

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

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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

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biomass (King and Hofmocker, 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 (Marciello 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:

$$T_i = \theta_k + e_i, \quad e_i \sim N(0, \sigma_i^2) \quad (1)$$

$$\theta_k = \mu + \varepsilon_k, \quad \varepsilon_k \sim N(0, \tau^2) \quad (2)$$

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 (\bar{Y}_{CC}) over that of the control (\bar{Y}_{NC}):

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

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 ($\hat{\sigma}_k^2$) was calculated from the following formulae:

$$s^2 = \frac{\sum_{i=1}^n (Y_i - \bar{Y})^2}{n} \quad (4)$$

$$\hat{\sigma}_k^2 = \frac{s_{CC}^2}{n_{CC} * \bar{Y}_{CC}^2} + \frac{s_{NC}^2}{n_{NC} * \bar{Y}_{NC}^2} \quad (5)$$

Here, s^2 is the reported variance of the mean of the response variable (\bar{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

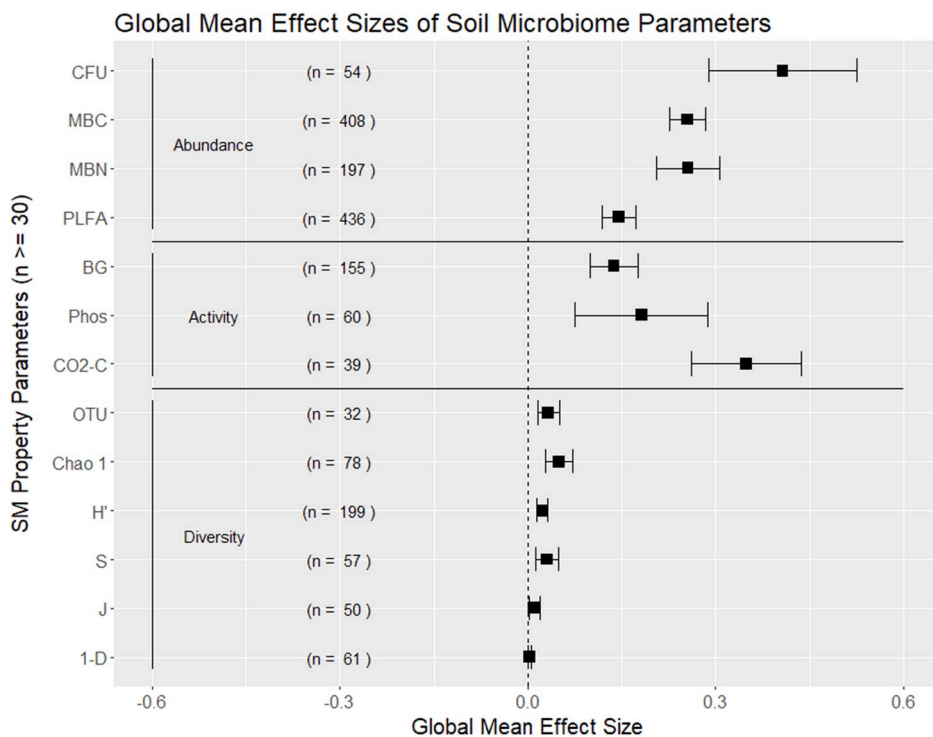


Fig. 1. Forest plot of global effect size means for 13 soil microbial properties with at least 30 observations: colony forming unit (CFU), microbial biomass C (MBC) and N (MBN), phospholipid fatty acid (PLFA), β -glucosidase activity (BG), phosphatase activity (Phos), respiration (CO₂-C), operational 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
CO ₂ -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 r_{ma} 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 r_{ma} 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

