Biochar (2021) 3:239–254
https://doi.org/10.1007/s42773-021-00099-x

REVIEW

Association of biochar properties with changes in soil bacterial, fungal and fauna communities and nutrient cycling processes

Zhongmin Dai[1,2,3,6] · Xinquan Xiong[1,2] · Hang Zhu[1,2] · Haojie Xu[1,2] · Peng Leng[4] · Jihui Li[4] · C. Tang[5] · Jianming Xu[1,2,3]

Received: 8 February 2021 / Accepted: 5 May 2021 / Published online: 29 June 2021

Abstract

Soil microorganisms play crucial roles in soil nutrient cycling, carbon sequestration, fertility maintenance and crop health and production. To date, the responses of microorganisms, such as microbial activity, diversity, community structure and nutrient cycling processes, to biochar addition have been widely reported. However, the relationships between soil microbial groups (bacteria, fungi and microscopic fauna) and biochar physicochemical properties have not been summarized. In this review, we conclude that biochar affects soil microbial growth, diversity and community compositions by directly providing growth promoters for soil biota or indirectly changing soil basic properties. The porous structure, labile C, high pH and electrochemical properties of biochar play an important role in determining soil microbial abundance and communities, and their mediated N and P cycling processes, while the effects and underlying mechanisms vary with biochar types that are affected by pyrolysis temperature and feedstock type. Finally, we highlight some issues related to research methodology and subjects that are still poorly understood or controversial, and the perspectives for further research in microbial responses to biochar addition.

Keywords Biochar property · Microbial communities · Diversity · Enzyme · Nutrient cycling · Crop health

1 Introduction

Biochar is the solid product of pyrolyzing biomass under the temperatures of 300–700 °C with limited oxygen (Lehmann and Joseph 2015). Biochar includes artificial biochar and natural biochar (usually formed by wildfire), and has a large range of physicochemical properties that are determined by pyrolysis condition and feedstock type. Due to its high alkalinity, porous structure, stable C content and surface area, biochar is widely applied for soil fertility improvement, soil carbon sequestration, crop promotion and contaminated soil remediation (Caporaso et al. 2012; Lehmann and Joseph 2012).

Over the last decade, the effects of biochar on soil microbial growth and communities, and the underlying mechanisms have been widely reported (Lehmann et al. 2011; Muhammad et al. 2014; Palansooriya et al. 2019; Yu et al. 2020) because soil microorganisms carry out a range of important ecosystem functions, such as soil nutrient cycling and plant growth (Fierer 2017). Soil microorganisms contribute greatly to decomposition of soil organic C, nitrification, denitrification and phosphorous solubilization,

✉ Jianming Xu
jmxu@zju.edu.cn

1 Institute of Soil and Water Resources and Environmental Science, College of Environmental and Resource Sciences, Zhejiang University, Hangzhou 310058, China

2 Zhejiang Provincial Key Laboratory of Agricultural Resources and Environment, Zhejiang University, Hangzhou 310058, China

3 The Rural Development Academy, Zhejiang University, Hangzhou 310058, China

4 Linyi City Academy of Agricultural Sciences, Linyi 276012, Shandong, China

5 Department of Animal, Plant and Soil Sciences, La Trobe University, Melbourne Campus, Bundoora, VIC 3086, Australia

6 Shangdong (Linyi) Institute of Modern Agriculture, Zhejiang University, Hangzhou 310058, China

and these processes are associated with soil fertility maintenance and global climate change (Fierer 2017). Furthermore, microorganisms interact with plant roots to enhance their nutrient uptake capacity and increase plant systemic resistance to environmental perturbation (e.g., pathogen invasion and drought), and finally benefit plant health and growth (Philippot et al. 2013). Bacteria are most diverse in terrestrial ecosystems and are susceptible to the availability of C sources and pH changes (Dai et al. 2018b). Most soil nutrient cycles, such as carbohydrate metabolism, C fixation, nitrification, denitrification and P solubilization, are primarily mediated by bacterial communities. Soil fungi, heterotrophic microorganisms, are saprophytic, parasitic or pathogenic (Madigan et al. 2008). They can either decompose plant residues or influence plant health and production by forming arbuscular mycorrhiza or cause diseases (Elmer and Pignatello 2011; Liu et al. 2015). Soil fauna, a major component of soil food webs are the consumers of bacteria, fungi, algae and nematodes, and are as parasites of plants and animals (Geisen et al. 2018). The fauna can exert top-down control effects and are affected by both soil properties (e.g., moisture, clay content and nutrient status) and associated bacterial and fungal communities (Xiong et al. 2018; Oliverio et al. 2020). Overall, any changes in soil properties, such as nutrient status, pH and texture, would alter the microbial abundance, diversity and communities and related functions. The effects of biochar on soil microbial biomass and communities have been widely reported across different biochar pyrolysis temperatures, biochar feedstocks, soil type and experimental condition.

The number of literature involved in biochar effects on soil biota increased rapidly from year 2011 to 2020 (Fig. 1). Previous reviews have widely reported the responses of soil biota and mediated nutrient cycling to biochar addition, while the relationships between biochar physicochemical properties and microbial responses, i.e. underlying mechanisms, still need further summary. In addition, previous reviews/meta-analysis only synthesized the responses of microbial community to biochar mainly based on the traditional techniques (e.g., PLFA and DGGE). With the recently rapid development of analytical techniques (e.g., high-throughput sequencing), we can observe the diversity and abundances of microorganisms at a higher taxonomic resolution (e.g., bacteria and fungi) in biochar-amended soils. The roles of fungal and protist keystones in biochar-soil–plant continuum and specific biogeochemical processes such as P solubilization in biochar-amended soils should not be negligible, while most studies have focused on bacterial roles and the N cycling process. Therefore, this review attempts to resolve the above deficiencies. It aims to (1) summarize biochar unique physicochemical properties, such as porous structure, pH, labile C and electron shuttle, that play important roles in microbial growth, (2) identify the relationships between biochar properties and soil bacterial, fungal and fauna communities, and (3) synthesize the effects of biochars on microbial-mediated soil N and P transformation processes and underlying mechanisms. Finally, the review highlights the issues related to research methodology and the need of further research.

