant Soil Orders. NRCS Soils [WWW Document]. https://www.nrcs.usda.gov/wps/portal/nrcs/detail/soils/survey/class/maps/?cid=nrcs142p2_053589. accessed 4.8.19.

NRCS, 2018. Recommended Soil Health Indicators and Associated Laboratory Procedures.

Nyerges, G., Han, S.-K., Stein, L.Y., 2010. Effects of ammonium and nitrite on growth and competitive fitness of cultivated methanotrophic bacteria. Applied and Environmental Microbiology 76, 5648–5651. https://doi.org/10.1128/AEM.00747-10.

Osipitan, O.A., Dille, J.A., Assefa, Y., Knezevic, S.Z., 2018. Cover Crop for Early Season Weed Suppression in Crops: Systematic Review and Meta-Analysis. Agron. J. 110, 2211–2221. https://doi.org/10.2134/agronj2017.12.0752.

Paustian, K., Lehmann, J., Ogle, S., Reay, D., Robertson, G.P., Smith, P., 2016. Climate-smart soils. Nature 532, 49–57. https://doi.org/10.1038/nature17174.

Poeplau, C., Don, A., 2015. Carbon sequestration in agricultural soils via cultivation of cover crops – a meta-analysis. Agriculture, Ecosystems & Environment 200, 33–41. https://doi.org/10.1016/j.agee.2014.10.024.

Preston-Mafham, J., Boddy, L., Randerson, P.F., 2002. Analysis of microbial community functional diversity using sole-carbon-source utilisation profiles – a critique. FEMS Microbiology Ecology 42, 1–14. https://doi.org/10.1111/j.1574-6941.2002.tb00990.x.

R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rohatgi, A., 2015. WebPlotDigitizer.

Sharma, V., Irmak, S., Padhi, J., 2018. Effects of cover crops on soil quality: Part I. Soil chemical properties-organic carbon, total nitrogen, pH, electrical conductivity, organic matter content, nitrate-nitrogen, and phosphorus. Journal of Soil and Water Conservation 73, 637–651. https://doi.org/10.2489/jswc.73.6.637.

Shewale, J.G., 1982. β-Glucosidase: its role in cellulase synthesis and hydrolysis of cellulose. International Journal of Biochemistry 14, 435–443. https://doi.org/10.1016/0020-711X(82)90109-4.

Soil taxonomy | NRCS soils [WWW Document], n.d. URL https://www.nrcs.usda.gov/wps/portal/nrcs/main/soils/survey/class/taxonomy/(accessed 4.21.19).

Stavi, I., Lal, R., 2015. Achieving zero net land degradation: challenges and opportunities. Journal of Arid Environments 112, 44–51. https://doi.org/10.1016/j.jaridenv.2014.01.016. Special Issue on the Fourth Drylands Deserts and Desertification "DDD" Conference.

Sturm, D.J., Peteinatos, G., Gerhards, R., 2018. Contribution of allelopathic effects to the overall weed suppression by different cover crops. Weed Research 58, 331–337. https://doi.org/10.1111/wre.12316.

Surucu, A., Ozyazici, M.A., Bayrakli, B., Kizilkaya, R., 2014. Effects of green manuring on soil enzyme activity. Fresenius Environmental Bulletin 23, 2126–2132.

Tabatabai, M.A., 2003. Soil enzymes. In: Encyclopedia of Agrochemicals. American Cancer Society. https://doi.org/10.1002/047126363X.agr354.

Tenuta, M., Beauchamp, E., 1996. Denitrification following herbicide application to a grass sward - Canadian Journal of Soil Science [WWW Document]. URL. http://www.nrcresearchpress.com/doi/abs/10.4141/cjss96-003#.XA2hJnRKi70. accessed 12.9.18.

Thapa, R., Mirsky, S.B., Tully, K.L., 2018. Cover crops reduce nitrate leaching in agroecosystems: a global meta-analysis. Journal of Environmental Quality 47, 1400–1411. https://doi.org/10.2134/jeq2018.03.0107.