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

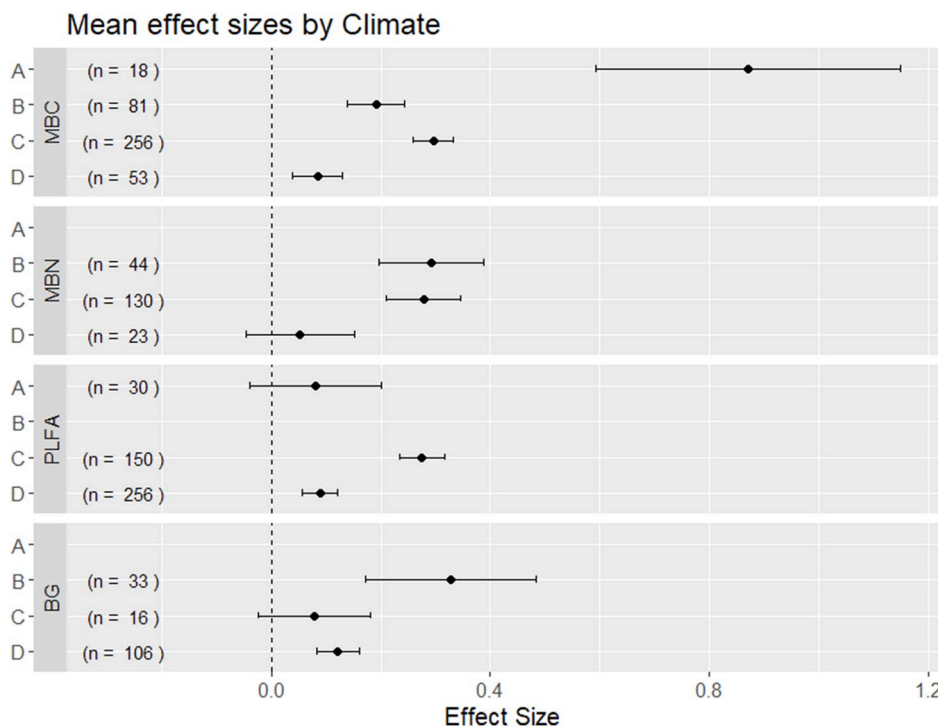


Fig. 2. Forest plots of interactions between soil microbial parameters and climate that had levels with significant differences between effect size means. Number of observations per level is noted in parentheses. Climate is classified by A (tropical), B (arid/semi-arid), C (temperate), and D (continental). 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.