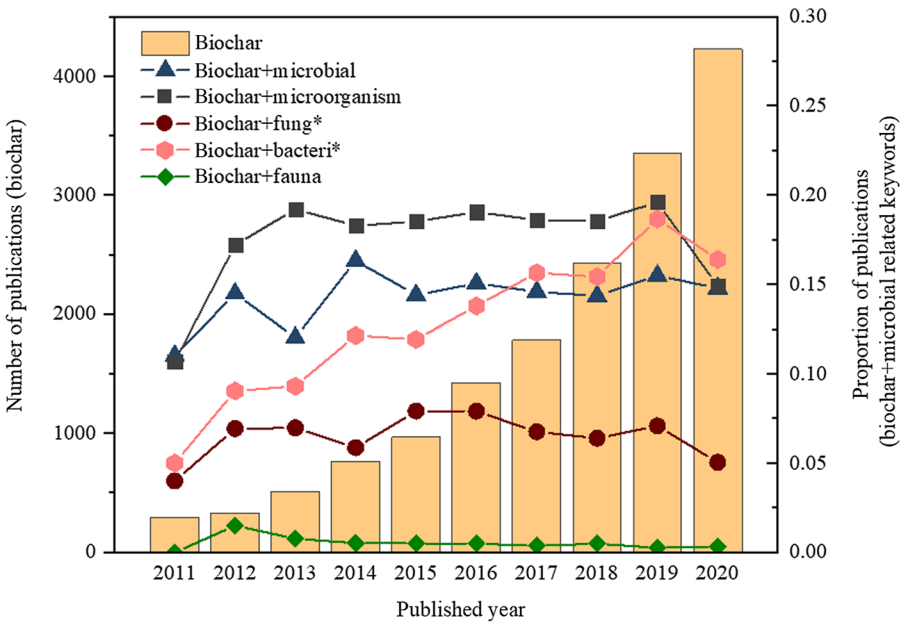

Fig. 1 The number and proportion of literatures involved in biochar effects on soil biota from year 2011 to 2020. The histograms presenting the number of biochar publications were corresponding to the left axis and the lines presenting the proportion of biochar publications were corresponding to the right axis

2 Relationship between biochar properties and microbial responses

Biochar can change soil physicochemical properties, which in turn alters soil microbial communities and related functions via following ways (Fig. 2). First, biochar can serve as a potential porous habitat for microbial growth and protection from predators. Second, it provides carbon source (in particular labile C) and mineral nutrients for microorganisms. Third, biochar changes soil basic properties such as increase in soil pH. Furthermore, it acts as an electron shuttle for microbial metabolisms (Dai et al. 2019; Saquing et al. 2016; Wu et al. 2018).

2.1 Porous structure

Biochar has porous aromatic structures that present high surface area and adsorption capacity. They can adsorb water, labile C and mineral nutrients from adjacent soils. The appropriate porous structure (i.e. macropores) can protect less competitive microorganisms from predator grazing (e.g., protists). Thus, microorganisms may use biochar particles as a habitat to colonize, grow and reproduce (Fig. 2). For instance, using a scanning electron microscope, Luo et al. (2013) observed the rich microbial colonization (i.e., diverse microbial shape and size) on the porous structure of lignocellulose-based biochar derived from *Miscanthus giganteus*. Dai et al. (2017a, b) showed that diverse microorganisms grew in manure-based biochar particles and that *Actinobacteria* with hyphae and spores were the dominant taxon in biochar particles, regardless of soil type. These studies also indicated that the presence of microorganisms is independent of biochar type and soil environments, as pyrolyzed biochar particles are always porous.

In general, the porosity and surface area of biochar increase with increasing pyrolysis temperature (Table 1) (Dai et al. 2013; Suliman et al. 2017). The microbial colonization would be more diverse in biochars pyrolyzed at high temperatures. This was consistent with more diverse microbial communities in manure biochar pyrolyzed at 700 °C compared to at 300 °C (Dai et al. 2017a, b). While the labile C reduces as pyrolysis temperature increases, biochar C availability also accounts greatly for microbial colonization (Table 1), which was supported by the higher number of microbes colonized in low-temperature biochar (Luo et al. 2013). Overall, the microbial colonization has resulted from the overall effects of porous structure and labile C content. Furthermore, the effects of porous structure were not apparent in aged biochar as soil succession, showed by sparse microbes being colonized in both external and internal surfaces of wood biochar aged for three years (Quilliam et al. 2013). This suggests that aging may reduce the microbial colonization in biochar particles, as the porous structure may collapse during aging and the adsorbed nutrients may be largely consumed by microorganisms.