Tsiafouli, M.A., Thebault, E., Sgardelis, S.P., de Ruiter, P.C., van der Putten, W.H., Birkhofer, K., Hemerik, L., de Vries, F.T., Bardgett, R.D., Brady, M.V., Bjornlund, L., Jorgensen, H.B., Christensen, S., Hertefeldt, T.D., Hotes, S., Gera Hol, W.H., Frouz, J., Liiri, M., Mortimer, S.R., Setala, H., Tzanopoulos, J., Uteseny, K., Pizl, V., Stary, J., Wolters, V., Hedlund, K., 2015. Intensive agriculture reduces soil biodiversity across Europe. Glob. Chang. Biol. 21, 973–985.

Venter, Z.S., Jacobs, K., Hawkins, H.-J., 2016. The impact of crop rotation on soil microbial diversity: a meta-analysis. Pedobiologia 59, 215–223. https://doi.org/10.1016/j.pedobi.2016.04.001.

Viechtbauer, W., 2010. Conducting meta-analyses in R with the metafor package. Journal of Statistical Software 36, 1–48. https://doi.org/10.18637/jss.v036.i03.

Vukicevich, E., Lowery, T., Bowen, P., Urbez-Torres, J.R., Hart, M., 2016. Cover crops to increase soil microbial diversity and mitigate decline in perennial agriculture. A review. Agronomy for Sustainable Development 36, 48. https://doi.org/10.1007/s13593-016-0385-7.

Wallenstein, M.D., Weintraub, M.N., 2008. Emerging tools for measuring and modeling the in situ activity of soil extracellular enzymes. Soil Biol. Biochem. Spec. Sect.: Enzymes Environ. 40, 2098–2106. https://doi.org/10.1016/j.soilbio.2008.01.024.

Wang, H., Li, X., Li, X., Li, X., Wang, J., Zhang, H., 2017. Changes of microbial population and N-cycling function genes with depth in three Chinese paddy soils. PLoS One 12. https://doi.org/10.1371/journal.pone.0189506.

Weber, K.P., Grove, J.A., Gehder, M., Anderson, W.A., Legge, R.L., 2007. Data transformations in the analysis of community-level substrate utilization data from microplates. Journal of Microbiological Methods 69, 461–469. https://doi.org/10.1016/j.mimet.2007.02.013.

Zabaloy, M.C., Allegrini, M., Tebbe, D.A., Schuster, K., Gomez, E.d.V., 2017. Nitrifying bacteria and archaea withstanding glyphosate in fertilized soil microcosms. Appl. Soil Ecol 117-118, 88–95.

Zang, X., Liu, M., Fan, Y., Xu, J., Xu, X., Li, H., 2018. The structural and functional contributions of β-glucosidase-producing microbial communities to cellulose degradation in composting. Biotechnology for Biofuels 11. https://doi.org/10.1186/s13068-018-1045-8.

Zuber, S.M., Villamil, M.B., 2016. Meta-analysis approach to assess effect of tillage on microbial biomass and enzyme activities. Soil Biology and Biochemistry 97, 176–187. https://doi.org/10.1016/j.soilbio.2016.03.011.

References

Acosta-Martínez, V., Dowd, S.E., Bell, C.W., Lascano, R., Booker, J.D., Zobeck, T.M., Upchurch, D.R., 2010. Microbial community composition as affected by dryland cropping systems and tillage in a semiarid sandy soil. Diversity 2, 910–931.

Barel, J.M., Kuyper, T.W., Paul, J., de Boer, W., Cornelissen, J.H.C., De Deyn, G.B., 2019. Winter cover crop legacy effects on litter decomposition act through litter quality and microbial community changes. Journal of Applied Ecology 56, 132–143.

Berthrong, S.T., Buckley, D.H., Drinkwater, L.E., 2013. Agricultural management and labile carbon additions affect soil microbial community structure and interact with carbon and nitrogen cycling. Microbial Ecology 66, 158–170.