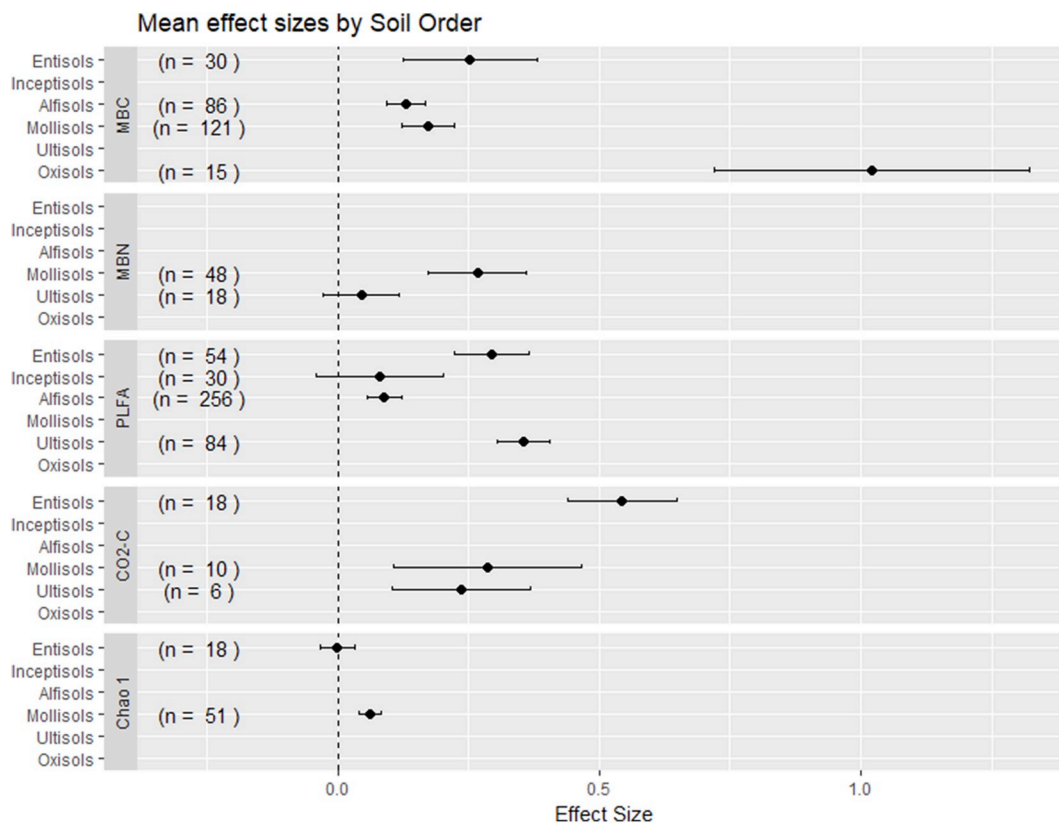


Fig. 3. Forest plots of interactions between soil microbial parameters and soil order that had levels with significant differences between effect size means. Number of observations per level is noted in parentheses. Significant soil microbial parameters were microbial biomass C (MBC) and N (MBN), phospholipid fatty acid (PLFA), respiration (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.

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

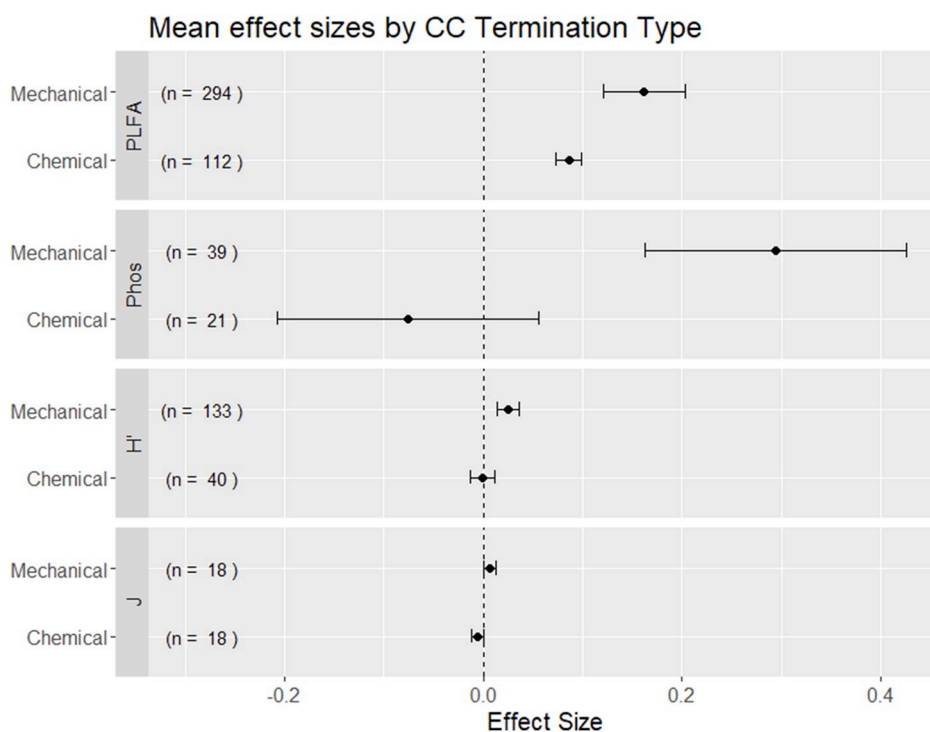


Fig. 4. Forest plots of interactions between soil microbial parameters and cover cropping termination method type that had levels with significant differences between effect size means. Number of observations per level is noted in parentheses. Significant soil microbial parameters were phospholipid fatty 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).

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			CO ₂ -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

