



## Global meta-analyses show that conservation tillage practices promote soil fungal and bacterial biomass

Huaihai Chen<sup>a,b</sup>, Zhongmin Dai<sup>c</sup>, Allison M. Veach<sup>a</sup>, Jianqiu Zheng<sup>b</sup>, Jianming Xu<sup>c</sup>, Christopher W. Schadt<sup>a,d,\*</sup>

<sup>a</sup> Biosciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, 37831, USA

<sup>b</sup> Biological Sciences Division, Pacific Northwest National Laboratory, Richland, WA, 99354, USA

<sup>c</sup> Institute of Soil and Water Resources and Environmental Science, Zhejiang Provincial Key Laboratory of Agricultural Resources and Environment, Zhejiang University, Hangzhou, 310058, China

<sup>d</sup> Department of Microbiology, University of Tennessee, Knoxville, TN, 37966, USA

### ARTICLE INFO

#### Keywords:

Agricultural practices  
Soil microbes  
Soil erosion  
Microbial biomass

### ABSTRACT

Despite a large number of published studies, a consensus has not been reached on how soil fungal and bacterial biomass, the primary regulators for soil organic matter decomposition, respond to conservation tillage, i.e., no or reduced tillage with > 30 % residue covers. In this study we conducted a global meta-analysis of 60 studies to investigate the effects of conservation versus conventional tillage on soil fungal and bacterial biomass, fungal-to-bacterial ratios, and their relationship to other soil properties. Our results showed that conservation tillage greatly increased overall soil microbial biomass (37 %), including both fungal (31 %) and bacterial biomass (11 %), especially in top 20-cm soils or no-till agro-ecosystems, but conservation tillage effects were non-significant in sandy soils. Regardless of soil depth and tillage intensity, fungal-to-bacterial ratios did not greatly increase in conservation tillage scenarios, but were significantly affected by soil texture. Conservation tillage was also associated with significant increases in soil total C and N, and reduced soil pH. Increases in soil total C were positively associated with both fungal and bacterial biomass increases. Years under conservation tillage, time between last convention tillage to soil sampling, may indirectly affect fungal and bacterial biomass through soil C accumulation. Our meta-analysis demonstrates that soil fungi and bacteria both respond positively to conservation tillage and are significantly associated with soil C content increase.

### 1. Introduction

Soils contain the largest pool of total carbon (C) compared to atmosphere and biota (Lal and Kimble, 1997) and soil C sequestration, the process that captures and stores C from atmosphere in terrestrial ecosystems, has the potential to mitigate global warming by slowing down the atmospheric accumulation of greenhouse gases released by burning fossil fuels (Lal, 2005). The processes leading to soil C sequestration and reduced turnover of soil organic C are largely mediated by soil microbes (Van Groenigen et al., 2010) and fungi and bacteria, comprising about 90 % of total soil microbial biomass, are primary regulators of soil organic matter decomposition (Six et al., 2006). Soil fungal and bacterial community composition can shift in response to agricultural management practices, and this compositional change may determine the rates of soil C accumulation and loss (Zhang et al., 2013). Soil ecology studies have often used the ratio of fungal-to-bacterial

biomass as an indicator of successful ecosystem self-regulation (Bardgett and McAlister, 1999), with biogeochemical pathways regulating nutrient turnover instead of reliance on N fertilizers, and soil fungal-to-bacterial biomass ratios have been found to be especially sensitive to the intensity of soil disturbance (Bailey et al., 2002). For example, soil microbial communities with a relatively high fungal biomass have been associated with low-input farming systems and with the potential for soil C sequestration (Chen and Ruan, 2018; Van Groenigen et al., 2010). This phenomenon has been attributed to the abilities of fungal hyphae to produce organic substrates that act as organic binding agents adhering soil particles into micro-aggregates, and thus provide for physical protection of soil organic matter (Beare et al., 1997). Additionally, fungal biomass is generally more recalcitrant to decomposition and has longer turnover times than bacteria, so microbial biomass C is thought to be retained longer in fungal-dominated ecosystems, potentially leading to greater C storage (Strickland and

\* Corresponding author at: Biosciences Division, Oak Ridge National Laboratory, 1 Bethel Valley Rd, Oak Ridge, TN, 37831, USA.

E-mail address: [schadtcw@ornl.gov](mailto:schadtcw@ornl.gov) (C.W. Schadt).

<https://doi.org/10.1016/j.agee.2020.106841>

Received 22 May 2019; Received in revised form 19 January 2020; Accepted 26 January 2020

Available online 09 February 2020

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Rousk, 2010). Other mechanisms for carbon sequestration in undisturbed agroecosystems include greater organic matter binding to inorganic clay particles (Blanco-Canqui and Lal, 2004), carbohydrate-rich extracellular polysaccharides (EPS) produced from bacteria and archaea that promote soil aggregate formation (Schimel and Schaeffer, 2012), and greater micro-niche formation and separation due to reduced disturbance (Zhang et al., 2013). Therefore, it is often postulated that less intensively managed agro-ecosystems that encourage a soil community dominated by fungal pathways of decomposition, are thought to be more “self-regulated” and have greater C sequestration potential (Bardgett and McAlister, 1999; Six et al., 2006).

