Science of the Total Environment 643 (2018) 926–935

Contents lists available at ScienceDirect

Science of the Total Environment

journal homepage: www.elsevier.com/locate/scitotenv

Responses of soil microbial community structure changes and activities to biochar addition: A meta-analysis

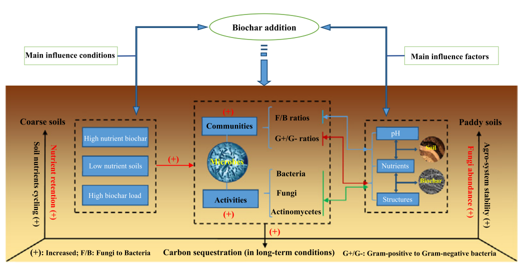
Leiyi Zhang [a], Yiming Jing [a], Yangzhou Xiang [b], Renduo Zhang [a,*], Haibo Lu [c]

[a] *Guangdong Provincial Key Laboratory of Environmental Pollution Control and Remediation Technology, School of Environmental Science and Engineering, Sun Yat-sen University, Guangzhou 510006, China*
[b] *Guizhou Institute of Forest Inventory and Planning, Guiyang 550003, China*
[c] *School of Atmospheric Sciences, Sun Yat-sen University, Guangzhou 510275, China*

HIGHLIGHTS

- Low temperature biochars addition in low pH soils greatly increased ratios of fungi to bacteria.
- Residue biochars application in dryland soils increased ratios of Gram-positive bacteria to Gram-negative bacteria the most.
- High load of biochar addition greatly enhanced microbial activities in low nutrients soils.
- Biochar nutrients and structural properties play the important role in soil microbial community structure changes and activities.

GRAPHICAL ABSTRACT



ARTICLE INFO

Article history:
Received 10 February 2018
Received in revised form 25 May 2018
Accepted 19 June 2018
Available online 28 June 2018

Editor: Baoliang Chen

Keywords:
Biochars
Soil bacteria
Soil fungi
Soil properties
Influence factors

ABSTRACT

The objective of this study was to investigate responses of soil microbial community structure changes and activities to biochar addition under different biochar characteristics, soil properties, and experiment conditions. A meta-analysis was conducted based on 265 datasets from 49 published studies. Results showed that biochar addition significantly increased the ratios of soil fungi to bacteria (F/B) and the ratios of Gram-positive bacteria to Gram-negative bacteria (G+/G−), and microbial biomass and activities. The enhancement of F/B ratios was most significant with addition of biochars produced at low temperatures to soils with lower pH and nutrients in a long-term condition, which improved ecosystem stability of agricultural soils. The F/B ratios were mainly affected by biochar nutrients, soil nutrients, and soil pH values. Biochar nutrients and structural properties (i.e., surface area and porosity) also played the important role in enhancing G+/G−, total microbial biomass, and activities of bacteria, fungi, and actinomycetes. The G+/G− ratios increased the most with addition of biochars produced with medium temperatures and residue accompanied with fertilizers in dry land (dried farmland) soils. High biochar load greatly improved the total phospholipid fatty acids, and activities of bacteria, fungi, and actinomycetes in fine/coarse, paddy soils, and soils with low nutrients, in turn increased the soil nutrient cycling. In addition, the structural properties of biochars were the most influencing factor to increase total microbial biomass and actinomycete activity. Overall, the enhancement of microbial activities and community structure shifts under biochar addition should promote soil nutrients cycling and carbon sequestration, and improve crop yields.

* Corresponding author.
E-mail address: zhangrd@mail.sysu.edu.cn (R. Zhang).

https://doi.org/10.1016/j.scitotenv.2018.06.231
0048-9697/

1. Introduction

Biochar generally refers to a carbon-rich solid that is produced by the pyrolysis of biomass in oxygen-limited conditions (Lehmann et al., 2011). Biochar application in soils may be beneficial to carbon (C) sequestration, soil fertility, and ecosystem functioning (Cao et al., 2009; Liu et al., 2013). Soil microorganisms play a vital role in soil nutrient cycling, soil ecosystem stability, and soil C changes under biochar addition (Lehmann et al., 2011; Zhu et al., 2017). Microbial activities and community compositions are affected by biochar characteristics (e.g., feedstock materials, pyrolysis temperature, pH, and specific surface area (SSA)), soil physiochemical properties (e.g., pH, soil organic carbon (SOC), and soil total nitrogen (STN), and texture), and experiment conditions (e.g., biochar load, fertilization, and study duration) (Singh et al., 2010; Spokas et al., 2011; Biederman and Harpole, 2013; Rutigliano et al., 2014; Mitchell et al., 2015; Tian et al., 2016). Therefore, it is critical to determine responses of soil microbial community structure changes and activities to biochar addition with different biochar characteristics, soil properties, and experiment conditions.

Effects of biochar application on soil microbial community structure changes and activities remain controversial under different biochar characteristics, soil properties, and experiment conditions. Castaldi et al. (2011) showed that wood biochar addition had no or little effect on soil microbial activities and community compositions. However, addition of wood and cotton straw biochars or low pyrolysed biochar, particularly at high biochar addition rates, increased microbial activities and altered the community composition towards a more Gram-negative bacteria dominated (relative to fungi and Gram-positive bacteria) community (Nelissen et al., 2012; Gomez et al., 2014; Liao et al., 2016). Straw biochar addition increased activities and community structure changes of fungi, Gram-negative bacteria, and actinomycetes, while wheat husk biochar addition did not affect the microbes (Lu et al., 2014; Watzinger et al., 2014; Wang et al., 2015; Muhammad et al., 2016; Luo et al., 2017). In terms of soil properties, biochar addition in red soil reduced microbial activities of Gram-positive bacterial and fungal phospholipid fatty acids (PLFAs), whereas biochar amendment in black soil increased the ratios of fungi to bacteria, Gram-negative bacteria, and action-bacterial PLFAs (Wang et al., 2012). Biochar application in sandy clay loam and silt loam soils reduced the total PLFA, but increased the total PLFA in clay loam soil (Ameloot et al., 2014). In addition, biochar amendment in the fine textured soil reduced microbial activities compared to in coarse textured soil (Wang et al., 2017).