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

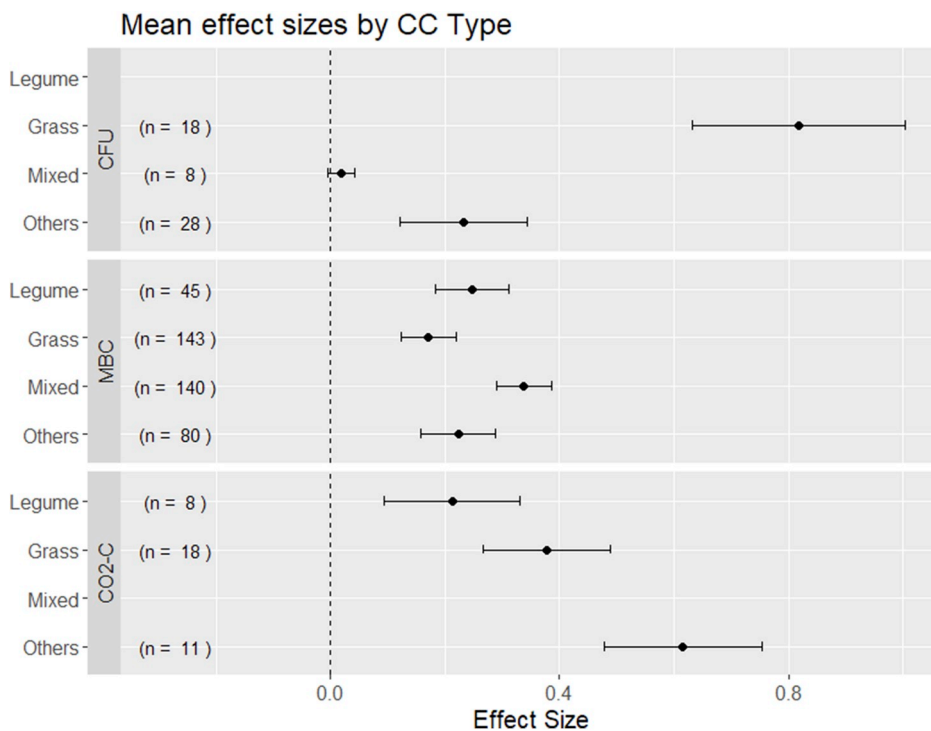


Fig. 5. Forest plots of interactions between soil microbial parameters and cover cropping type that had levels with significant differences between effect size means. Number of observations per level is noted in parentheses. Significant soil microbial parameters were colony forming unit (CFU), microbial 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

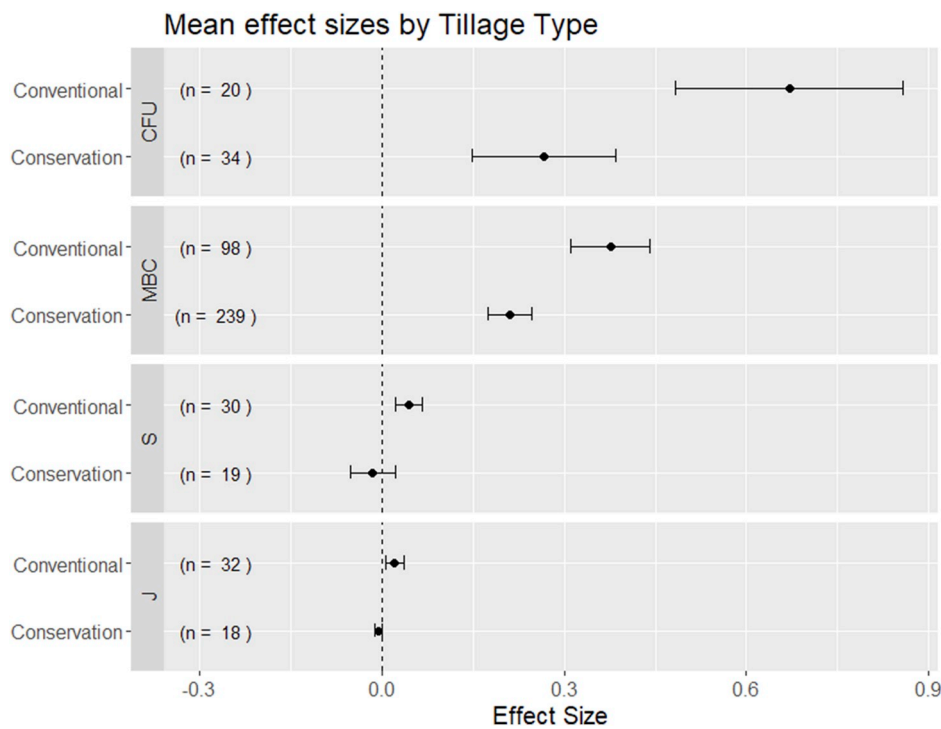


Fig. 6. Forest plots of interactions between soil microbial parameters and tillage type that had levels with significant differences between effect size means. Number of observations per level is noted in parentheses. Significant soil microbial parameters were colony forming unit (CFU), microbial biomass 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.