Conservation tillage, i.e., no or reduced tillage, are tillage systems that minimize the degree and frequency of tillage passes to reduce soil aggregate disruption, and keep a minimum of 30 % of the soil surface covered with residues for soil conservation (Singh et al., 2018). Along with diverse crop rotations and the incorporation of cover crops, conservation tillage approaches are some of the key agricultural practices widely implemented across cropping systems for the mitigation of soil erosion and organic matter losses (Van Kessel et al., 2013). By developing a model based on published data, it was predicted that conversion from conventional to conservation tillage from 27 % to 76 % of all cultivated area in the U.S. from 1990 to 2020 would increase soil organic matter accumulation of 0.3–0.5 Pg C in total, equivalent to 0.7–1.1 % of the total projected CO<sub>2</sub> emissions from fossil fuel combustion for the 30 year period (Kern and Johnson, 1993). Compared to conventional tillage, not only does conservation tillage protect soil aggregate structure and reduce soil erosion and surface runoff, but it also decreases the exposure of soil organic matter to extremes in environmental variation. Therefore, conservation tillage may slow the decomposition and mineralization of soil organic matter, and thus constrain greenhouse gas production (Lal and Kimble, 1997; Van Kessel et al., 2013). In addition, it has been shown that reduced disturbance in agro-ecosystems can promote microbial C-use efficiency (CUE) to reduce respiration, and thus increase soil C storage and stabilization (Manzoni et al., 2012). Undisturbed soil conditions may also favor a complete denitrification cycle (dinitrogen gas production), rather than incomplete denitrification leading to the production of nitrous oxide (Elmi et al., 2003). Consequently, how soil microbial community structure, and especially fungal and bacterial biomass, responds to conservation tillage practices may be of great importance in understanding and managing soil C stocks and greenhouse gas emissions.

The general consensus of research in this area has been that conventional tillage encourages bacterial dominance in soil microbial communities, while conservation tillage promotes fungal dominance (Beare et al., 1997; Frey et al., 1999; Pankhurst et al., 2002; Six et al., 2006; Strickland and Rousk, 2010; Van Groenigen et al., 2010). Three main reasons have been proposed to explain why bacterial and fungal biomass react differently in conventional-till and conservation-till farming systems (Six et al., 2006). Firstly, conservation tillage favors fungal growth due to the prevention of soil disturbance effects on fungal hyphae, thus enhancing the establishment and maintenance of extensive hyphal networks (Beare et al., 1997). In addition, increased retention of soil moisture in conservation tillage soils may also greatly influence soil bacteria and fungi either by directly favoring microbial growth or indirectly changing substrate availability and detrital food webs (Frey et al., 1999). Lastly, plant residue retention may alter relative bacterial and fungal population sizes as it is thought that presence of surface residues in conservation-till favors fungal growth (Beare et al., 1997) and they can connect across the soil-residue interface through their hyphal networks.

Prior studies have reviewed conservation tillage effects on soil organic C (Luo et al., 2010), overall microbial biomass C (Zuber and Villamil, 2016), and greenhouse gas production (González-Sánchez et al., 2012; Van Kessel et al., 2013), however review and synthesis work to investigate how soil fungi and bacteria respond to conservation tillage is lacking. Here, we conducted what is to our knowledge the first

global meta-analysis on the published literature to date to assess if conservation tillage differentially promotes below-ground fungal or bacterial biomass, and in turn, how this translates to soil fungal-to-bacterial ratios. Specifically, we tested the following hypotheses: (1) conservation tillage would promote overall soil microbial biomass including both soil fungal and bacterial populations; (2) due to the increase of both soil fungal and bacterial biomass in conservation-till soils, tillage practices would not significantly modify the fungal-to-bacterial ratios; (3) both fungal and bacterial abundance would exhibit a positive correlation with soil C content as well as relationships to other soil properties.

## 2. Materials and methods

### 2.1. Data collection

To investigate the effects of conservation tillage in comparison with conventional tillage on soil fungal and bacterial biomass, we collected data from peer-reviewed publications from 1994 to 2016 using the Web of Science database for our literature survey and review. Search terms included “no/reduced-till”, “conservation tillage”, “fungi”, “bacteria”, and “microbial biomass”, etc. in the title, keyword, or abstract. Conventional tillage is a tillage system that includes a sequence of soil ploughing and harrowing to produce a fine seedbed for cultivation, and removes plant residues from soil surface (Singh et al., 2018). The following additional criteria were applied to the results prior to inclusion: (1) studies were at least one-year tillage field experiments conducted in agro-ecosystems; (2) studies reported the means of fungal and bacterial biomass for both conservation tillage treatments and conventional tillage controls. Generally in our dataset, the methods used to estimate fungal and bacterial biomass are phospholipid-derived fatty acids (PLFA) analysis, direct microscopic observation (MO) to count fungal hyphal length or colony-forming units (CFU) after dilution of soil suspension and staining, selective inhibition of substrate-induced respiration (SIR), and biomarker-based quantitative polymerase chain reaction (qPCR). From these publications, data on years between tillage and sampling were included to assess how tillage treatment duration affects fungal and bacterial biomass. Generally, most studies included in this meta-analysis conducted soil sampling and analyses at or shortly after harvest. However, if studies reported data from multiple time points within one year, the average number across dates was used. This resulted in a total of 60 publications for inclusion in the meta-analysis database, which was comprised of 233 paired experimental observations that originated from 20 countries globally (Fig. 1, Supplementary Table 1).

For fungal and bacterial biomass, means (M), standard deviations (SD), and sample sizes (*n*) of both conservation tillage treatments and conventional tillage controls were extracted. If only the standard errors (SE) were given, SD was calculated as:

$$SD = SE \sqrt{n} \quad (1)$$

While 78 % of studies (82 % of dataset) reported measures of variability, for those studies missing both standard deviations and standard error, the average coefficient of variation of the datasets with known standard deviations was used (Dai et al., 2018). If studies also reported total soil microbial biomass, fungal-to-bacterial (F:B) ratios, soil total C and N, soil pH, and soil bulk density of both treatments and controls, these data were also extracted to explain the effects of conservation tillage on fungal and bacterial biomass compared to conventional tillage. If studies did not directly report data on overall soil microbial biomass or F:B ratios, soil microbial biomass was calculated as the sum of fungal and bacterial biomass, while F:B ratios were calculated as fungal biomass divided by bacterial biomass. Most studies reported data in tables that could be transferred into our database directly. However, when data was given only in figures, it was extracted