The experiment conditions, including different biochar application rates, experiment durations (residence time) of biochar addition in soil, and fertilization amendment with biochar, significantly influence soil microbial activities and community structure shifts. Mitchell et al. (2015) found PLFA concentrations specific to Gram-positive and Gram-negative bacteria as well as actinomycetes decreased during the first 16 weeks of biochar addition, while the PLFA concentrations and the ratio of bacteria to fungi increased during weeks 16–24 of biochar application. Soil Gram-positive bacterial and fungal activities decreased with 0.5% of biochar addition, but fungi activity increased with higher biochar application rates (Wang et al., 2012; Muhammad et al., 2014). Biochar addition with fertilizers significantly increased ratios of fungi to bacteria, but the opposite result was reported (Kelly et al., 2015; Luo et al., 2017). Therefore, it remains unclear how the soil microbial community structure changes and activities respond to different conditions of biochar amendment. So far a comprehensive synthesis to reveal the general responses of soil microbial activities and community structure changes to biochar addition under different conditions is still not available (Gul et al., 2015; Zhu et al., 2017).

Therefore, the purpose of this study was comprehensive and quantitative to synthesize responses of soil microbial community structure shifts and activities to biochar addition with different biochar characteristics, soil properties, and experiment conditions. Using the meta-analysis, we aimed to answer the following questions: How do soil microbial community structure changes and activities change with different biochar characteristics under different soil properties and experiment conditions? What are the main influencing factors on soil microbial community structure shifts and activities under biochar addition?

2. Materials and methods

2.1. Data sources

The peer-reviewed articles reporting effects of biochar addition on soil microorganisms with different biochars under different soil and experiment conditions were collected globally using Web of Science (http://apps.webofknowledge.com) and China National Knowledge Infrastructure (CNKI, http://www.cnki.net). Keywords and terms used for the literature online-searching were "biochar" and "soil microbial biomass, or soil microbial activity, or microbial community structure, or total PLFA, fungi, bacteria and actinomycetes" and "phospholipid fatty acids or PLFAs". Articles satisfying the following criteria were included for the meta-analysis: at least three replicates per treatment, biochar and control treatments in the same experimental site (i.e., the same experimental conditions), clearly reported biochar addition rates, and analyzed data of soil microbial activities (bacteria, fungi and actinomycetes), total microbial biomass and activities (total PLFA), and microbial community structure changes (fungi to bacteria ratios and Gram-positive bacteria to Gram-negative bacteria ratios) using the PLFA method (Kong et al., 2011). In addition, some datasets of soil bacterium, fungus and actinomycete activities, total microbial biomass, and microbial community structure changes were extracted from tables and figures of the publications, including values of the mean and standard deviation (SD) or standard error (SE). For two datasets with mean values but without SE or SD values, 1/10 of the mean values were assigned as the SD values (Luo et al., 2006; Luo et al., 2010; Liu et al., 2013).

Totally 265 biochar addition experiments from 49 papers met the criteria above and were utilized in this study (Text S1 and Tables S1–3). We only adopted the microbial community structure shifts and activities measured with the PLFAs, which was the most commonly used methods for microbial measurements and for similar meta-analysis (Z. Zhou et al., 2017). Total PLFA were used to estimate the total microbial biomass and activities. The activities of fungi (F), bacteria (B), and actinomycetes (Actino), Gram-positive bacteria (G+) and Gram-negative bacteria (G−) were measured with taxa-specific PLFAs. The datasets of community structure changes included the ratios of fungi to bacteria (F/B) and the ratios of Gram-positive bacteria to Gram-negative bacteria (G+/G−).

2.2. Data collection

The raw data were obtained numerically from the tables, texts, or extracted from the figures in the original papers with the Get-Data Graph Digitizer 2.26 software. To the multiple sampling dates, only the result of biochar effect on the latest sampling time and the uppermost soil layer was chosen (Geisseler et al., 2016). Data were collected based on paired measurements between the control and biochar treatments. The control was subject to the same experimental conditions without a biochar treatment (Nguyen et al., 2017). SE and pH ($CaCl_2$/KCl) were unified into SD and pH (H_2O), respectively (Liu et al., 2013; Jian et al., 2016; Nguyen et al., 2017). Biochar load was converted from t ha^{-1} to % using soil bulk density and soil depth where biochar was applied. If bulk density was not reported, the Hydraulic Properties Calculator program was used to determine the bulk density based on soil texture (Biederman and Harpole, 2013; Nguyen et al., 2017).

The data were extracted from each study, including biochar characteristics (i.e., feedstock, pH, pyrolysis temperature, and SSA), soil properties (i.e., texture, pH, source, SOC, and STN), and experimental conditions, including biochar load (application rate), residence time of biochar in soil (study duration), and fertilization. Experimental factors to affect soil microorganisms under biochar amendment were categorized into the following groups to facilitate the analysis (Omondi et al., 2016; Peng et al., 2018; H. Zhou et al., 2017). According to feedstock materials, biochars were categorized as wood (pyrolyzed from wood residues), herb (feedstocks of crop straw, grass, green waste, and bulrush), residue (lignocellulosic waste of peanut, nut, pine needle, walnut shells, leaves, and chaff), manure (pyrolysis of livestock waste) and sludge (pyrolysis of sewage or deinking sludge) biochars. To the pyrolysis temperatures, biochars were grouped as low (≤350 °C), medium (350–600 °C), and high (≥600 °C) temperature biochars. Soil sources included soils from grassland, forest, dry land (dried farmland), and paddy (e.g., flooded paddy rice fields). Soil texture classes were categorized into fine (clay, clay loam, silty clay loam, and silty clay), medium (silt, loam, silty loam, and sandy silt loam), and coarse (sandy loam, sandy clay loam, loamy sand, silty sand, and sand) soils with the USDA Soil Classification System. Soil pH were grouped into acid (<6.5), neutral (6.5–7.5 including 6.5 and 7.5), and alkaline (>7.5). For soil nutrients, SOC values were categorized into <10, 10–20 (including 10 and 20), and >20 g kg^{-1}, and STN values <1, 1–2 (including 1 and 2), and >2 g kg^{-1}. Fertilization included practices with and without applications of inorganic and organic fertilizers.