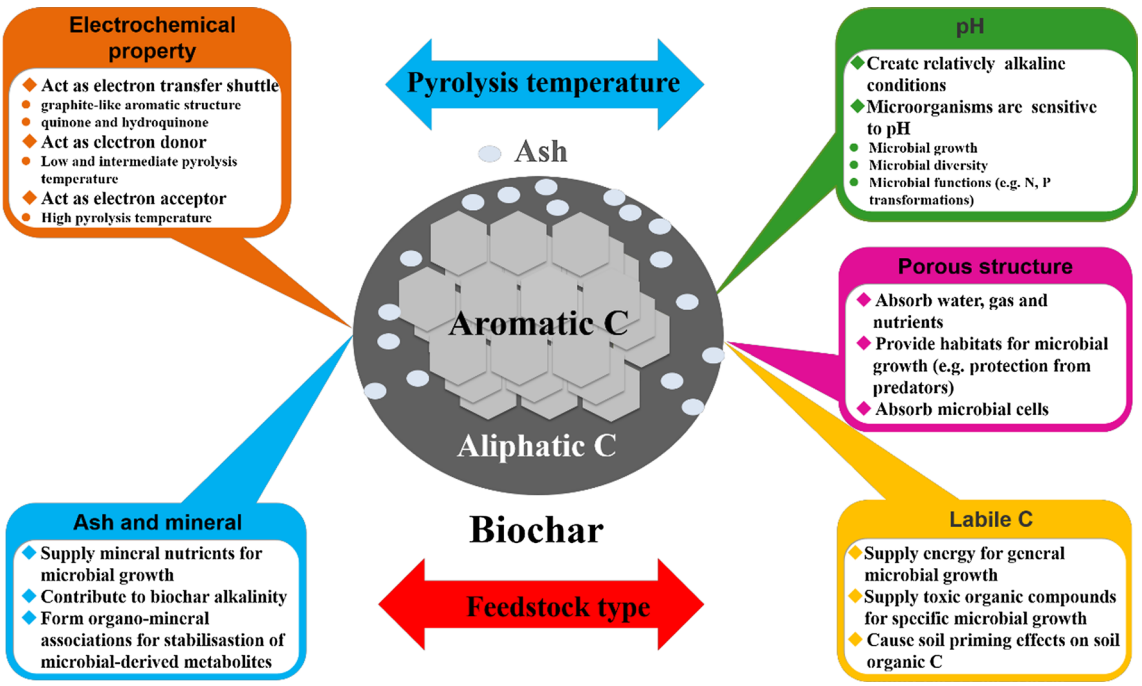

Fig. 2 The special physicochemical properties (i.e., pH, labile C, porous structure, electron shuttle and ash) of biochars that play important roles in altering the activity, diversity and community structure of bacteria, fungi and fauna

Table 1 The effects of pyrolysis temperature and feedstock type on biochar physicochemical properties that influence microbial communities

Biochar properties	Pyrolysis temperature (from 300 °C to 700 °C)	Feedstock type (from lignocellulose to manure)	References
pH	Increase	Increase	Yuan et al. (2011), Enders et al. (2012), Dai et al. (2017a, b)
Labile C	Decrease	Decrease	Cross and Sohi (2011), Enders et al. (2012), Spokas (2012)
Aromatic C	Increase	Decrease	
Ash	Increase	Increase	Lehmann and Joseph (2012), Novak et al. (2014), Dai et al. (2016b)
Porosity (Porous structure)	Increase (may decrease from 600 to 700 °C)	Decrease	Tsai et al. (2012), Gray et al. (2014)
Electron shuttle	Increase	Decrease	Kluepfel et al. (2014), Yu et al. (2015), Saquing et al. (2016), Sun et al. (2017), Yuan et al. (2019)
Electron donor	Decrease	Decrease	

2.2 Labile C

The labile C, which can serve as C substrates for microbial growth and metabolism, increases with decreasing pyrolysis temperature and is higher in lignocellulose-based biochar than manure-based ash-rich biochar (Table 1) (Cross and Sohi 2011; Dai et al. 2016b). The labile C can directly increase the microbial population and alter microbial communities by supplying energy sources such as carbohydrates. Some other bio-oils and condensates, such as polycyclic aromatic hydrocarbons, xylenol in labile C, are toxic to most microorganisms (Freddo et al. 2012), while they may selectively stimulate the growth of specific microorganisms (Table 2).

Table 2 Current research status and future perspectives for biochar effects on soil microbial communities

Key topic	Current research	Future research
1. From relative abundance to absolute abundance	1. Widely using amplicon sequencing (e.g., 16S and ITS sequencing); 2. Traditional methods, such as PLFA and DGGE	1. Using multi-omics, e.g., metagenomics, transcriptomics, proteomics and metabolomics; 2. Measuring the absolute abundance of microorganisms, e.g., using modified 16S rRNA sequencing
2. From individual microorganism types to microbial interactions	1. Bacterial, fungal and fauna growth and biomass; 2. Bacterial, fungal and fauna diversity and community structure	1. Lack of investigation of virus; 2. Insufficient investigations of protist; 3. Focus on the food-web where microbial interactions occur and find keystones responsive to biochar addition
3. From soil to biochar particles and char-sphere	1. Microbial diversity, community structure, dominant taxa in biochar-soil continuum 2. The influencing factors, such as pH, labile C, porous structure	1. Microbial communities, dominant taxa and functions in biochar particles and colonization mechanisms 2. Distribution patterns of microbial communities and functions across char-sphere gradients; 3. Differences in microbial communities and functions between biochar particles, char-sphere and adjacent soils
4. From individual nutrient transformation processes to coupled transformation processes	1. Transformation processes of individual nutrients (C, N or P) 2. Abundances of transformation genes of individual nutrients (C, N or P)	1. Coupled transformation processes of nutrients, such as C-P, N-P, C-N and C-N-P, and abundances of associated genes 2. Microbial anabolic and catabolic processes for C, N or P cycling
5. From microbial communities to plant growth and health	1. Microbial biomass, diversity and community structure in bulk soils; 2. Microbial biomass, diversity and community structure in rhizosphere	1. Specific microbial communities (e.g., N_2-fixing bacteria, growth-promoting bacteria and arbuscular mycorrhiza) that benefit plant growth and health 2. Connections between specific microorganisms and plant roots