Bini, D., Santos, C.A.D., Bernal, L.P.T., Andrade, G., Nogueira, M.A., 2014. Identifying indicators of C and N cycling in a clayey Ultisol under different tillage and uses in winter. Applied Soil Ecology 76, 95–101.

Brooks, J.P., Tewolde, H., Adeli, A., Shankle, M.W., Way, T.R., Smith, R.K., Pepper, I.L., 2018. Effects of subsurface banding and broadcast of poultry litter and cover crop on soil microbial populations. Journal of Environmental Quality 47, 427–435.

Buyer, J.S., Baligar, V.C., He, Z., Arevalo-Gardini, E., 2017. Soil microbial communities under cacao agroforestry and cover crop systems in Peru. Applied Soil Ecology 120, 273–280.

Buyer, J.S., Teasdale, J.R., Roberts, D.P., Zasada, I.A., Maul, J.E., 2010. Factors affecting soil microbial community structure in tomato cropping systems. Soil Biology and Biochemistry 42, 831–841.

Chavarria, D.N., Pérez-Brandan, C., Serri, D.L., Meriles, J.M., Restovich, S.B., Andriulo, A.E., Jacquelin, L., Vargas-Gil, S., 2018. Response of soil microbial communities to agroecological versus conventional systems of extensive agriculture. Agriculture, Ecosystems & Environment 264, 1–8.

Chavarría, D.N., Verdenelli, R.A., Muñoz, E.J., Conforto, C., Restovich, S.B., Andriulo, A. E., Meriles, J.M., Vargas-Gil, S., 2016. Soil microbial functionality in response to the inclusion of cover crop mixtures in agricultural systems. Spanish Journal of Agricultural Research 14.

Chen, S., Xu, C., Yan, J., Zhang, X., Zhang, X., Wang, D., 2016. The influence of the type of crop residue on soil organic carbon fractions: an 11-year field study of rice-based cropping systems in southeast China. Agriculture, Ecosystems & Environment 223, 261–269.

Chirinda, N., Olesen, J.E., Porter, J.R., Schjønning, P., 2010. Soil properties, crop production and greenhouse gas emissions from organic and inorganic fertilizer-based arable cropping systems. Agriculture, Ecosystems & Environment 139, 584–594.

de Queiroz Cunha, E., Stone, L.F., de Brito Ferreira, E.P., Didonet, A.D., Moreira, J.A.A., Leandro, W.M., 2011. Soil tillage systems and cover crops in organic production of common bean and corn. II-soil biological properties. Revista Brasileira de Ciência do Solo 35, 603–611.

Dinesh, R., 2004. Long-term effects of leguminous cover crops on microbial indices and their relationships in soils of a coconut plantation of a humid tropical region. Journal of Plant Nutrition and Soil Science 167, 189–195.

Fernandez, A.L., Sheaffer, C.C., Wyse, D.L., Staley, C., Gould, T.J., Sadowsky, M.J., 2016. Associations between soil bacterial community structure and nutrient cycling functions in long-term organic farm soils following cover crop and organic fertilizer amendment. The Science of the Total Environment 566–567, 949–959.

Fernandez, A.L., Sheaffer, C.C., Wyse, D.L., Staley, C., Gould, T.J., Sadowsky, M.J., 2016. Structure of bacterial communities in soil following cover crop and organic fertilizer incorporation. Applied Microbiology and Biotechnology 100, 9331–9341.

Finney, D.M., Buyer, J.S., Kaye, J.P., 2017. Living cover crops have immediate impacts on soil microbial community structure and function. Journal of Soil and Water Conservation 72, 361–373.

Frasier, I., Noellemeyer, E., Figuerola, E., Erijman, L., Permingeat, H., Quiroga, A., 2016. High quality residues from cover crops favor changes in microbial community and enhance C and N sequestration. Glob. Ecol. Conserv. 6, 242–256.