2.3. Data meta-analysis

The meta-analysis was conducted to evaluate responses of soil microbes to biochar addition using Meta-Win 2.1 software. Specifically, the effect of biochar addition was estimated using the following response ratio (R) (Gurevitch and Hedges, 1999):

$$R = \ln\left(\frac{X_t}{X_c}\right) \tag{1}$$

where X_t and X_c are the results of the biochar treatments and control treatments, respectively. Values of $R = 0$, >0, and <0 represents no biochar effect, an increased (i.e., positive) effect, and a reduced (i.e., negative) effect, respectively (Luo et al., 2006). The variance (ν_R) associated with the effects was calculated by:

$$\nu_R = \frac{S_c^2}{n_c X_c^2} + \frac{S_t^2}{n_t X_t^2} \tag{2}$$

where S_t and S_c are the standard deviations of the biochar and control treatments, respectively, n_t and n_c are the data points of the biochar and control treatments, respectively. The following weighted response ratio (R_+) was utilized to identify the overall effect of the biochar treatments vs. the control treatments (Jian et al., 2016):

$$R_+ = \frac{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij} R_{ij}}{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij}} \tag{3}$$

where w is the weighting factor, j and i are the jth data point in the ith dataset in each category group, $w_{ij} = 1/\nu_R$, m and k are the number of datasets and data points in each dataset, respectively, in the category groups. The SE of R_+ was calculated by:

$$s(R_+) = \sqrt{\frac{1}{\sum_{i=1}^{m}\sum_{j=1}^{k} w_{ij}}} \tag{4}$$

The 95% confidence interval (95% CI) of R_+ can be calculated using results of Eqs. (3) and (4). The percentage change (P_c) between a certain categorical and control groups was related to the weighted response ratio by (Jian et al., 2016):

$$P_c = 100\%[\exp(R_+) - 1] \tag{5}$$

Values of the mean (i.e., P_c) and 95% CI of the overall effect of biochars on soil microorganisms were calculated using the random-effect models in the Meta-Win software and the datasets. The Pearson correlation and regression analyses were conducted to examine relationships of the responses of microbial community structure changes and activities vs. the various factors. The chi-square test was applied to determine significant difference between groups at $P < 0.05$. To elucidate the publication bias, the fail-safe numbers were presented (Table S4). A fail-safe number $> 5n + 10$ (n is the number of datasets used) indicated the result without publication bias (Xiang et al., 2017). To evaluate the sensitivity of response ratios to changes in the dataset and variability of the results, the response ratios were evaluated with successively reduced datasets (i.e., starting from all datasets, then randomly removing five datasets each time) (Fig. S1) (Jian et al., 2016). The categorical group analysis was conducted to calculate heterogeneity values between the groups (Q_b) and the chi-square test was applied to determine the significant difference in heterogeneities between groups (Jian et al., 2016). A larger Q_b value indicates a more significant effect of a main influence factor on soil microbial activities and community structure changes (Liu et al., 2016).

3. Results and discussion

3.1. Effects of biochar addition on soil microbial community structure changes under different conditions

Our meta-analysis revealed that biochar addition overall increased soil F/B ratios by 6.4% under different conditions (Table 1 and Fig. 1a). Especially low pyrolysis temperature biochars increased soil F/B ratios by 37% (Fig. 1a). Pyrolysis temperatures were negatively correlated with the response ratios of soil F/B ($P < 0.01$) (Table 2). Low pyrolysis temperature biochars contain a larger amount of non-pyrolyzed organic residue and organic nutrients than high temperature biochars (Wang et al., 2017; Zhu et al., 2017). The higher organic C and total N of nutrients in low pyrolysis temperature biochars facilitate the formation soil macro-aggregates and are more favorable for fungi to grow than for bacteria (Zhang et al., 2015). Our analysis showed that additions of biochars with lower pH values resulted in higher F/B ratios (Table 2). Biochar pH values increase with the pyrolysis temperatures (Gul et al., 2015; Liang et al., 2016). A low pH condition, such as addition of low pyrolysis temperature biochars, should be more favorable to fungus growth than to bacterium growth (Aciego Pietri and Brookes, 2009). As shown in Table 4, biochar pyrolysis temperature was the most significant factor to soil F/B, fungi, and bacteria among the influence factors. Therefore, the above analyses suggest that biochar pyrolysis temperatures play a main role in influencing soil F/B and microbial community structure shifts.

To the soil properties, low SOC content (<10 g kg^{-1}) of soil under biochar addition increased soil F/B ratios by 38% (Fig. 1a), and the response ratios of soil F/B were negatively correlated with soil pH ($P < 0.05$) (Table 2), that is, lower soil pH values resulted in higher

Table 1
Values of the mean and 95% confidence interval (CI) of the percentage changes (%) of soil microbial community structure changes and activities in response to biochar addition.

Variable	Percentage change (%)	95% CI (%)	Sample size (n)
Total PLFA	8.34	3.82–13.0	147
Bacteria	19.8	14.7–25.0	154
Fungi	19.4	15.1–23.7	242
Actino	9.09	5.07–13.3	197
G+	10.9	6.80–15.1	189
G−	13.4	9.22–17.7	192
F/B	6.35	1.83–11.1	154
G+/G−	10.0	3.73–16.7	74

Note: G+, G−, and Actino represent Gram-positive bacteria, Gram-negative bacteria, and actinomycetes, respectively; F/B and G+/G− represent ratios of fungi to bacteria, and Gram-positive bacteria to Gram-negative bacteria, respectively.

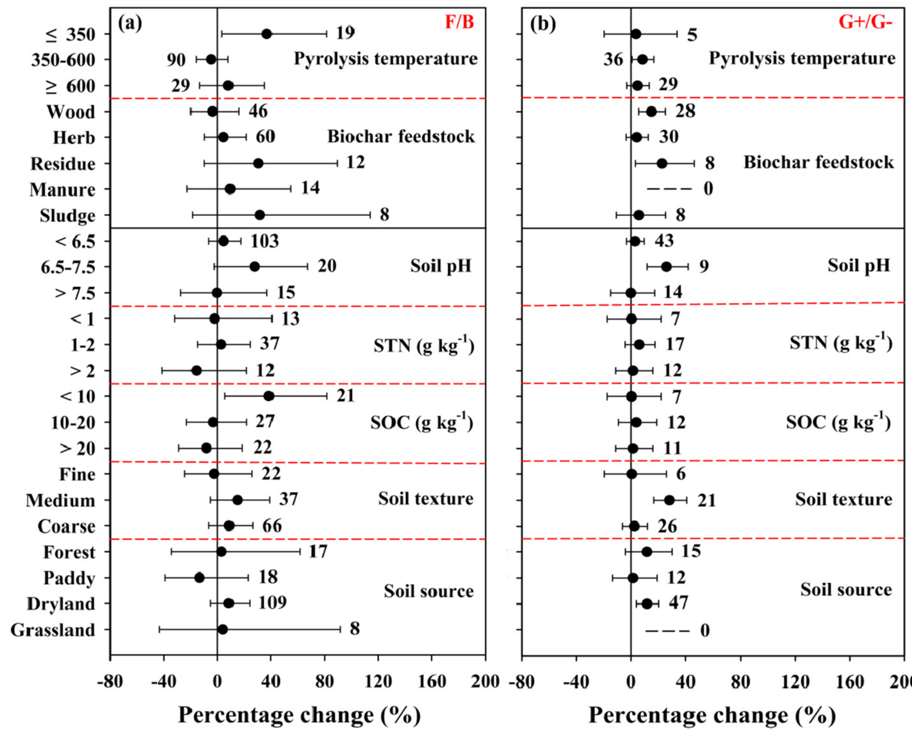


Fig. 1. Effects of biochar addition on (a) ratios of soil fungi to bacteria (F/B) and (b) ratios of soil Gram-positive bacteria to Gram-negative bacteria (G+/G−) under different biochar characteristics and soil properties. The bars represent the 95% confidence intervals, and the numbers of data pairs are showed near the bars.