Dai et al. (2019) used acetone to extract the major fraction of labile C from manure biochar and found that acetone-extracted C largely affected microbial biomass, community structure and microbial-mediated N cycling processes in both farmland and forest soils (Dai et al. 2018a, 2019). These effects were significantly greater than the aromatic C and ashes of biochar, supporting the importance of labile C in determining microbial communities. Moreover, isotopic tracing methods also verified that the labile C fraction of biochar was highly associated with microbial respiration and community succession in different soils, regardless of biochar type and incubation condition (Luo et al. 2013, 2017; Watzinger et al. 2014). Although the aliphatic C (volatile matter) accounts for 13.2% to 70.0% of biochar (Enders et al. 2012), microorganisms only utilize a small amount of the volatile matter (less than 5%), and the mineralization rate of labile C dramatically decreased to a minimum level during one year of incubation (Nguyen et al. 2014; Watzinger et al. 2014). For instance, only 4.3% of the ryegrass biochar C was mineralized by microorganisms after 158 days of incubation and only 0.45% of the biochar C was incorporated into microbial biomass (Maestrini et al. 2014). This implies that the effects of labile C on microbial communities are usually short-lived and diminishing over time. We point out that ash can supply inorganic nutrients for microbial growth and form organo-mineral bonds as the major driver for the microbial-metabolite stabilization (Fig. 2). However, the maximum content of ash from biochar only caused a small change in microbial communities (Dai et al. 2018a), again emphasizing the importance of labile C in determining microbial communities.

2.3 Biochar pH

Biochar is usually alkaline (pH > 7.0), resulting in a large increase in soil pH, especially for acid soils. Its alkalinity increases with increasing pyrolysis temperature and in most cases the manure-based biochars have higher pH compared to lignocellulose-based biochars (Table 1) (Dai et al. 2013; Enders et al. 2012). In general, soil microbial growth, community changes and relevant functions were highly sensitive to pH changes. An increase in bacterial growth and a decrease in fungal growth were observed with increasing soil pH at the gradient pH range of 4.0 to 8.3 (Rousk et al. 2009). In addition, the diversity and community structure of bacteria and the relative abundance of dominant phyla revealed by 16S sequencing were positively associated with soil pH, while the fungi and protist were not responsive to soil pH (Oliverio et al. 2020; Rousk et al. 2010). The abundances of bacterial phyla are also sensitive to pH, and for example the abundances of *Acidobacteria* are negatively related to soil pH (Madigan et al. 2008). Furthermore, the abundances of microbial genes involved in soil nutrient cycling, such as nitrification (e.g., *amoA* genes) and P mineralization (e.g., *phoD* genes), were affected by soil pH (Dai et al. 2020; DeForest and Otuya 2020).

Therefore, the effects of biochar on soil microbial communities, in particular bacterial communities, via increasing soil pH have been widely emphasized. For instance, the biochars with higher pH contributed greatly to the increases in bacterial diversity (Zhou et al. 2020). Also, the variances in bacterial communities after biochar addition were dominantly determined by soil pH rather than other properties such as organic C, regardless of agricultural soils or forest soils (Dai et al. 2016a; Wang et al. 2020). Wildfire-produced biochar consistently showed the similar trends for microbial evolution/succession (Zackrisson et al. 1996), as microbiomes in biochar significantly interact with those in adjacent soils, and this interaction is ascribed to niche differentiation between habitat specialists in biochar and soil (Zhang et al. 2021).

2.4 Electrochemical properties

The electrochemical properties of biochar have received an increasing attention, due to its (1) redox-active moieties that enable biochar to donate and accept electrons and (2) graphite-like aromatic structures for electron transfer (Sun et al. 2017). Low pyrolysis temperatures (e.g., 400–500 °C) induce redox-active moieties (e.g., quinone and hydroquinone) dominated by electron donating, while high temperatures (e.g., 650–800 °C) induce electron-accepting moieties and graphite-like aromatic structure (Table 1) (Kluepfel et al. 2014; Yu et al. 2015; Sun et al. 2018). Thus, biochar can act as an electron shuttle for microorganisms, which participate in redox reactions, such as nitrification and denitrification. The examples include the stimulated microbial reduction of Fe(III) oxyhydroxide mineral ferrihydrite by biochar (Kappler et al. 2014) and the suppression of N_2O emission in biochar-amended soils (Harter et al. 2014). The oxidized biochar by H_2O_2 increased soil N_2O emission rates, again indicating the suppressive effect of biochar redox-active moieties on N_2O emissions from soil denitrification (Yuan et al. 2019).

3 Biochar effects on soil microbial activity, biomass and enzyme activities

3.1 Biochar effects on soil CO_2 evolution and microbial biomass

Biochar addition significantly affects soil CO_2 evolution and microbial biomass by altering soil C substrate quality and quantity, while the effects are short-term and decrease over time as the C substrates are gradually consumed by

microorganisms. For example, the application of corn and nutshell biochars significantly enhanced the cumulative microbial respiration and C-use efficiencies during short-term incubation (Khadem and Raiesi 2017; Xu et al. 2018b). The transitory and large increase in soil CO_2 evolution after biochar addition is mainly attributed to: (1) increased microbial respiration using labile C or toxic organic compounds as C substrates; (2) increased decomposition priming effect of native organic C pools in soil; and/or (3) the metabolism of microbial necromass by other microorganisms (Lehmann and Joseph 2015).

By contrast, some studies have reported that biochar has inhibiting effects or no effects on soil CO_2 evolution (Zhou et al. 2017; Li et al. 2018; Chen et al. 2019). For instance, biochar application to a subtropical bamboo plantation reduced soil microbial heterotrophic respiration (Li et al. 2018). This was attributed to increased aromatic C content and the decreased activities of β-glucosidase and cellobiohydrolase which are responsible for decomposition of carbohydrates and celluloses (Li et al. 2018). No changes in soil respiration in temperate forests and reduced microbial respiration in paddy soils with the application at 40 t ha^{-1} also supported the inhibiting effects of biochar on soil CO_2 evolution (Zhou et al. 2017; Chen et al. 2019). The decrease in CO_2 evolution over time in incubation and field experiments is mainly attributed to: (1) the enhancement of C recalcitrancy and the decrease of labile C pool (Chen et al. 2019), and (2) the presence of toxic compounds which are only utilized by a minority of microorganisms.