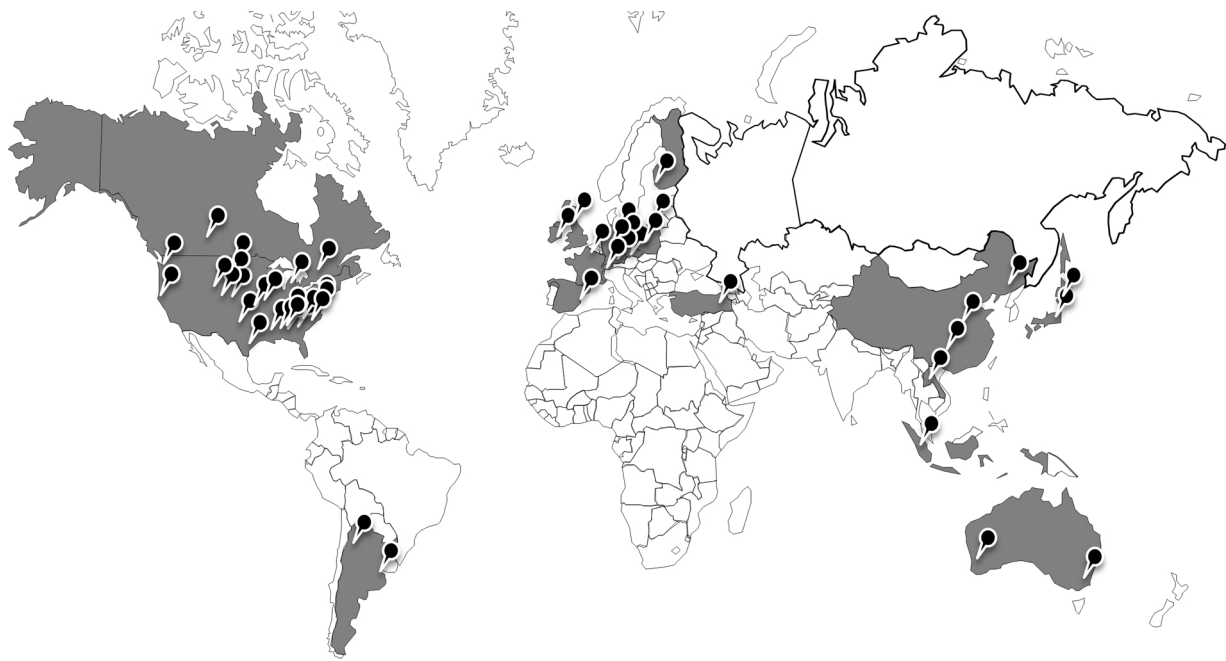


Fig. 1. World map showing the distribution of 233 paired observations in 20 countries of gray color from 60 tillage studies in agro-ecosystems included in this meta-analysis.

using the software Data Thief (Bas Tummer, Eindhoven, The Netherlands).

## 2.2. Meta-analysis

Impacts of conservation tillage in comparison with conventional tillage on soil fungal and bacterial biomass and soil properties were evaluated using the treatment against the pairwise control (Chen et al., 2013). The natural log-transformed response ratio was calculated as:

$$\ln R = \ln(X_t) - \ln(X_c) \quad (2)$$

where  $\ln R$  denotes the natural log of response ratio and is defined as the effect size,  $X_t$  and  $X_c$  are the means in the treatment and control groups, respectively (Hedges and Olkin, 1985). The variance ( $v$ ) is computed as:

$$v = \frac{SD_t^2}{n_t X_t^2} + \frac{SD_c^2}{n_c X_c^2} \quad (3)$$

where  $SD_t$  and  $SD_c$  are standard deviation of treatment and control groups, and  $n_t$  and  $n_c$  are sample sizes of treatment and control groups, respectively. The weighted response ratios and 95 % confidence intervals were calculated using both MetaWin 2.0 (Rosenberg et al., 1999) and the R package Metafor 2.0 (Viechtbauer, 2010). As between-study heterogeneity measures are important to understand the quality of our dataset, an analysis of the  $I^2$  statistic was also conducted (Higgins and Thompson, 2002) to facilitate the interpretation of the heterogeneity present in our dataset. Our results showed that fungal and bacterial biomass had  $I^2$  (total heterogeneity/total variability) of 42.58 % and 62.93 %, respectively, indicating moderate to substantial heterogeneity in our dataset. Funnel plots created using the funnel function in Metafor to visually represent the heterogeneity and publication bias of our database showed that the majority of our data points fell within the asymmetric funnels (Supplementary Fig. S1), and the frequency distribution of weighted response ratio of soil microbial biomass, fungal and bacterial biomass, and F:B ratios was unimodal (Supplementary Fig. S2). Metafor was used together with MetaWin to account for the non-independent sampling errors due to the inclusion of multiple studies. Specifically in Metafor a mixed-effect multivariate model was constructed using the `rma.mv` function and restricted maximum

likelihood (REML) estimation to include study (i.e., publications used in this meta-analysis) (Supplementary Table 1) as random factors in the models. The conclusions from two meta-analysis approaches remained the same, and thus only grand means and 95 % confidence interval of effect sizes calculated by Metafor are reported.

In this meta-analysis, each categorical variable, i.e., soil microbial biomass, fungal and bacterial biomass, F:B ratios, and the soil properties of soil C and N, soil pH, and bulk density was separated into groups including: two soil depths, two tillage intensities, and three soil texture categories, to examine if there were any significant differences in effect size between groups. The two groups of soil depths (< 20 cm and > 20 cm) were chosen as typical plow depths, to assess if microbial biomass reacts differently to tillage above and below the plow layer. However, because plow layer properties and depths were quite different among regions and cropping regimes, soil layers of < 20 cm and > 20 cm are here referred "topsoil" and "subsoil" for the purposes of comparison. The two groups of conservation tillage intensity (no-till and reduced-till) were used and we defined them as reported within each publication but this of course also varied across the literature. Generally, reduced-till had a plow depth that was approximately half of the conventional-till to reduce the tillage intensity and thus soil disturbance. For soil texture, three categories were included: sandy (Sandy loam/Loamy sand), loamy (Loam/Silt loam/Silty clay loam), and clayey (Clay loam/Clay) soils. Because soil property information was only available for a limited number of publications, grouping by soil texture was only performed for categorical variables of soil microbial biomass, fungal and bacterial biomass, and F:B ratios.