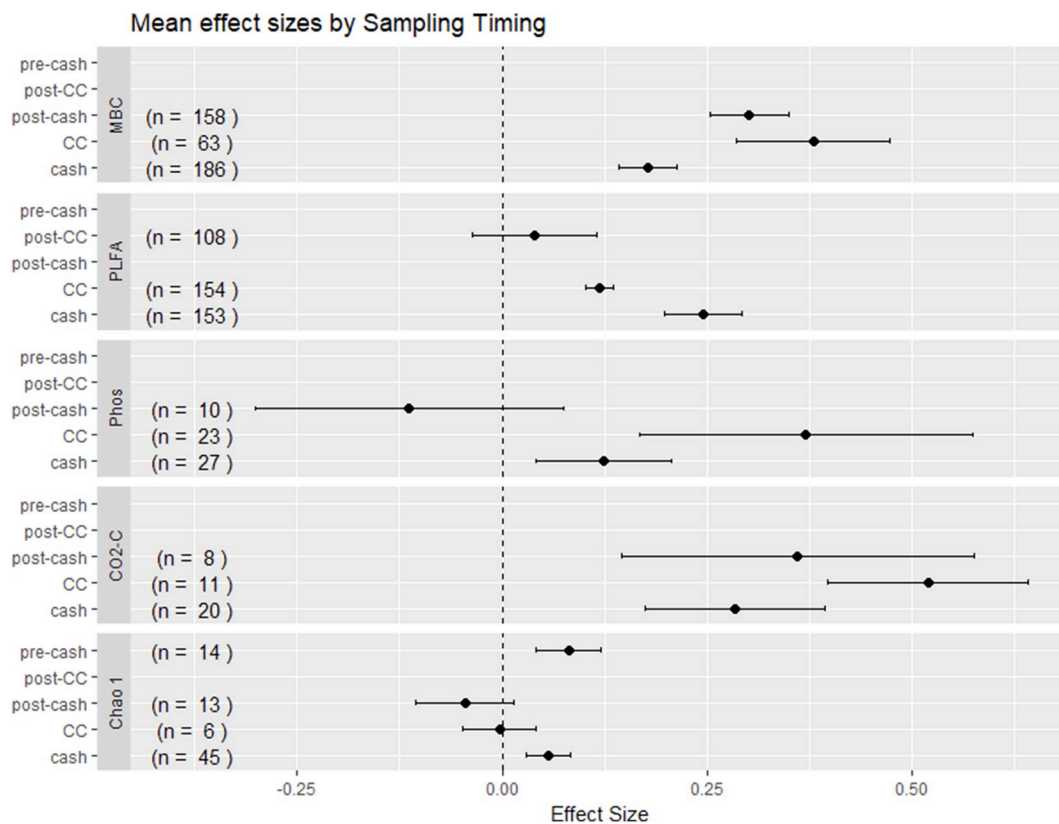


Fig. 7. Forest plots of interactions between soil microbial parameters and soil sampling timing that had levels with significant differences between effect size means. Number of observations per level is noted in parentheses. Significant soil microbial parameters were microbial biomass C (MBC), phospholipid 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 exude 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 to 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