Our review showed that biochar addition significantly increased microbial biomass C and N (Fig. 3), which was consistent with the study of Pokharel et al. (2020). The microbial biomass C and N in biochar-amended soils were 455 and 24.0 mg kg^{-1}, while the biomass C and N in non-amended soils were 412 and 20.2 mg kg^{-1}, respectively (Fig. 3). In addition, we pointed out that biochar produced at low temperatures had larger increasing effects on microbial biomass than those at high temperatures due to its higher content of labile C (Table 1), since biochar provides C substrates for microbial growth. This was supported by the increased microbial biomass C and N increased with the application of biochar pyrolyzed at 350 °C but were not affected by the biochars pyrolyzed at high temperatures of 500 and 700 °C (Guo et al. 2020). In another study, increasing application rate of wheat-straw biochar (350–550 °C) increased the amount of labile C which in turn increased microbial biomass C (Chen et al. 2016). Although biochars produced at high pyrolysis temperatures provide more living space for microorganisms, the abundant labile C substrates in biochars with low pyrolysis temperatures are the basic biogenic resource for the majority of microbial growth. Thus, we suppose the more important role of C substrates than porous structure in increasing microbial biomass.

3.2 Biochar effects on soil microbial enzyme activities

Biochar affects the activities of soil extracellular enzymes which are responsible for organic C degradation and other important enzymes for N mineralization or P solubilization. Such effects vary with biochar property, soil type and enzyme type (Zhang et al. 2019; Pokharel et al. 2020). A meta-analysis investigated the biochar effects on the activities of soil C-degrading enzymes and showed that biochar reduced the activities of total enzymes involved in C cycling by 6.3% (Zhang et al. 2019). The deceases were larger when biochar addition rates and pyrolysis temperature increased (Zhang et al. 2019). These C-degrading enzymes include α-glucosidase, β-cellobiosidase and β-glucosidase (Chen et al. 2016). On the contrary, Infan et al. (2019) indicated that biochar at the application rate of 1% C (w/w) stimulated the activities of dehydrogenase, which was consistent with the increased dehydrogenase activities by 19.8% in a meta-analysis (Pokharel et al. 2020). Some studies revealed that the activities of organic C-degrading enzymes reduced while those of C:N-acquiring enzymes increased moderately with increasing pyrolysis temperature of biochar (Guo et al. 2020). We attributed the contrasting responses of C-cycling enzyme activities to the ratio of biochar labile C to recalcitrant C, which determines microbial C-use efficiency.

Contrasting effects of biochar on the activities of N mineralization or P solubilization enzymes were observed in our study (Fig. 3) and other studies (Chen et al. 2016, 2020; Zhang et al. 2017). Based on a meta-analysis, biochar significantly increased the activities of urease and alkaline phosphatase by 23.1% and 25.4% (Pokharel et al. 2020). Other individual observations also showed the significant increase in the activities of urease, nitrite reductase, N-acetylglucosaminidase and alkaline phosphatase in different soils following biochar additions (Chen et al. 2016, 2020; Zhang et al. 2017). However, the activities of N and P enzymes were related to the application rate and biochar type. For example, the addition of 10 mg kg^{-1} biochar stimulated the activities of alkaline phosphatase and urease, whereas 50 mg kg^{-1} inhibited alkaline phosphatase and invertase activities (Huang et al. 2017). Similarly, the activity of N acquisition (N-acq) enzyme increased with the application rate of 1% but was unaffected with the application rate of > 1%. In addition, biochars produced at pyrolysis temperature of 350–550 °C with a pH of > 10 and C/N ratio of < 50 increased the urease activity to a greater extent than those produced at other pyrolysis conditions (Pokharel et al. 2020).