To access whether different methods used to determine fungal and bacterial biomass influence the results of the meta-analysis, fungal and bacterial biomass was also grouped by biomass quantification methods, i.e., PLFA, MO, SIR, and qPCR. However, SIR and qPCR had very limited sample sizes, eight and five for SIR and qPCR, respectively (Supplementary Table 1), so for the final analyses fungal and bacterial biomass could only be compared between the PLFA and MO methods.

## 2.3. Statistics

For each categorical variable, total heterogeneity ( $Q_T$ ) was partitioned into within-group ( $Q_w$ ) and between-group ( $Q_b$ ) variations. The

Q statistic follows a Chi-square distribution with  $k-1$  degrees of freedom; here  $k$  is the number of paired observations between treatments and controls for a categorical variable. The effect size was considered to be significantly positive or negative at  $\alpha = 0.05$  level when 95 % CIs did not overlap zero (Gurevitch et al., 2018; Hedges et al., 1999). The effect size results of  $\ln R$  were also back-transformed and reported as percentage change under treatments relative to controls:

$$(R - 1) \times 100 \% \quad (4)$$

where  $R$  denotes the response ratio. Rank correlation tests and fail-safe numbers were conducted to explore publication bias; both indicated no publication bias for all categorical variables (Supplementary Table 2).

We also tested whether average local temperature and precipitation patterns affect the response of fungal and bacterial biomass to conservation tillage by conducting a cumulative meta-analysis. Specifically, mean annual temperature (MAT) and precipitation (MAP) from each study location (Supplementary Table 1) were implemented as independent variables to construct a continuous random-effect regression model. MAT and MAP in studied sites were derived from the WorldClim dataset (Fick and Hijmans, 2017). Furthermore, a linear regression was constructed to examine the relationships between effect sizes of soil C and those of fungal and bacterial biomass.

A structural equation model (SEM) was constructed using AMOS 25.0 (SPSS Inc., Armonk, NY, USA) to determine how tillage years and the effect sizes of soil properties, such as soil C, pH, and bulk density influence the effect sizes of fungal and bacterial biomass. All data were tested for a normal distribution and log transformed if needed prior to modeling. First, a full model including all possible factors was constructed. To find the best-fit model, nonsignificant pathways between factors were iteratively removed, starting with the pathway with the highest  $P$  value, until no non-significant pathways remained. To test the overall goodness of fit for this SEM, a Chi-square test was conducted, and a Chi-square value  $\chi^2$  and  $P$  value as well as several goodness-of-fit indices were calculated to validate the proposed model. The model was thus considered to have a good fit when  $P > 0.05$ , suggesting that the proposed model produces a population covariance matrix that is consistent with the sample covariance matrix (Schermelleh-Engel et al., 2003).

### 3. Results and discussion

#### 3.1. Response of fungal and bacterial biomass to conservation tillage

The grand mean of effect size ( $d_{++}$ ) of conservation tillage relative to conventional tillage on soil microbial biomass was significantly greater than zero ( $P < 0.05$ ) (Fig. 2), indicating that conservation tillage, on average, enhanced soil microbial biomass by  $\sim 37\%$  compared to conventional tillage. However, the effect size was only significant in soil depths of  $< 20$  cm, which increased by 38 % ( $P < 0.05$ ), but was not significant in soil depths of deeper than 20 cm. The two conservation tillage intensity levels of no-till and reduced-till both showed significant increase of soil microbial biomass at 38 % and 32 %, respectively ( $P < 0.05$ ).

Increases in overall soil microbial biomass in the topsoil layers under conservation tillage has been observed in many geographic locations and agroecosystem types (Frey et al., 1999; Helgason et al., 2009; Jiang et al., 2011; Minoshima et al., 2007; Spedding et al., 2004; Van Groenigen et al., 2010; White and Rice, 2009; Zhang et al., 2014). In both no-till and reduced-till systems, more crop residues are left at the soil surface than conventional-till, leading to increased C substrate availability, and thus likely the enhancement of soil microbial biomass in topsoils (Zhang et al., 2014). However, compared to topsoils, deeper soil layers might experience a reduction in incorporated residues under conservation tillage (Frey et al., 1999), and thus positive conservation tillage effects on soil microbial biomass have mostly been reported in

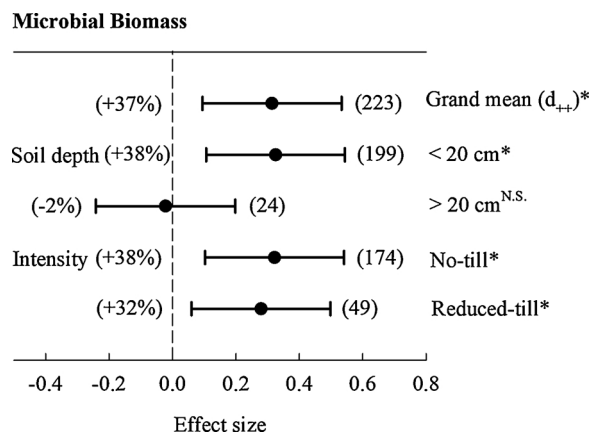
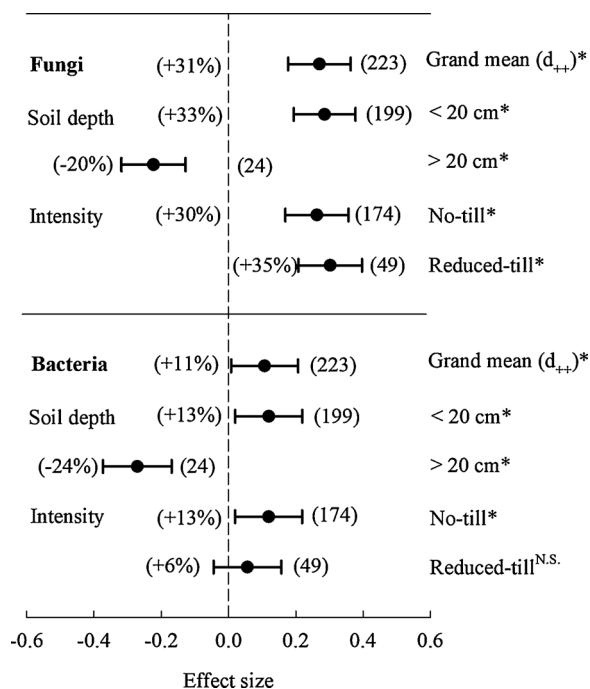