F/B ratios. With higher C assimilation efficiency than bacteria, fungi can better utilize the C from biochar addition in low C soils, resulted in greater fungal abundance (Steinbeiss et al., 2009; Lehmann et al., 2011; Siciliano et al., 2014). Similar to addition of low pyrolysis temperature biochars, soils with low pH should be more favorable to fungus growth than to bacterium growth (Strickland and Rousk, 2010). As one of the main factors, pH changes alone can greatly influence soil microbial community structure changes (Warnock et al., 2007; Farrell et al., 2013). Among the soil properties, SOC content was the most significant factor to affect soil F/B, while soil pH was not a significant influence factor (Table 4). Meanwhile, SOC content was correlated with soil pH (Table S5). Therefore, nutrient supply (by biochars and soils) and soil pH interactively influenced the F/B ratios.

For the experiment conditions, the response ratios of soil F/B were positively correlated with biochar load ($P < 0.001$) and study duration ($P < 0.01$) (Fig. 2a and Table 2). Several studies have observed that the high application rates of biochar (≥5%) in the long-term condition significantly increased soil F/B ratios with preferential stimulation of soil fungi (Steinbeiss et al., 2009; Farrell et al., 2013; Zornoza et al., 2016). Compared to bacteria, fungi can assimilate C sources more efficiently. Under high biochar loads, hyphae grow into biochar pores using more degradable and stable C sources (Demoling et al., 2007; Lehmann et al., 2011). During a long study duration, with reduction of available biochar C and declined soil pH, fungi should have better chances to survive through mineralizing recalcitrant C than bacteria (Warnock et al., 2007; Zornoza et al., 2016). As shown by Yu et al. (2018), because of a shift in mineralization from biochar C to soil organic matter (SOM), the microbial community structure changed from bacterium dominance to fungus dominance (e.g., *Sordariomycetes* and *Tremellomycetes*) after 40 d. Meanwhile, signal molecules (e.g., flavonoid) stored in biochars can be desorbed into soil water over time, which should stimulate fungus growth (Warnock et al., 2007). An increased F/B ratio indicates a more sustainable agricultural system, in which C decomposition and N

Table 2
Pearson correlation coefficients of the relations between the response ratios of soil microbial community structure changes (F/B and G+/G−) and activities (the total soil microorganisms (total PLFA), bacteria, fungi, and actinomyctes) vs. different influence factors.

Factors	F/B	G+/G−	Total PLFA	Bacteria	Fungi	Actino
Biochar pH	−0.370**	−0.119	0.076	−0.310**	−0.293**	−0.051
	(126)	(70)	(118)	(132)	(190)	(152)
Pyrolysis temperature	−0.241**	0.022	0.073	−0.338**	−0.244**	−0.015
	(138)	(70)	(135)	(134)	(222)	(187)
Biochar SSA	−0.143	0.120	0.373**	−0.025	−0.016	0.234*
	(60)	(28)	(52)	(83)	(108)	(84)
Soil pH	−0.205*	−0.014	−0.028	0.033	−0.003	0.274**
	(138)	(66)	(130)	(140)	(216)	((179)
Soil total nitrogen	−0.241	0.011	0.092	0.097	−0.194	−0.396**
	(62)	(36)	(92)	(80)	(125)	(110)
Soil organic carbon	−0.175	0.003	−0.065	−0.081	−0.171*	−0.317**
	(70)	(30)	(96)	(95)	(127)	(104)
Study duration	0.197**	0.105	0.178*	0.008	0.021	0.144*
	(154)	(74)	(147)	(154)	(242)	(197)

Note: F/B, G+/G−, Actino, and SSA represent fungi to bacteria ratios, Gram-positive bacteria to Gram-negative bacteria ratios, actinomycetes, and specific surface area, respectively. *, **Indicate significant correlation at $P < 0.05$ and $P < 0.01$, respectively. The numbers are sample sizes in the parentheses.