Frasier, I., Quiroga, A., Noellemeyer, E., 2016. Effect of different cover crops on C and N cycling in sorghum NT systems. The Science of the Total Environment 562, 628–639.

Gao, S., Cao, W., Zou, C., Gao, J., Huang, J., Bai, J., Zeng, N., Shimizu, K.Y., Wright, A., Dou, F., 2018. Ammonia-oxidizing archaea are more sensitive than ammonia-oxidizing bacteria to long-term application of green manure in red paddy soil. Applied Soil Ecology 124, 185–193.

Gao, S.J., Chang, D.N., Zou, C.Q., Cao, W.D., Gao, J.S., Huang, J., Bai, J.S., Zeng, N.H., Rees, R.M., Thorup-Kristensen, K., 2018. Archaea are the predominant and responsive ammonia oxidizing prokaryotes in a red paddy soil receiving green manures. European Journal of Soil Biology 88, 27–35.

Grantina, L., Kenigsvalde, K., Eze, D., Petrina, Z., Skrabule, I., Rostoks, N., Nikolajeva, V., 2011. Impact of six-year-long organic cropping on soil microorganisms and crop disease suppressiveness. Zemdirbyste 98, 399–408.

Higo, M., Takahashi, Y., Gunji, K., Isobe, K., 2018. How are arbuscular mycorrhizal associations related to maize growth performance during short-term cover crop rotation? Journal of the Science of Food and Agriculture 98, 1388–1396.

Hontoria, C., García-González, I., Quemada, M., Roldán, A., Alguacil, M.M., 2019. The cover crop determines the AMF community composition in soil and in roots of maize after a ten-year continuous crop rotation. The Science of the Total Environment 660, 913–922.

Jackson, L.E., Ramirez, I., Yokota, R., Fennimore, S.A., Koike, S.T., Henderson, D.M., Chaney, W.E., Calderón, F.J., Klonsky, K., 2004. On-farm assessment of organic matter and tillage management on vegetable yield, soil, weeds, pests, and economics in California. Agriculture, Ecosystems & Environment 103, 443–463.

Khan, M.I., Hwang, H.Y., Kim, G.W., Kim, P.J., Das, S., 2018. Microbial responses to temperature sensitivity of soil respiration in a dry fallow cover cropping and submerged rice mono-cropping system. Applied Soil Ecology 128, 98–108.

King, A.E., Hofmockel, K.S., 2017. Diversified cropping systems support greater microbial cycling and retention of carbon and nitrogen. Agriculture, Ecosystems & Environment 240, 66–76.

Kravchenko, A.N., Negassa, W.C., Guber, A.K., Hildebrandt, B., Marsh, T.L., Rivers, M.L., 2014. Intra-aggregate pore structure influences phylogenetic composition of bacterial community in macroaggregates. Soil Science Society of America Journal 78, 1924–1939.

Li, L.N., Xi, Y.G., Chen, E., He, L.P., Wang, L., Xiao, X.J., Tian, W., 2018. Effects of tillage and green manure crop on composition and diversity of soil microbial community. Journal of Ecology and Rural Environment 34, 342–348.

Longa, C.M.O., Nicola, L., Antonielli, L., Mescalchin, E., Zanzotti, R., Turco, E., Pertot, I., 2017. Soil microbiota respond to green manure in organic vineyards. Journal of Applied Microbiology 123, 1547–1560.

Lupwayi, N.Z., Larney, F.J., Blackshaw, R.E., Kanashiro, D.A., Pearson, D.C., 2017. Phospholipid fatty acid biomarkers show positive soil microbial community responses to conservation soil management of irrigated crop rotations. Soil and Tillage Research 168, 1–10.

Lupwayi, N.Z., Larney, F.J., Blackshaw, R.E., Kanashiro, D.A., Pearson, D.C., Petri, R.M., 2017. Pyrosequencing reveals profiles of soil bacterial communities after 12 years of conservation management on irrigated crop rotations. Applied Soil Ecology 121, 65–73.