Fig. 2. Effects of conservation tillage, i.e., no/reduced tillage compared to conventional tillage on soil microbial biomass, grouped by soil depths of  $< 20$  cm and  $> 20$  cm, and tillage intensity of no-till and reduced-till. Data are expressed as mean effect size with 95 % confidence intervals. Percentage change for means and observation numbers for the category and each group are given in parentheses. Asterisks indicate  $P < 0.05$ ; N.S. indicates not significant.

the upper soil layers (Van Groenigen et al., 2010). Greater residue coverage on topsoils also can increase soil water holding capacity, and result in less fluctuation in moisture content and temperature in conservation-tillage soils (Lienhard et al., 2013). It has been reported that moisture content in the 0–5 cm layer with no-till is significantly higher than other treatments (Helgason et al., 2009); conventional tillage may have lower microbial biomass due to reduced soil moisture, and changing soil temperature and humidity (Horwath, 2003). Perhaps more importantly, conventional tillage may ultimately change microbial biomass due to the direct change in soil macro-aggregate structure. It has been shown that conventional tillage can lead to a 67 % decrease in the proportion of macro-aggregates with corresponding reductions of soil microbial biomass (Jiang et al., 2011). Our analyses are also consistent to the only previous meta-analysis study that explored the effects of various tillage practices on microbial biomass C (Zuber and Villamil, 2016) and showed that conventional tillage techniques reduced microbial biomass C when compared to no-till systems.

The overall responses of fungal and bacterial biomass to conservation tillage were significantly positive, at approximately 31 % and 11 % increase, respectively, in soils with conservation tillage ( $P < 0.05$ ) (Fig. 3), showing that both fungi and bacteria contributed positively to the increased microbial biomass from conservation tillage. However, the effect sizes were only significantly positive in soil depths of top 20 cm, in which fungal and bacterial biomass significantly increased by 33 % and 13 % ( $P < 0.05$ ), respectively, while there were significantly negative effects on both fungi and bacteria by conservation tillage in soil depths of deeper than 20 cm ( $P < 0.05$ ). Although tillage intensity did not change the effects of conservation tillage on fungal biomass, positive effect sizes on bacterial biomass were not found in reduced-till treatments.

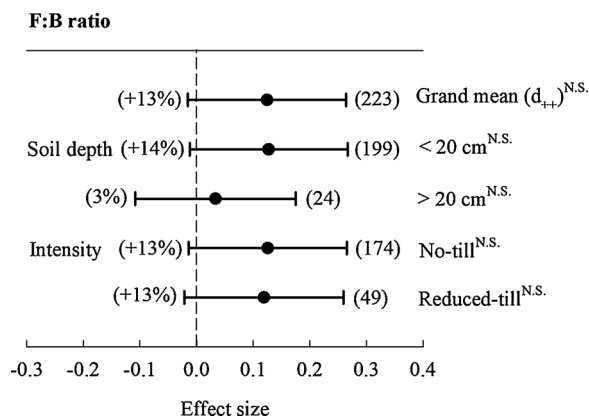
Our global meta-analysis confirmed a significant increase in both bacterial and fungal populations in top 20-cm soil depths by 33 % and 13 % ( $P < 0.05$ ), respectively, regardless of intensity in conservation-till agro-ecosystems, which was in agreement with many field studies reporting an increased biomass of both fungi and bacteria under no-till scenarios (Helgason et al., 2009; Jiang et al., 2011; Minoshima et al., 2007; Toyota et al., 2013; Van Groenigen et al., 2010; White and Rice, 2009). The increase of bacterial biomass by 13 % in upper 20-cm soils suggests that soil conditions created by conservation tillage may likewise be suitable for bacteria as well, although perhaps to a lesser degree when compared to fungi. Plant residue placement on the soil surface can ameliorate large fluctuations in soil temperature and humidity



**Fig. 3.** Effects of conservation tillage, i.e., no/reduced tillage compared to conventional tillage on fungal and bacterial biomass, grouped by soil depths of < 20 cm and > 20 cm, and tillage intensity of no-till and reduced-till. Data are expressed as mean effect size with 95 % confidence intervals. Percentage change for means and observation numbers for the category and each group are given in parentheses. Asterisks indicate  $P < 0.05$ ; N.S. indicates not significant.

(Frey et al., 1999), which could indeed be favorable to soil bacterial communities. For example, it has been shown that fungal communities remain more compositionally consistent across temperature and moisture changes than bacterial communities (Bell et al., 2009). Additionally, soil environments dominated by fungi may also promote bacterial growth, as fungi in terrestrial ecosystems act as ecosystem engineers by creating novel niche space for bacteria (Boer et al., 2005). This global synthesis suggests that conservation tillage practices do not necessarily select for fungal growth only, but do promote overall greater microbial growth for both bacteria and fungi. Therefore, future studies of reduced-disturbance agricultural management, such as conservation tillage, should focus on both fungi and bacterial responses. These findings have important implications for advancing our understanding of microbe-carbon cycling feedbacks across global agro-ecosystems implementing no-till practices.