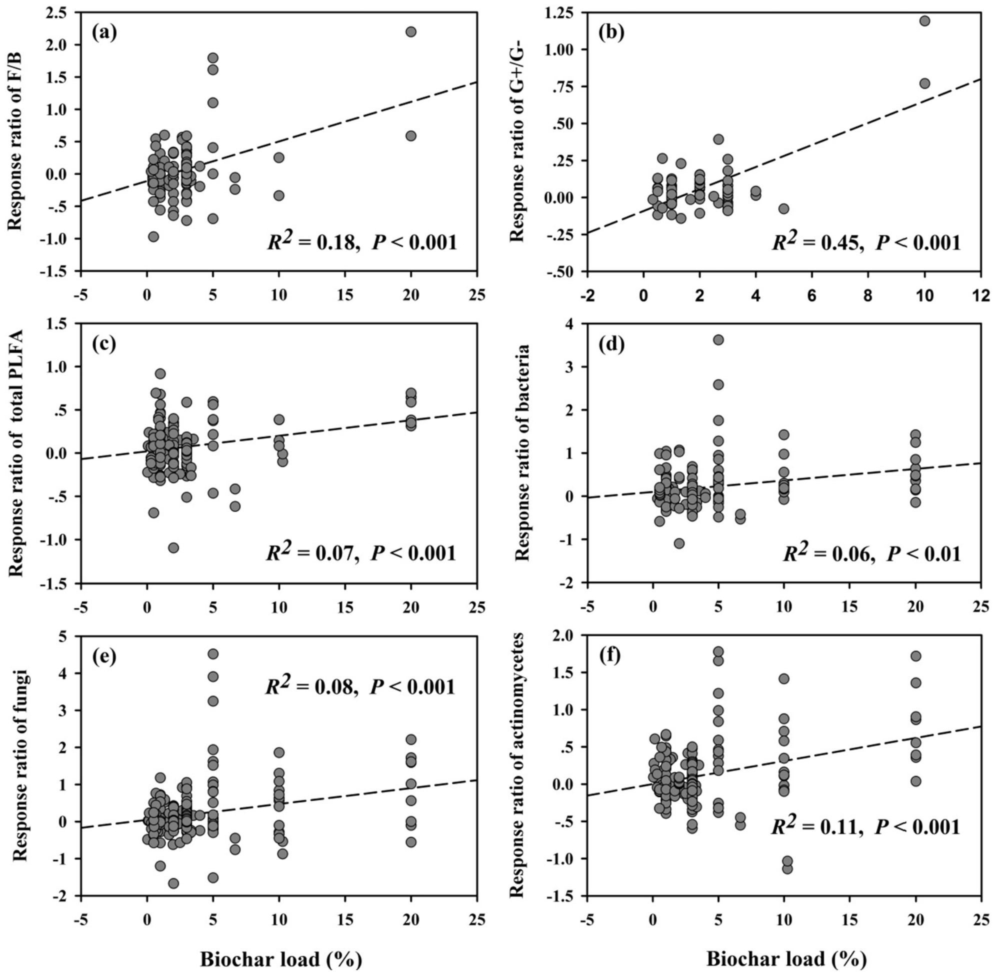


Fig. 2. Relationships between the response ratios of (a) ratios of fungi to bacteria (F/B), (b) ratios of Gram-positive bacteria to Gram-negative bacteria (G+/G−), and activities of (c) the total soil microorganisms (total PLFA), (d) soil bacteria, (e) fungi, (f) actinomycetes vs. biochar load.

mineralization mediated by fungi result in more efficient plant nutrient uptake, thus promoting crop growth (de Vries et al., 2006; Luo et al., 2017).

Biochar addition increased soil G+/G− by 10% (Table 1), and medium temperatures (350–600 °C) and residue biochars enhanced G+/G− values by 8.5% and 23%, respectively (Fig. 1b). Gram-negative bacteria favor soils with high nutrients (easily degradable organic substances) and carry out "specialized" or "narrow" functions in soils, while G+ bacteria (as oligotrophic communities) can use recalcitrant C as an energy source in soils and are more inherently resistant to environmental stress than G− bacteria (Fierer et al., 2003; Schimel et al., 2007; Farrell et al., 2013; Z. Zhou et al., 2017). Thus, G− bacteria become dominant immediately after biochar addition, but shift to G+ bacteria with time due to decrease of available C (Mitchell et al., 2015). The relatively higher recalcitrant and available C of medium temperature biochars improved nutrient supply to increasing G+/G− (Ameloot et al., 2013; Gul et al., 2015). In addition, the moderate porosity of medium temperature biochars could provide habitats to shelter and more direct contact with recalcitrant C for G+ bacteria (Zhu et al., 2017). The higher nutrients (recalcitrant and available C) and pore structure of residue biochars greatly enhanced G+/G− compared to wood, manure and sludge biochars (Akhter et al., 2015; Zhu et al., 2017). A recent ^{13}C-PLFA analysis revealed that soil microorganisms (especially G+ bacteria) utilized biochar-C as the substrate much more in biochar produced at 350 °C than that at 700 °C (Luo et al., 2017a). Therefore, the above analysis suggests that moderate biochar nutrients and pore structure should be beneficial to increase G+/G− in long-term conditions.

Biochar applications in neutral, medium-textured, and dry land soils enhanced soil G+/G− values by 26%, 28%, and 12%, respectively (Fig. 1b). The enhancement of soil G+/G− values was attributable to ample aeration and water, moderate nutrition, and microbial community structure changes (e.g., greater abundance of G+ bacteria in medium-textured soils) under biochar addition (Aciego Pietri and Brookes, 2009; Butnan et al., 2015; Zhu et al., 2017). Gram-positive bacteria are the major microbes responsible for the breakdown of litter and SOM in neutral, medium-textured, and dry land soils, and biochar additions can bind SOM to form a larger number of stable aggregates, thus enhance growth of G+ bacteria (Soinne et al., 2014; Gul et al., 2015; Wang et al., 2016; Z. Zhou et al., 2017). As shown in Fig. 1b, SOC and STN did not affect G+/G−. However, biochar addition suppressed SOC decomposition with altered microbial community structure by increasing G+ bacteria (Lu et al., 2014), which could potentially increase soil C sequestration.

Response ratios of soil G+/G− were positively correlated with biochar load (P < 0.001) (Fig. 2b), and biochar addition combined with fertilization greatly increased soil G+/G− by 17% (Table 3). The biochar load can influence physical and chemical properties of the soil, thus affect microbial community structure shifts (Gul et al., 2015). The increased nutrients (recalcitrant and labile C) and pores with higher application rates of biochars can increase soil ability to induce greater retention of ions and organic compounds with low molecular weights, in turn promote growth of G+ bacteria (Ameloot et al., 2013; Gul et al., 2015). The combination of biochar and fertilizer applications should reduce nutrients limitation for microbial competition and nutrients leaching, increase nutrients availability and the excretion of plant root, and thus provide sufficient nutrients for improving microbial growth (Nelissen et al., 2012; Tian et al., 2016; Xiang et al., 2017). Nevertheless, the growth and activity of G+ bacteria are more easily stimulated under adequate nutrients conditions than those of G− bacteria (Ameloot et al., 2013, 2014, 2015; Farrell et al., 2013).

3.2. Effects of biochar addition on soil microbial activities under different conditions

Across all the studies, biochar addition significantly increased activities of the total soil microorganisms (total PLFA), bacteria, fungi, actinomycetes, G+ bacteria, and G− bacteria by 8.3%, 20%, 19%, 9.1%, 11%, and 13%, respectively (Table 1). In general, the increase of total abundance and/or activities of soil microorganisms with biochar addition can be explained according to following three main mechanisms. First, biochar nutrients can directly stimulate soil microbial activities attributable to the co-metabolisms and soil priming effects (Kuzyakov et al., 2009; Luo et al., 2011, 2013). Second, biochar addition can change various soil physicochemical properties, such as soil pH, cation exchange capacity, and water and nutrient availability, thus indirectly affect microbial growth and activities (Abel et al., 2013; Luo et al., 2013; Gul et al., 2015). Thirdly, the interactions of biochars and soils lead to the formation of organic coating and organo-mineral layers to enhance water and nutrients retention to enhance microbial biomass over time (Archanjo et al., 2017; Hagemann et al., 2017). The increased soil microbial biomass and activities promote the decomposition and mineralization organic matter and plant uptake, i.e., the soil nutrients cycling (Biederman and Harpole, 2013; Ameloot et al., 2014).