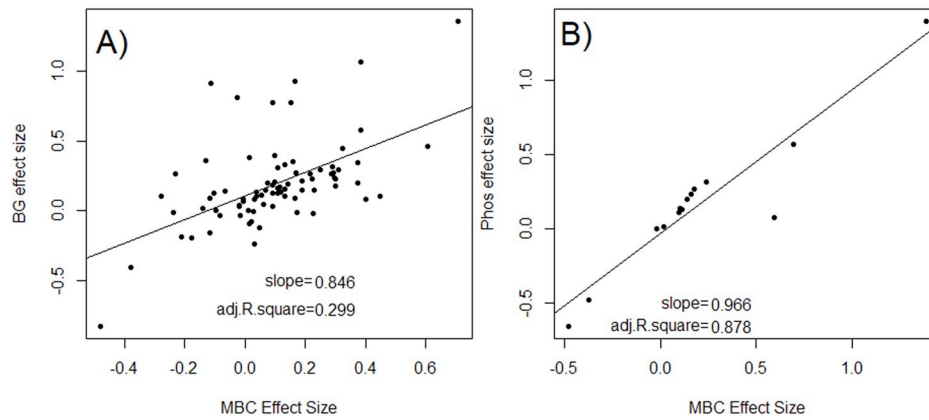


Fig. 8. Scatter plot and linear regression of cover cropping effect sizes of β -glucosidase (BG; A) and those of phosphatase activity (Phos; B) on those of microbial biomass C (MBC). The linear coefficient of the model (slope) and R^2 are noted. Both linear coefficients had significant (p -values). These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

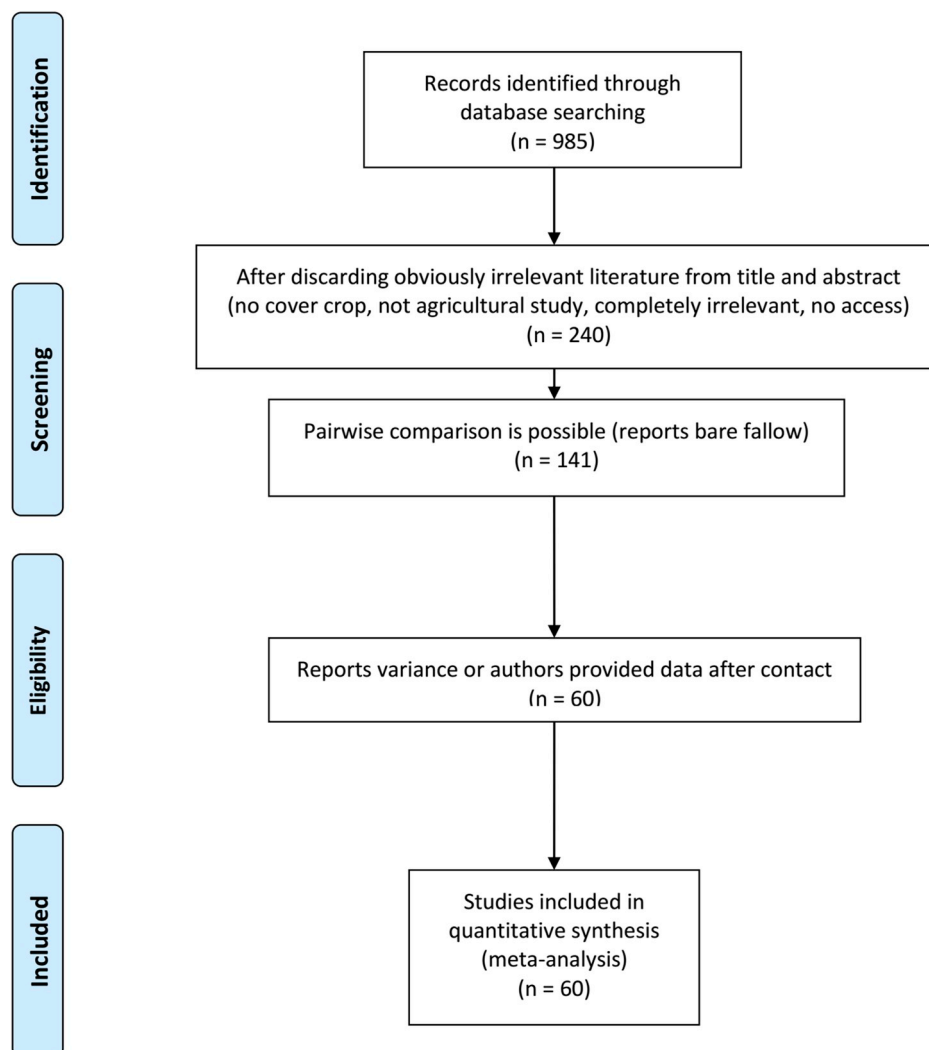


Fig. 9. PRISMA flow diagram modified from that by Moher et al. (2009). The chart shows what criteria was applied and how many literature remained at each stage ($n =$).

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.

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Appendix A. Supplementary data

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

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