In tests as to whether the response ratios of fungal and bacterial biomass significantly differed between PLFA and MO methods, our results showed that there was no significant between-group heterogeneity for either fungal ( $Q_{\text{Chi-square}} = 0.09$ ,  $P_{\text{Between}} = 0.77$ ) or bacterial ( $Q_{\text{Chi-square}} = 0.83$ ,  $P_{\text{Between}} = 0.36$ ) biomass determination methods, indicating that different biomass quantification methods likely had little to no influence on the results of this meta-analysis. Variation in microbial abundance may be due to local climatic conditions, specifically moisture and temperature differences, which may be an important driver of microbial abundance. To find out whether average local temperature and precipitation influence the response of fungal and bacterial biomass to conservation tillage, our results of a cumulative continuous meta-analysis showed that fungal and bacterial biomass were not significantly associated with either MAT ( $Q_{\text{Fungi}} = 0.22$ ,  $P_{\text{Fungi}} = 0.64$ ;  $Q_{\text{Bacteria}} = 0.01$ ,  $P_{\text{Bacteria}} = 0.93$ ) or MAP ( $Q_{\text{Fungi}} = 0.30$ ,  $P_{\text{Fungi}} = 0.58$ ;  $Q_{\text{Bacteria}} = 1.21$ ,  $P_{\text{Bacteria}} = 0.27$ ), so the variation attributed to our large-scale estimates of climate on microbial biomass was not supportive of a significant role in this meta-analysis. However these

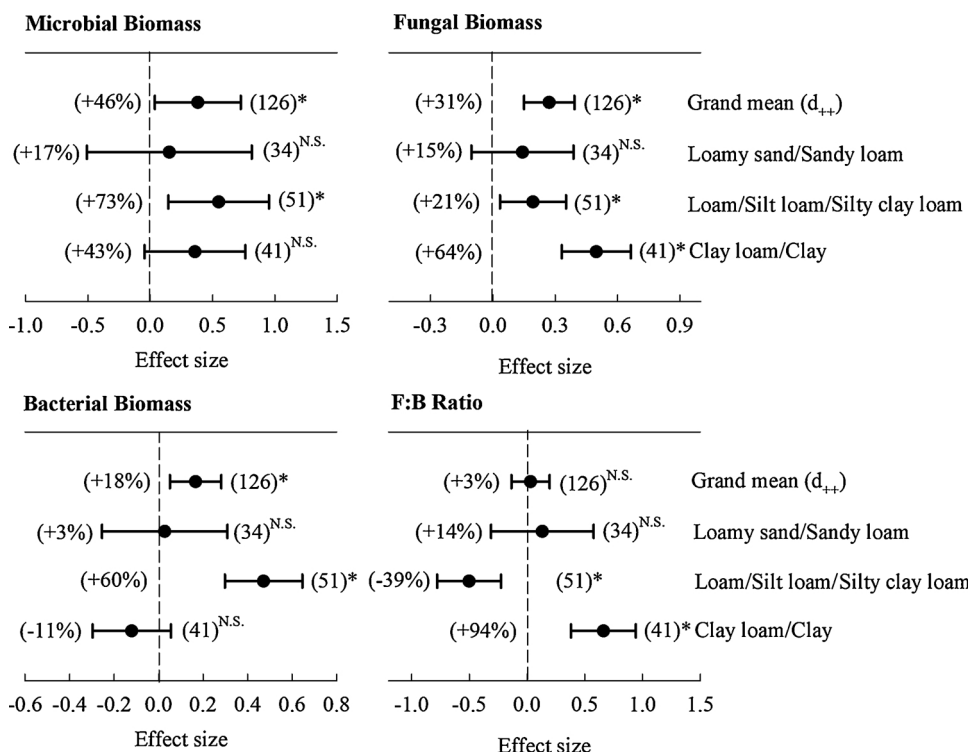


**Fig. 4.** Effects of conservation tillage, i.e., no/reduced tillage compared to conventional tillage on fungi-to-bacteria (F:B) ratios, grouped by soil depths of < 20 cm and > 20 cm and tillage intensity of no-till and reduced-till. Data are expressed as mean effect size with 95 % confidence intervals. Percentage change for means and observation numbers for the category and each group are given in parentheses. Asterisks indicate  $P < 0.05$ ; N.S. indicates not significant.

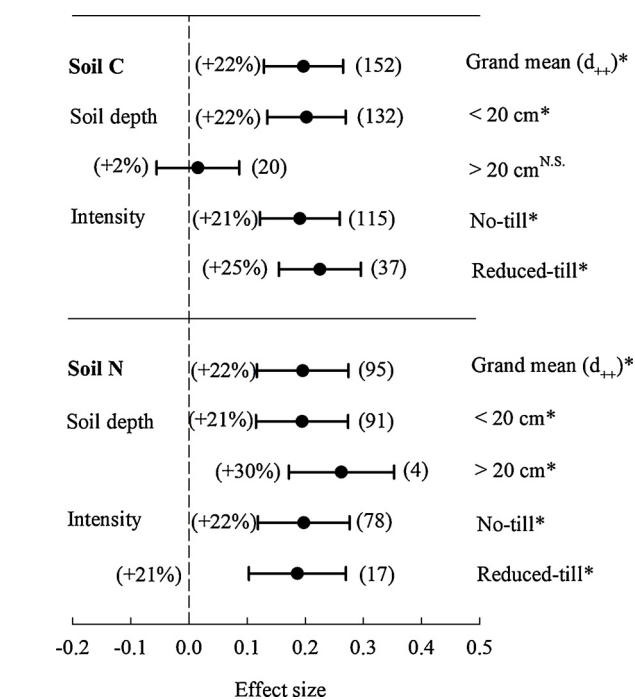
interpolated climatic data used here must be approached with a greater degree of caution than direct observations of infield conditions, that was not consistently available from the published studies.

Fungal-to-bacterial biomass (F:B) ratios were not significantly affected by conservation tillage, even with an increase of the mean effect size by 13–14 % in soil depths of top 20 cm (Fig. 4). However, our results should not be interpreted to necessarily deemphasize the importance of fungi in soil C sequestration. Some studies (Helgason et al., 2009) have suggested that even without an increased fungal-to-bacterial abundance, fungal communities were still relatively more important for soil organic matter decomposition as the key driver of C accumulation in no-till systems, due to dominance of fungal enzyme activity in litter decomposition (Voříšková and Baldrian, 2013). While the F:B ratio may be a commonly used indicator in soil ecology (Lienhard et al., 2013), our compiled evidence analysis supports that not only fungal but also bacterial biomass appears to be favored by conservation tillage conditions.