Recent studies have shown that feedstock materials and pyrolysis temperatures greatly affect biochar-induced microbial activities (Zhu et al., 2017; Yu et al., 2018). Our analysis showed that low (≤ 350 °C) temperature and residue biochars improved activities of soil bacteria, fungi, and actinomycetes the most, while biochars with medium pyrolysis temperatures and wood greatly enhanced total PLFA (Fig. 3a–d). The response ratios of bacteria and fungi were negatively correlated with biochar pyrolysis temperature ($P < 0.01$), and biochar SSA were positively correlated with the response ratios of the total PLFA ($P < 0.01$) and actinomycete activity ($P < 0.05$) (Table 2). Low temperature biochars generally contain higher organic nutrients content than medium and high temperature, which can increase the interaction between biochars and microorganisms by the co-metabolism, resulting in enhancement of microbial biomass and activities, especially activities of bacteria and fungi (the dominant decomposers) (Luo et al., 2013; Gul et al., 2015; Z. Zhou et al., 2017). Residue biochars contain higher porosity and surface areas than manure and sludge biochars, which form more organo-mineral layers to provide nutrient shelter for microbes, thus improve microbial activities (Hagemann et al., 2017; Nguyen et al., 2017; Zhu et al., 2017). Steinbeiss et al. (2009) also reported that yeast-derived (i.e., a model residue material) biochar strongly promoted fungus growth. Medium temperature biochars contain the moderate organic nutrients content, pore structure, and surface areas compared with high and low temperature biochars to increase the total microbial abundance and activities (Gul et al., 2015; Zhu et al., 2017). The high porosity and SSA of wood biochars enhance the total microbial biomass and actinomycete activity (Zhu et al., 2017). Our comprehensive analysis showed that biochar pyrolysis temperature was a more significant influence factor on soil bacteria and fungi than biochar feedstock (Tables 4 and S6). However, Yu et al. (2018) indicated that biochar feedstock type explained more variation in the soil bacteria and fungi than pyrolysis temperature. The different responses of microorganisms to the different biochar properties indicate the needs of further quantitative studies (Lehmann et al., 2011). Overall, the above results showed that pyrolysis temperature, organic nutrients content, porosity, and SSA of biochars collaboratively influenced soil microbial growth and activities. Among the biochar characteristics, biochar organic nutrient was the most influencing factor to increase activities of bacteria and fungi, and biochar structural properties (porosity and SSA) were the most influencing factor to increase the total microbial abundance and actinomycete activity.

Table 3
Values of the mean and 95% confidence interval (CI) of the percentage changes (P_C) of soil microbial community structure changes and activities under biochar addition with and without fertilization.

Index	Biochar alone			Biochar with fertilizers		
	PC (%)	Sample size	95% CI (%)	PC (%)	Sample size	95% CI (%)
F/B	3.84	101	−7.60–16.7	11.1	53	−5.76–30.9
G+/G−	4.16	39	−2.75–11.6	17.0	35	8.83–25.7
Total PLFA	16.0	86	12.6–19.4	−0.68	61	−3.93–2.70
Bacteria	33.5	103	26.3–41.1	−1.68	51	−8.94–6.17
Fungi	27.1	160	18.2–36.6	8.00	82	−2.17–19.2
Actino	11.3	135	7.91–14.7	1.52	62	−2.92–6.15

Note: F/B and G+/G− represent the ratios of fungi to bacteria, and Gram-positive bacteria to Gram-negative bacteria, respectively. Actino is for actinomycetes.

It has been reported that microbial biomass increases with pH values up to 7 but decreases at higher pH values (Rousk et al., 2010; Lehmann et al., 2011). Our analysis showed that biochar application into acidic soil increased bacterial activity by 26%, and biochar addition in neutral soil increased activities of the total soil microorganisms (total PLFA), fungi, and actinomycetes by 22%, 46%, and 28%, respectively (Fig. 4a–d). The increased bacterial activity with biochar addition in acidic soil is related to the surface functional groups, silicates, and carbonates of biochars, which bind H^+ ions to increase soil pH and reduce the toxicity of exchangeable Al in acidic soil (Rousk et al., 2010; Qian and Chen, 2013; Stewart et al., 2013). Biochar addition in acidic soils can increase soil pH, which should enhance bacterial growth. With better pH buffering capacity and physicochemical properties, the neutral soils with biochar addition should stimulate the total microbial abundance and different microbial activities (Lauber et al., 2009; Gul et al., 2015). More biochar C is mineralized by microorganism in soils with higher pH than with low pH (Luo et al., 2011). Biochar addition in soils with high nutrients (i.e., STN > 2 and SOC > 20 g kg^{-1}) greatly increased the total PLFA and bacterial activity (Fig. 4a–b). This could be attributed to the sorption of high SOC on the biochar surfaces. In addition, the biochar surfaces can provide a favorable habitat for the soil microorganisms (Zhu et al., 2017). Biochar addition greatly stimulated microbial colonization and utilization of biochar C through the potential co-metabolism of biochar with SOC mineralization (Luo et al., 2011, 2013). High STN should compensate for large C/N ratios after biochar application to increase soil microorganism growth (Tian et al., 2016). It was also revealed that both SOC and soil texture significantly affected total PLFA, bacteria, fungi, and actinomycetes (Tables 4 and S6), suggesting that soil structure and nutrients were the most influencing factors to soil microbial activities under biochar amendment. The enhancement of total microbial biomass and activities by biochar addition in soils with high nutrients have been widely reported in the literature (Gul et al., 2015; Wang et al., 2016; Luo et al., 2017b; Zhu et al., 2017).

Biochar addition in soils with low nutrients (STN < 1 and SOC < 10 g kg^{-1}) and in fine/coarse soils obviously increased the activities of total soil microorganisms (total PLFA), bacteria, fungi, and actinomycetes (Fig. 4a–d). The SOC was negatively correlated with the response ratios of activities of fungi ($P < 0.05$) and actinomycetes ($P < 0.01$) (Table 2). With biochar addition, the changes of soil properties are mainly observed in the near vicinity of biochar (i.e., charsphere), and the interface between biochar and soil have unique properties (Luo et al., 2013). In the charsphere as a unique environment, enzymes and labile organic matter are adsorbed from the bulk soil to the biochar surface, which increases microbial growth, especially in drought or coarse-textured soils and soils with low pH or limited nutrients (Luo et al., 2013). In addition, biochar can adsorb clay minerals (especially in fine-textured soils) and organic matter as binding agents to enhance