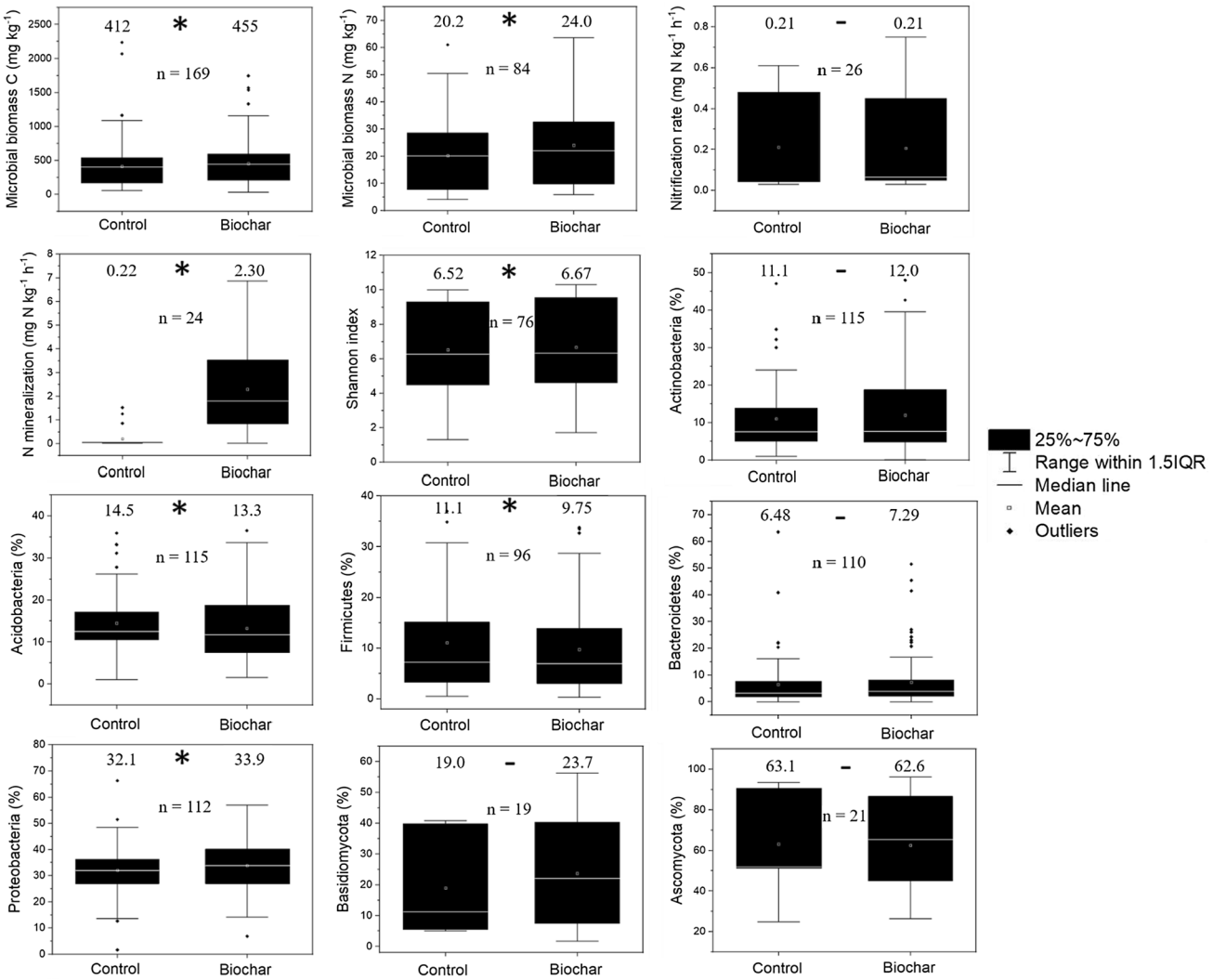

Fig. 3 The effects of biochar on soil microbial biomass C and N, N mineralization rate, nitrification rate, microbial alpha diversity and the relative abundances of soil dominant bacterial and fungal taxa. "*"and "-"represent the significant and non-significant differences in microbial parameters between control and biochar-amended soils at $p \leq 0.05$, respectively. The values above the black box are the average values of the microbial parameters, and the n represents the sample size. The references that provide the data are shown in the Supporting Information

4 Biochar effects on soil microbial diversity and community structure

4.1 Soil bacterial diversity and community structure

Overall effects of biochar on soil bacterial diversity and community structure depend on biochar type, soil type and agricultural managements, such as crop type and planting duration (Abujabhah et al. 2016; Dai et al. 2016a; Hermann et al. 2019; Liu et al. 2018; Yu et al. 2018a). With biochar type, the bacterial diversity was higher in forest soils amended with leaf biochar than with woodchip biochar, probably attributed to the higher pH with the leaf biochar (Zhou et al. 2020). The *Proteobacteria* was the dominant taxon in biochar pyrolyzed at low temperature (300 °C), while the *Chloroflexi* tended to be more prevalent in biochar pyrolyzed at high temperature (700 °C) (Dai et al. 2017a, b). Soil type impacted the responses of bacterial diversity and community structure to biochar addition. For instance, biochars at addition rates of 20 and 40 t ha^{-1} increased the relative abundance of *Betaproteobacteria* and *Deltaproteobacteria* in the soil with pH 4.89 and soil organic C of 17.7 g kg^{-1}, while decreased the abundance of *Betaproteobacteria* and increased the abundance of *Chloroflexi* in the soil with pH 5.99 and soil organic C of 20.1 g kg^{-1}. No significant changes were found in the soils with pH 6.21 and soil organic C of 18.8 g kg^{-1} (Chen et al. 2015). A

field experiment also showed that straw biochar increased the relative abundances of *Proteobacteria* and *Chloroflexi* in bulk soils while it enhanced the relative abundances of *Gemmatimonadetes* in rhizosphere soils (Cheng et al. 2019). Woolet and Whitman (2020) identified the positive responders, such as *Nocardioides*, *Micromonospora*, and *Ramlibacter*, to biochar at the genus level by re-analyzing publicly available raw data from 16S Illumina sequencing, while most bacterial taxa did not consistently respond to biochar addition across soil types.

Crop type and planting duration also impacted the responses of bacterial diversity and community structure to biochar addition. For example, the addition of biochar increased the abundances of bacterial (16S rRNA) gene, and Gram +, Gram − and *Pseudomonas* bacteria in the soils planted with mash bean but not with wheat (Azeem et al. 2020). In cotton-cropping soils, biochar amendment increased the abundances of *Sphingomonas* and *Pseudomonas* in biochar-amended cotton soils compared to the un-amended control, while the abundances of these bacteria decreased after continuous cropping for 11 years and 14 years (Han et al. 2017). Nguyen et al. (2018) compared the differences in bacterial diversity and communities between newly applied (1 year) and aged biochar (9 year), and observed that the abundances of *Cyanobacteria*, N_2-fixation bacteria, nitrification and denitrification bacteria were lower after 9 years of biochar history although the similar bacterial diversity and community structure (e.g., Chao 1 and Shannon index) were found between 1 and 9 years of biochar amendment (Nguyen et al. 2018). Although the variable effects on bacterial diversity were reported, a new meta-analysis concluded that the increased diversity was generally observed in acidic and sandy soils with biochar pyrolyzed under low temperature and derived from nutrient-rich feedstocks, as well as with low application rates (Li et al. 2020). Furthermore, our statistical analyses collected the abundance of bacterial taxa from high-throughput sequencing from published literatures (references listed in Supporting Information) and showed that biochar significantly increased the bacterial alpha diversity and the relative abundances of *Firmicutes* and *Proteobacteria* and decreased the relative abundance of *Acidobacteria* by paired t test (Fig. 3). This synthesis gives a supplement to the understanding of bacterial communities based on the traditional techniques.