While overall F:B ratio was not significantly enhanced by conservation tillage in our analyses, it remains likely that shifts in the composition within both the bacterial and fungal community could be driven by conservation tillage practices (Yin et al., 2010). Using pyrosequencing of the 16S rRNA gene, it has been shown that the relative abundance of several bacterial phyla were significantly altered under limited tillage compared with traditional tillage (Navarro-Noya et al., 2013). Indeed, microbial compositional changes are often associated with shifts in ecological conditions and processes in soils, perhaps more so than microbial abundance (Liu et al., 2018). Both fungal and bacterial community composition may be altered by varying tillage intensity, but some evidence suggests soil bacterial communities may be more responsive than fungal communities (Hartman et al., 2018). Others have reported that no-till approaches typically increase the relative abundance of Acidobacteria and reduces other bacterial phyla (Sengupta and Dick, 2015), while still others showed that Acidobacteria are repressed by conservation tillage (Dong et al., 2017). In the face of such contradictory conclusions, additional research is necessary to elucidate the interactions of fungal and bacterial community dynamics and how they are affected by conservation tillage practices. Such studies should incorporate both microbial biomass and more fine grained compositional information on fungal and bacterial taxa, as well as C sequestration potential to reveal the relative importance of microbial structure contributing to soil function in agro-ecosystems.



**Fig. 5.** Effects of conservation tillage, i.e., no/reduced tillage compared to conventional tillage on soil microbial biomass, fungal and bacterial biomass, and fungi-to-bacteria (F:B) ratios, grouped by three soil texture categories. Data are expressed as mean effect size with 95 % confidence intervals. Percentage change for means and observation numbers for the category and each group are given in parentheses. Asterisks indicate  $P < 0.05$ ; N.S. indicates not significant.



**Fig. 6.** Effects of conservation tillage, i.e., no/reduced tillage compared to conventional tillage on soil total C and N contents, grouped by soil depths of < 20 cm and > 20 cm, and tillage intensity of no-till and reduced-till. Data are expressed as mean effect size with 95 % confidence intervals. Percentage change for means and observation numbers for the category and each group are given in parentheses. Asterisks indicate  $P < 0.05$ ; N.S. indicates not significant.

**3.2. Effect sizes of fungal and bacterial biomass are influenced by soil texture**

Generally, the effect sizes of conservation tillage on soil microbial

biomass, fungal and bacterial biomass were significantly positive in loamy soils ( $P < 0.05$ ) (including loam, silt loam, and silty clay loam), but not significant in sandy soils ( $P > 0.05$ ) (including loamy sand and sandy loam) (Fig. 5). Additionally, the effect sizes on fungal biomass were greater in clayey soils (including clay loam and clay) ( $P < 0.05$ ). Correspondingly the effect sizes of F:B ratios were significantly positive in clayey soils, but significantly negative in loamy soils ( $P < 0.05$ ).

The relatively reduced impact of conservation tillage on soil microbial biomass in sandy soils has also been reported in other studies (Cookson et al., 2008; Spedding et al., 2004). It has been posited that coarse soil textures may constrain the effects of conservation tillage on labile C pools, including soil microbial C and extractable C (Spedding et al., 2004), because soils rich in silt and clay have greater initial amounts of organic matter, which could protect microbial biomass from being disrupted by tillage disturbance. The high percentage of sand, and the resulting lack of soil structure, may thus lead to little protected organic matter in soil aggregates, so that although conservation tillage management may increase soil microbial biomass in coarse textured soils in the short term, the capacity for further increases in a long term may be reduced (Cookson et al., 2008). However, the greater increase of bacteria than fungi in loamy soils, and the negative response of F:B ratios, further indicate that bacteria could contribute to microbial biomass increases even more than fungi under these soil conditions. Thus, future soil research of tillage practices should include data of soil texture that can be potentially used to improve our capability to predict fungal and bacterial biomass changes under varying soil conditions.

**3.3. Response of soil C, N, pH, and bulk density to conservation tillage**

In studies that reported data on soil properties, such as soil total C and N, soil pH, and bulk density, the effect sizes were also calculated to further examine their association with fungal and bacterial biomass as driven by conservation tillage. In total, there were 152 and 95 observation pairs measuring soil total C and N, respectively (Fig. 6). Regardless of soil depths and tillage intensity, conservation-tillage significantly promoted soil total C and N by 22 % in comparison with conventional tillage ( $P < 0.05$ ). The effect sizes on soil C at soil depths

greater than 20 cm were not significant, while the positive effects of conservation tillage on soil N were significant in both soil depth ranges ( $P < 0.05$ ). However, soil N in subsoils consisted only of 4 observations and thus this difference between soil C and N responding to conservation tillage in subsoils might be due to sampling bias. Tillage intensity did not influence the effect sizes of soil C and N, indicating that even reduced tillage can result in nearly equal enhancement of soil C and N contents as no-till scenarios.

There were strong positive relationships between effect sizes of conservation tillage on soil total C versus effect sizes of conservation tillage on soil microbial biomass, including both fungal and bacterial biomass ( $P < 0.0001$ ,  $n = 152$ ) (Supplementary Fig. S3), with fungal and bacterial biomass having similar slopes. These results confirm the value of microbial biomass as an indicator of enhanced soil C under conservation tillage. It is generally acknowledged that changes in soil microbial biomass could reflect conditions affecting the accumulation of soil organic matter (Minoshima et al., 2007), which could be also attributed to the deposition and accumulation of plant residues in surface soil (Jiang et al., 2011). A positive correlation between soil microbial biomass and soil total C has been found frequently (Minoshima et al., 2007), but our demonstration of similar responses of both fungal and bacterial biomass with soil total C increase is novel. These results support our working hypothesis that both fungal and bacterial communities are associated with soil C increase as a result of transition from conventional to conservation-till managed ecosystems.