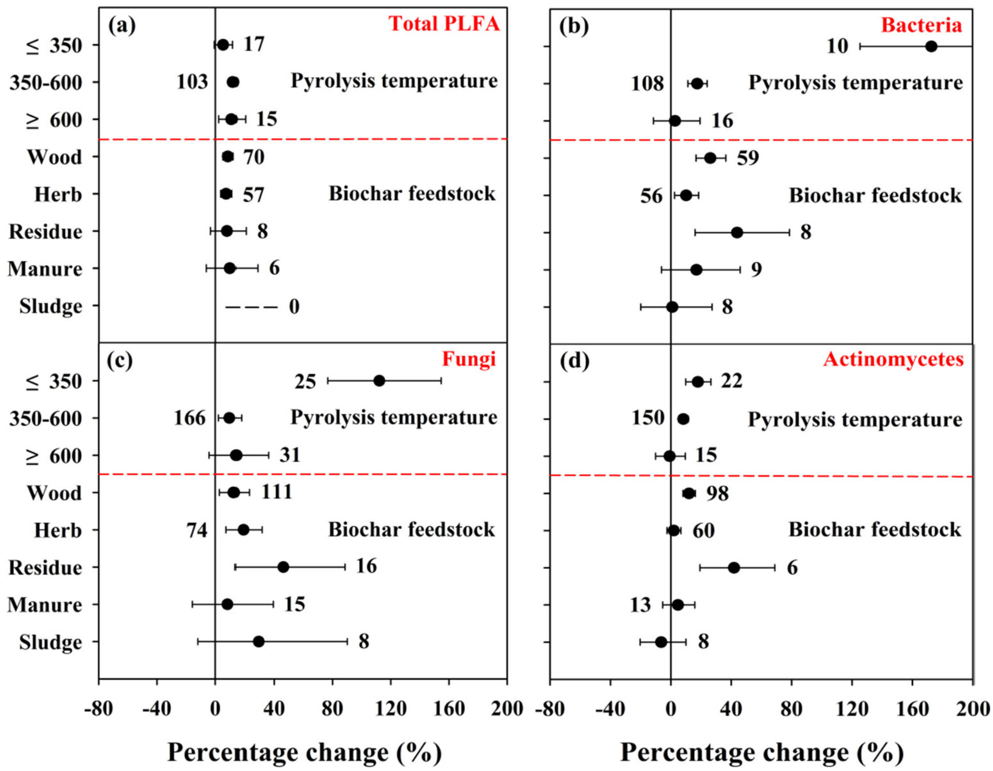


Fig. 3. Effects of biochar addition on activities of (a) the total soil microorganisms (total PLFA), (b) soil bacteria, (c) fungi, and (d) actinomycetes under different biochar characteristics. The bars represent the 95% confidence intervals, and the numbers of data pairs are showed near the bars.

aggregates formation and to increase aggregates stability, which can provide functions, such as protection of organic matter and increase of retention of soil water and nutrients, thus provide a suitable environment for soil biota and increase microbial activities (Lehmann et al., 2011; Soinne et al., 2014; Zhu et al., 2017). Biochar addition can also increase the bulk density of fine texture soil and decrease the bulk density of coarse texture soil to enhance oxygen and water content of soils, in turn to improve microbial activities (Lehmann et al., 2011). Compared to dry land and forest soils, biochar addition to paddy soils had more significant effects on the total soil microorganisms (total PLFA), bacteria, fungi, and actinomycetes (Fig. 4a–d). Because of the limited availability of oxygen under flooding conditions, more SOC or SOM are accumulated in paddy soils than in dry land soils (Geisseler et al., 2017). Biochar addition can increase oxygen content and pH of paddy soils, which promotes SOM and N mineralization, thus greatly increases soil microbial activities and rice growth (Tian et al., 2016; Zhu et al., 2017). Moreover, biochar amendment in paddy soils with high native SOC can cause soil priming effects by the co-metabolisms to significantly increase the activated microorganisms (Kuzyakov et al., 2009; Luo et al., 2017b). Moreover, temperature changes can alter the activities and compositions of soil microbial community (Sun et al., 2016; Tian et al., 2016). Elevated soil temperature can increase microbial activities and F/B ratios under biochar addition (Bamminger et al., 2016, 2018). Intermediate soil temperatures (i.e., 20–40 °C) greatly enhance the co-metabolism processes (i.e., the positive priming effects) of native SOC (i.e., water-soluble labile SOC, labile SOC, and relatively stable SOC) and biochar C (i.e., labile organic C and recalcitrant C), whereas high and low temperatures may reduce microbial activities and the priming effects (Fang et al., 2014, 2017).

Biochar load were positively correlated with the response ratios of activities of bacteria ($P < 0.01$), the total soil microorganisms (total PLFA), fungi, and actinomycetes ($P < 0.001$) (Fig. 2c–f). The response ratios of activities of the total soil microorganisms (total PLFA), and actinomycetes were positively correlated with the study duration ($P < 0.05$) (Table 2). Higher biochar application rates provide more biochar surfaces and pores to the habitat of microorganisms, and improve soil bulk density, pH, and retention of water and nutrients. These changes of soil physico-chemical properties greatly promote microbial abundance and activities (Lehmann et al., 2011; Ameloot et al., 2013; Gul et al., 2015). Aging biochars in soils over time form meso-

Table 4
Between-group heterogeneities (Q_b) of the main influence factors of biochar amendment on ratios of fungi to bacteria (F/B), ratios of Gram-positive bacteria to Gram-negative bacteria (G+/G−), and activities of the total soil microorganisms (total PLFA), soil bacteria, fungi, and actinomycetes.

Influence factor	F/B	G+/G−	Total PLFA	Bacterium	Fungus	Actinomycetes
Pyrolysis temperature	24.0***	1.01	4.26	127***	84.7***	9.55**
Biochar feedstock	2.70	4.58	0.66	14.0**	3.81	30.7***
Soil pH	2.85	18.7***	11.7**	2.03	11.6**	30.6***
Soil textures	1.00	20.3***	29.7***	12.7**	6.71*	13.7**
Soil organic carbon	12.7**	7.20*	12.3**	25.0***	15.5***	9.59**
Soil total nitrogen	9.94**	12.9**	4.37***	104***	4.11	20.4***
Soil sources	1.53	1.74	30.9***	27.4***	1.00	20.3***
Fertilizer addition	0.25	7.14**	51.6***	39.6***	6.46*	14.0***

Note: *, **, and *** represent the significance levels of $P < 0.05$, <0.01, and <0.001, respectively.