Lupwayi, N.Z., May, W.E., Kanashiro, D.A., Petri, R.M., 2018. Soil bacterial community responses to black medic cover crop and fertilizer N under no-till. Applied Soil Ecology 124, 95–103.

Lupwayi, N.Z., Rice, W.A., Clayton, G.W., 1998. Soil microbial diversity and community structure under wheat as influenced by tillage and crop rotation. Soil Biology and Biochemistry 30, 1733–1741.

Lupwayi, N.Z., Soon, Y.K., 2016. Soil microbial properties during decomposition of pulse crop and legume green manure residues in three consecutive subsequent crops. Canadian Journal of Soil Science 96, 413–426.

Mancinelli, R., Campiglia, E., Di Tizio, A., Marinari, S., 2010. Soil carbon dioxide emission and carbon content as affected by conventional and organic cropping systems in Mediterranean environment. Applied Soil Ecology 46, 64–72.

Marinari, S., Mancinelli, R., Brunetti, P., Campiglia, E., 2015. Soil quality, microbial functions and tomato yield under cover crop mulching in the Mediterranean environment. Soil and Tillage Research 145, 20–28.

Mbuthia, L.W., Acosta-Martinez, V., DeBruyn, J., Schaeffer, S., Tyler, D., Odoi, E., Mpheshea, M., Walker, F., Eash, N., 2015. Long term tillage, cover crop, and fertilization effects on microbial community structure, activity: implications for soil quality. Soil Biology and Biochemistry 89, 24–34.

McDaniel, M.D., Grandy, A.S., Tiemann, L.K., Weintraub, M.N., 2014. Crop rotation complexity regulates the decomposition of high and low quality residues. Soil Biology and Biochemistry 78, 243–254.

Nevins, C.J., Nakatsu, C., Armstrong, S., 2018. Characterization of microbial community response to cover crop residue decomposition. Soil Biology and Biochemistry 127, 39–49.

Nivelle, E., Verzeaux, J., Habbib, H., Kuzyakov, Y., Decocq, G., Roger, D., Lacoux, J., Duclercq, J., Spicher, F., Nava-Saucedo, J.-E., Catterou, M., Dubois, F., Tetu, T., 2016. Functional response of soil microbial communities to tillage, cover crops and nitrogen fertilization. Applied Soil Ecology 108, 147–155.

Peregrina, F., Pilar Perez-Alvarez, E., Garcia-Escudero, E., 2014. Soil microbiological properties and its stratification ratios for soil quality assessment under different cover crop management systems in a semiarid vineyard. Journal of Plant Nutrition and Soil Science 177, 548–559.

Perez Brandan, C., Chavarria, D., Huidobro, J., Meriles, J.M., Perez Brandan, C., Vargas Gil, S., 2017. Influence of a tropical grass (Brachiaria brizantha cv. Mulato) as cover crop on soil biochemical properties in a degraded agricultural soil. European Journal of Soil Biology 83, 84–90.

Petersen, S.O., Schjonning, P., Olesen, J.E., Christensen, S., Christensen, B.T., 2013. Sources of nitrogen for winter wheat in organic cropping systems. Soil Science Society of America Journal 77, 155–165.

Pooniya, V., Shivay, Y.S., Rana, A., Nain, L., Prasanna, R., 2012. Enhancing soil nutrient dynamics and productivity of Basmati rice through residue incorporation and zinc fertilization. European Journal of Agronomy 41, 28–37.

Qian, X., Gu, J., Pan, H.-j., Zhang, K.-y., Sun, W., Wang, X.-j., Gao, H., 2015. Effects of living mulches on the soil nutrient contents, enzyme activities, and bacterial community diversities of apple orchard soils. European Journal of Soil Biology 70, 23–30.

Reddy, K.N., Zablotowicz, R.M., Locke, M.A., Koger, C.H., 2003. Cover crop, tillage, and herbicide effects on weeds, soil properties, microbial populations, and soybean yield. Weed Science 51, 987–994.