Overall, our dataset contained 61 and 31 paired observations of changes in soil pH and bulk density, respectively. Specifically, soil pH was modestly, but significantly reduced by 3 % under conservation tillage ( $P < 0.05$ ) (Supplementary Fig. S4), which was independent of soil depths and tillage intensity. Soil bulk density also significantly increased under conservation tillage relative to conventional tillage practices, but only in no-till agro-ecosystems. Although the effect size of bulk density was negative in soil depths below 20 cm, there were only 2 paired observations available and thus the significance of the results is questionable. Most studies have reported no significant change in soil pH among different tillage management scenarios (Frey et al., 1999; Minoshima et al., 2007; Pankhurst et al., 2002). Surprisingly, in our meta-analysis, there was a minor but consistent reduction of soil pH in both depths of no-till and reduced-till soils. It has been also found that surface soil pH decreased with increasing tillage, which could be attributed to greater incorporation of lime that is often also applied at tillage (Cookson et al., 2008). Moreover, base cations might be distributed deeper in the soil layers with ploughing in conventional tillage when compared to conservation tillage where they may remain on the surface (Lewis et al., 2011). Generally, it is thought that a more acidic soil environments might favor ecological niches for fungi over bacteria as it is often reported that fungal communities dominate over bacteria under lower pH conditions (Chen et al., 2015; Rousk et al., 2010a, 2009, 2010b). However, caution should be taken that the reduction of soil pH by only 3 % found in our study may have very limited effects on microbial communities. Besides the decrease in soil pH, we also observed a significant increase by 4 % in soil bulk density in the no-till soils in our study. In an undisturbed soil environment, the heavy rainfall and consequential soil wetting-drying cycles might be responsible for the general increase in soil bulk density under conservation tillage (Osunbitan et al., 2005). Alternatively, the change of soil physical and chemical properties due to management practices may be linked to the shift of microbial abundances in conservation-tilled soils.

### 3.4. Effect sizes of fungal and bacterial biomass as influenced by tillage years

There was no significant effect of the number of years under conservation tillage on the microbial biomass effect sizes, suggesting that both fungal and bacterial biomass may quickly respond to conservation tillage and that the rapid growth rates of fungal and bacterial biomass

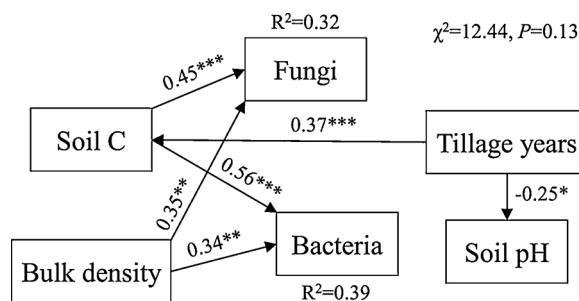


Fig. 7. Structural equation model (SEM) depicting the direct and indirect effects of tillage years and the effect sizes of soil total C, pH, and bulk density on the effect sizes of fungal and bacterial biomass. The numbers associated with single-headed arrows are standardized path coefficients (\*\*\* $P < 0.001$ , \*\* $P < 0.01$ , \* $P < 0.05$ ). Nonsignificant factors and pathways were eliminated.  $R^2$  represent the amount of variation explained by all paths. To show the overall goodness of fit for this SEM,  $\chi^2$  and  $P$  value were given as the model has a good fit when  $P > 0.05$ .

may be an important consideration and indicator for management changes (Kallenbach and Grandy, 2011), such as reduced-tillage and residue incorporation, even before measurable changes of soil total C (Carter, 1991). We constructed a structural equation model (SEM) to further investigate how tillage years influence the effect sizes of fungal and bacterial biomass through changing soil properties. Our results showed that neither fungal nor bacterial biomass was directly affected by tillage years (Fig. 7). Instead, tillage years played an indirect role in driving the effect sizes of fungal and bacterial biomass through soil total C ( $P < 0.001$ ). Therefore, our results suggest that regardless of the dynamic response of fungal and bacterial biomass, the build-up of soil total C pools depends on the numbers of years under conservation tillage. The SEM indicates that bulk density increases under conservation tillage may also have a direct positive effects on fungal and bacterial biomass ( $P < 0.01$ ) and that the reduction of soil pH by conservation tillage was further enhanced over tillage years ( $P < 0.05$ ). Our SEM model indicated that neither in a direct relationship, nor through modifying soil pH or bulk density, did conservation tillage years affect fungal and bacterial biomass. However, the positive relationship between soil total C and soil microbial biomass to conservation tillage further demonstrates that both fungi and bacteria are likely associated with soil C increases.

## 4. Conclusions

The meta-analysis approach implemented in this study has brought some new insights into how fungal and bacterial biomass and soil C storage are influenced by conservation tillage practices. Firstly, not only fungal, but also bacterial biomass clearly benefits from conservation tillage management, especially in top soils, as both fungi and bacteria significantly contributed to the enhancement of soil microbial biomass and were associated with total soil C increases. However the positive effects of conservation tillage on soil microbial biomass, including both fungi and bacteria, were absent in soils with coarse sandy textures. These data also challenge the viewpoint that conservation tillage practices result in fungal dominated ecosystems, as we found that increases of fungal-to-bacterial biomass ratios were not significant under conservation tillage practices no matter the soil depth and tillage intensity. Contrastingly in loamy soils we show that bacteria responded more significantly to tillage practices than fungi and result in a reduction of F:B ratios. Future studies of tillage management practices should thus not be only concerned with conditions that favor fungi, but also pay close attention to bacteria. While fungi are undoubtedly involved in the dynamics of soil organic matter formation and decomposition, it seems possible that bacteria benefit both directly and indirectly and that a soil environment favorable for fungal growth likely

promotes bacterial growth as well. However, the lack of significant fungal-to-bacterial ratio changes under conservation tillage does not necessarily mean that the phylogenetic and functional class distributions of fungi and bacteria will remain stable during the transition from conventional to conservation tillage practices, and thus future work should target a greater understanding of microbial community composition using high-resolution DNA sequencing or other methods to pinpoint the specific microbial groups responsive to sustainable agricultural practices.

### 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.

### Acknowledgments

This study was funded by Laboratory Directed Research and Development Program of Oak Ridge National Laboratory and the Department of Energy Bioenergy Technology Programs, Oak Ridge National Laboratory is managed by UT-Battelle, LLC for the U. S. Department of Energy under Contract No. DE-AC05-00OR22725. Dr. Zhongmin Dai was supported by National Science Foundation of China # 41807033.

### Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agee.2020.106841>.

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