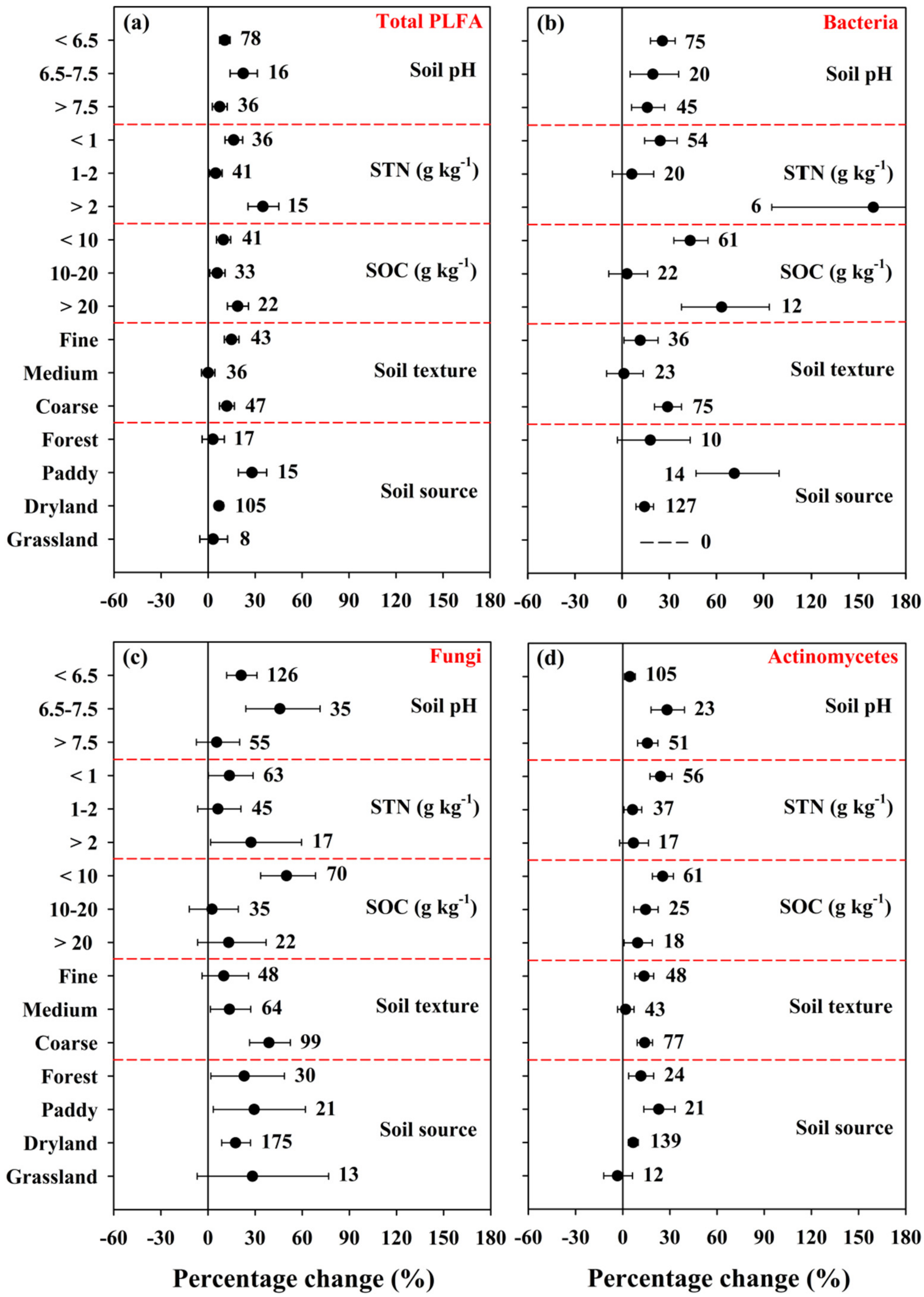


Fig. 4. Effects of biochar addition on activities of (a) the total soil microorganisms (total PLFA), (b) soil bacteria, (c) fungi, and (d) actinomycetes under different soil properties. The bars represent the 95% confidence intervals, and the numbers of data pairs are showed near the bars.

porous and hydrophilic organic coatings and organo-mineral layers on the high pore surfaces of biochars. These coatings and layers should strengthen biochar-water interactions and enhance nutrients retention, thus increase habitats into the surface and pores of biochars and microbial growth as well as activities (Archanjo et al., 2017; Hagemann et al., 2017). Ye et al. (2017) revealed that long-term exposure of biochar to the soil likely depleted organic compounds suitable to support heterotrophic growth, which could support chemolithotrophic processes that provide energy for *Oxalobacteraceae* and *Thiobacillus* bacteria. Therefore, high biochar load could be beneficial to improve soil microbial activities in long-term conditions. With less available degradable substances in soils, actinomycetes can utilize persistent and complex substrates by long-term priming effect, such as aromatic compounds in biochar (Watzinger et al., 2014; Yu et al., 2018). In addition, among the microorganisms, actinomycetes with the smallest size can be better protected by biochar macropores and directly use biochar C to growth (Warnock et al., 2007; Gul et al., 2015). Therefore, the activities of actinomycetes increased over time. Our analysis indicated that biochar with fertilizer applications did not significantly affect soil microbial activities (Table 2), whereas fertilization was a great influencing factor for the microbial activities (Tables 4 and S6). Biederman and Harpole (2013) showed that the nutrients pool contributed by biochar and fertilizer was not available to plants and microbes. In contrast, several studies indicated that biochar and fertilizer applications could reduce nutrients limitation for microbial competition and nutrients leaching, thus improve plant root biomass and microbial growth (Nelissen et al., 2012; Tian et al., 2016; Xiang et al., 2017). Therefore, it should be interesting to study how biochar with fertilizer (especially inorganic fertilizer) applications affect soil microbial activities in the future.

4. Conclusions

This meta-analysis found that additions of low temperature and high application rates of biochars significantly increased soil F/B ratios in low soil pH and SOC over time, which was collectively attributable to the biochar nutrients, soil nutrients, and pH values. Biochar nutrients and structural properties (pore structure, SSA, and porosity) played the main role in shifting soil G+/G− ratios and affecting soil microbial activities and growth. Applications of medium temperature biochars and high application rates of biochars greatly increased G+/G− in dry land soils. The microbial community structure changes were related to that fungi and G+ bacteria could efficiently and persistently utilize the labile and recalcitrant C over time. Biochar pyrolysis temperature, soil texture, and SOC were the main influence factors of activities of soil microorganisms. Amendment of low temperature and residue biochars and with high application rates significantly enhanced activities of bacteria, fungi, and actinomycetes in fine/coarse, low nutrient, and paddy soils. The main mechanisms of the above results were as follows: the co-metabolism process stimulated by biochar amendment, the formation of a microenvironment (i.e., the charsphere) with biochar addition to improve soil physicochemical and biological properties, and the formation of organic coatings or organo-mineral layers between biochar and soil to enhance water and nutrients retention. The improvement and changes of soil microbial activities and community structure changes under biochar amendment are beneficial to soil C sequestration, farmland systems stability, and promoting soil nutrients cycling, thus improving crop yields.

Acknowledgements

We are thankful to all the scientists whose primary studies were used to perform this meta-analysis. This study was supported by grants from the National Natural Science Foundation of China (Nos. 41471181, 41503085, and 31270544) and Forestry Science and Research Program of Guizhou Province (GZFSTC [2015] No. 6).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2018.06.231.

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