4.2 Soil fungal diversity and community structure

In general, the effects of biochar on fungal diversity and community structure have been widely assessed, while the soil dominant taxa of *Basidiomycota* and *Ascomycota* were not responsive to biochar addition (Fig. 3). At the functional perspective, fungi encompass three functional groups with saprotrophs, pathotrophs and symbiotrophs (Madigan et al. 2008). Among them, saprotrophs decompose soil organic matter and biochar particles, and the pathotrophs cause crop diseases. The symbiotrophs promote plant growth by forming the root-fungal mutualists in soil ecosystems.

Saprophytic fungi rely on C substrates as the energy source and hence biochar addition always enhances the growth of fungal saprotrophs. For instance, Dai et al. (2018a) found that the labile C of biochar as a microbial C source increased the abundance of saprotroph, enhancing their competitive capacity with pathotrophs and symbiotrophs, and finally decreased fungal diversity. The inorganic minerals and aromatic C had less effects compared to labile C. This indicates that C substance is likely more important to determine saprotroph growth rather than microbial habitats and mineral nutrients. Except the mineralization of biochar itself, biochar addition to soil may accelerate the decomposition of soil organic C (priming effects) mediated by fungal communities (Luo et al. 2011). For instance, the microbial succession altered from bacterial to fungal communities during soil incubation with biochar, and *Sordariomycetes* and *Tremellomycetes* contributed more to soil priming effects in a late phase (i.e., 40 day) compared to bacterial communities (Yu et al. 2018b). Some studies report that saprophytic fungi have the capacity to utilize the recalcitrant C fraction of biochar when the labile-C substances have been utilized (Dai et al. 2018a). Overall, saprophytic fungi play an important role in soil C biochemical cycling by decomposing both soil organic C and biochar C.

Biochar can reduce plant disease by suppressing soil-borne pathogens. Dai et al. (2018a) found that biochar favors the growth of saprotrophs over soil-borne fungal pathogens by providing labile C for saprotroph growth and enhance their competitive capacity to pathogens. The application of biochar for 3 years decreased the relative abundances of potential soil-borne plant pathogens (e.g. *Fusarium*) and suppressed crop diseases in a black soil (Yao et al. 2017). The infection of *Fusarium* on asparagus roots was suppressed by coconut biochar (Matsubara et al. 2002) and hardwood-dust biochar (Elmer and Pignatello 2011). Other studies involved in the soil-borne pathogen suppression caused by biochar and the pathogens varied from the *Phytophthora* spp. in tree seedlings (Zwart and Kim 2012) to *Rhizoctonia solani* in cucumber (Jaiswal et al. 2014). The possible mechanisms are described as follows. First, soil microorganisms promoted by biochar addition can compete the C resources with pathogens, produce toxic compounds to pathogens or parasitizing pathogens (Dai et al. 2018a; Graber et al. 2010). Second, biochar indirectly increases plant systemic resistance by supplying nutrients, improving root architecture and enhancing arbuscular mycorrhizal colonization (Lehmann and Joseph 2015).

Mycorrhizae are one of the ubiquitous symbiotrophs in soil–plant systems. They build a vast connection between

plant roots and soils to increase plant nutrient uptake, such as N, P and water (Elmer and Pignatello 2011). Biochar has been considered as a micro-habitat for mycorrhizal growth and interaction with plant roots (Ameloot et al. 2015), while most studies have reported the negative effects or no effects of biochar on mycorrhizae communities. For instance, biochars significantly decreased the biomass of arbuscular mycorrhizal fungi (AMF) in a soil with low soil organic C (8.9 g C kg^{-1}), while did not affect it in a soil with high soil organic C (16.1 g C kg^{-1}). The poultry-litter biochar had larger decreasing effects on AMF biomass compared to pine-chip biochars (Ameloot et al. 2015). Similarly, mycorrhizal colonization in tallgrass roots was suppressed by royal-oak biochar addition (5.2%) in the first year of study and had no effects in the second or third year (Biederman et al. 2017). This trend was also reported by Elzobair et al. (2016), showing no effects of biochars on arbuscular mycorrhizal fungal colonization on corns in an Aridisol (Elzobair et al. 2016) and cowpea plants growing in Mollisol/Alfisol (Cobb et al. 2018). Furthermore, biochars derived from switchgrass, hardwood, or softwood feedstocks all reduced the colonization in roots of *Allium porrum* L. by the AMF (Han et al. 2016). By contrast, for potato plants, straw biochar significantly increased AMF root colonization, and plant N, P, and K uptake and plant biomass (Yang et al. 2020). Further work should be focused on understanding the underlying mechanisms and design of the targeted biochar for mycorrhizal colonization.

4.3 Soil fauna diversity and community structure

Soil fauna communities are the consumers of bacteria, fungi and other microorganisms. Biochar can change soil fauna communities and contribute greatly to soil nutrient cycling. For instance, biochar significantly increased the abundance of soil total nematodes and affected nematode community structure, with bacterivores dominant in the biochar treatments based on a 5-year field experiment (Liu et al. 2020b). The altered nematode community by biochar contributed to the improvement of soil quality and the enhancement of productivity in yellow cinnamon soil (Liu et al. 2020b). A farm case study indicated that straw biochar increased protist population, but had no effect on earthworms (Hansen et al. 2017). In a cultivated acidic soil, biochar only increased the flagellates abundance and had negative effects on the growth of nematodes, such as bacterivorous, fungivorous, and herbivorous and the amoebae (protists), indicating the detrimental effect on multitrophic levels of soil fauna (Liu et al. 2020a).