Reilly, K., Cullen, E., Lola-Luz, T., Stone, D., Valverde, J., Gaffney, M., Brunton, N., Grant, J., Griffiths, B.S., 2013. Effect of organic, conventional and mixed cultivation practices on soil microbial community structure and nematode abundance in a cultivated onion crop. Journal of the Science of Food and Agriculture 93, 3700–3709.

Romaniuk, R., Beltran, M., Brutti, L., Costantini, A., Bacigaluppo, S., Sainz-Rozas, H., Salvagiotti, F., 2018. Soil organic carbon, macro-and micronutrient changes in soil fractions with different lability in response to crop intensification. Soil and Tillage Research 181, 136–143.

Sánchez de Cima, D., Tein, B., Eremeev, V., Luik, A., Kauer, K., Reintam, E., Kahu, G., 2016. Winter cover crop effects on soil structural stability and microbiological activity in organic farming. Biological Agriculture & Horticulture 32, 170–181.

Somenahally, A., DuPont, J.I., Brady, J., McLawrence, J., Northup, B., Gowda, P., 2018. Microbial communities in soil profile are more responsive to legacy effects of wheat-

cover crop rotations than tillage systems. Soil Biology and Biochemistry 123, 126–135.
Thomazini, A., Mendonça, E.S., Souza, J.L., Cardoso, I.M., Garbin, M.L., 2015. Impact of organic no-till vegetables systems on soil organic matter in the Atlantic Forest biome. Scientia Horticulturae 182, 145–155.
Tiemann, L.K., Grandy, A.S., Atkinson, E.E., Marin-Spiotta, E., McDaniel, M.D., 2015. Crop rotational diversity enhances belowground communities and functions in an agroecosystem. Ecology Letters 18, 761–771.
Venkateswarlu, B., Srinivasarao, C., Ramesh, G., Venkateswarlu, S., Katyal, J.C., 2007. Effects of long-term legume cover crop incorporation on soil organic carbon, microbial biomass, nutrient build-up and grain yields of sorghum/sunflower under rain-fed conditions. Soil Use & Management 23, 100–107.
Verzeaux, J., Alahmad, A., Habbib, H., Nivelle, E., Roger, D., Lacoux, J., Decocq, G., Hirel, B., Catterou, M., Spicher, F., 2016. Cover crops prevent the deleterious effect of nitrogen fertilisation on bacterial diversity by maintaining the carbon content of ploughed soil. Geoderma 281, 49–57.
Wortman, S.E., 2012. Diversification of Organic Cropping Systems with Cover Crop Mixtures: Influence on Weed Communities, Soil Microbial Community Structure, Soil Moisture and Nitrogen, and Crop Yield. Dissertation. University of Nebraska, Lincoln.
Wortman, S.E., Drijber, R.A., Francis, C.A., Lindquist, J.L., 2013. Arable weeds, cover crops, and tillage drive soil microbial community composition in organic cropping systems. Applied Soil Ecology 72, 232–241.
Wright, P.J., Falloon, R.E., Hedderley, D., 2017. A long-term vegetable crop rotation study to determine effects on soil microbial communities and soilborne diseases of potato and onion. New Zealand Journal of Crop and Horticultural Science 45, 29–54.
Wu, T., Chellemi, D.O., Graham, J.H., Martin, K.J., Rosskopf, E.N., 2008. Comparison of soil bacterial communities under diverse agricultural land management and crop production practices. Microbial Ecology 55, 293–310.
Xue, K., Wu, L., Deng, Y., He, Z., Van Nostrand, J., Robertson, P.G., Schmidt, T.M., Zhou, J., 2013. Functional gene differences in soil microbial communities from conventional, low-input, and organic farmlands. Applied and Environmental Microbiology 79, 1284–1292.
Zhang, J., Zhang, Y., Zheng, L., Shi, Y., Kong, F., Ma, X., Tian, L., Zhang, Z., 2017. Effects of tobacco planting systems on rates of soil N transformation and soil microbial community. International Journal of Agriculture and Biology 19, 992–998.