The mechanisms by which biochar affects soil fauna communities are related to (1) specific biochar properties, (2) soil physicochemical property changes and (3) changes in soil bacterial and fungal communities. Noyce et al. (2016) showed that the microorganisms living in or around the biochars had higher diversity than the adjacent soil, in particular, with the dominant taxa of *Aveolata* superphylum from protist, suggesting that biochar particles provide a unique habitat for soil protists. Biochar-induced changes in soil physicochemical properties, such as soil pH, C availability and moisture, may affect fauna (e.g., protist) growth and community succession (Geisen et al. 2018). This was supported by the Asiloglu et al. (2021a) revealing that the increase in the relative abundance of *Stramenopiles* in biochar-amended soils was highly correlated with the increases in soil total pore volume and C/N ratio. The increases in the relative abundances of protists, such as *Alveolata*, *Amoebozoa* and *Excavata*, were associated with increased soil pH and nutrient status (Asiloglu et al. 2021a). In addition, as the predators in food web, the shifts in bacterial and fungal communities after biochar addition would also affect the behaviors of fauna (Xiong et al. 2018). For instance, both poultry-litter and rice-husk biochars significantly altered soil bacterial communities and trophic interactions, resulting in the changes in protist communities and relevant N cycling processes (Asiloglu et al. 2021b).

5 Biochar effects on soil microbial-mediated nutrient transformation processes

5.1 Soil microbial-mediated N cycling

Biochar pH, labile C content, mineral N availability and electrochemical properties play an important role in mediating soil N cycling (Fig. 4). Biochars increase soil pH (Yuan et al. 2011) that can change the activity and community of nitrifiers and affect soil nitrification and N_2O emission (Yuan et al. 2011; Liu et al. 2017; Yu et al. 2019). For example, Lin et al. (2017) found that straw biochar increased the abundance of the bacterial *amoA* genes (ammonia-oxidizing bacteria) in the nitrification process, due to the increased soil pH. The importance of biochar pH in determining N-cycling microorganisms is clearly supported by a char-sphere study. Yu et al. (2019) found that soil pH and bacterial *amoA* abundance increased in the proximity to the biochar surface, while pH decreased with increasing the distance from the biochar. However, some studies have reported that the archaeal *amoA* abundance was not pH-sensitive or negatively correlated with soil pH (Hu et al. 2014; Nicol et al. 2008; Ying et al. 2017; Yu et al. 2021). This indicates that pH changes caused by biochar effects are mainly attributed to changes in AOB abundance and community. Although biochar contains a small amount of NH_4^+, which is the substrate for nitrification, the concentration of NH_4^+ in biochar is approximately equivalent to soil NH_4^+ concentration (Enders et al. 2012), except for biochar derived from high-ammonium feedstocks.

Nitrification

Attributes	Nitrification rate	Nitrifier-mediated N_2O emission	Bacterial *amoA* abundance	Archeal *amoA* abundance
Increase soil pH	+	+	+	- ; variable
Provide NH_4^+ for nitrifiers	+	+	+	- ; variable
Absorb NH_4^+ from soils	-	-	-	-

Denitrification

Attributes	Denitrification rate	Denitrifier-mediated N_2O emission	Denitrifier-mediated N_2O/N_2 emission	*nirK* and *nirS* abundance	*nosZ* abundance
Provide labile C for denitrifiers	+	+	-	+	+
Act as electron acceptor	-	-	+	-	-
Act as electron donors	+	+	-	+	+
Provide NO_3^- for denitrifiers	+	+	/	+	+
Cause more anaerobic microsites	+	+	-	+	+

P solubilization

Attributes	Available P	Fixed inorganic P fraction	Organic P fraction	Alkaline phosphatase	Acid phosphatase
Provide nutrients and habitats for P solubilizing microorganisms	+	-	-	+	+
Increase soil pH	+	variable	-	+	-
Increase water holding capacity	+	-	-	/	/

Fig. 4 The effects of biochar on soil nitrification, denitrification and P solubilization processes and the underlying mechanisms. "+"and "−"represent the stimulatory and inhibitory effects of biochar on nutrient transformation processes, respectively. "variable" and "/"represent the unknown and no effects of biochar on nutrient transformation processes, respectively

We assume that biochar addition does not change soil NH_4^+ availability and not strongly affect soil nitrification. Furthermore, due to the high adsorption capacity, biochar may adsorb NH_4^+ from soils when N fertilization is applied, and reduce soil NH_4^+ availability for nitrifiers compared to soils without biochar addition. This assumption has been verified by Yang et al. (2015) and Wang et al. (2015), reporting that biochar significantly decreased NH_4^+-N availability and thus decreased nitrification and the abundance of ammonia-oxidizing microorganisms, regardless of biochar and soil type (Wang et al. 2015; Yang et al. 2015).

Studies of the biochar effects on denitrification rates and denitrifier-mediated N_2O emission are inconsistent, with the increased denitrification in some studies but decreased denitrification in others. Such discrepancies can be explained by the differences in labile C content and electrochemical properties of biochars used in different studies (Fig. 4). A meta-analysis showed that biochar overall increased the abundance of denitrification process and relevant genes of *nirK*, *nirS* and *nosZ* (Xiao et al. 2019), which was probably due to the amount of labile C in biochar. The labile C could be directly utilized by N-cycling heterotrophic denitrifiers. In addition, the labile C may stimulate the priming effects on decomposition of soil organic C, leading to a quick consumption of O_2 and formation of anaerobic localized sites in soil (Harter et al. 2014). Both processes can increase soil denitrification and hence N_2O emission. Dai et al. (2019) showed that biochars with high labile C contents stimulated soil denitrification and had greater stimulatory effects on the abundances for denitrification genes, such as *nirK*, *nirS*, and *nosZ* and also N_2O emission, compared with biochar with low labile C. The close positive relationships between N_2O emission and biochar-increased dissolved organic C (Feng et al. 2018) and biochar volatile matter (Subedi et al. 2016) also indicated the C–N coupled cycling in soil denitrification and N_2O emission. As the labile C in biochar increased with decreasing pyrolysis temperature, we propose that the biochars produced at low pyrolysis temperatures (e.g., 300 °C) contribute to denitrification and N_2O emission to a greater extent than those produced at high temperatures. By contrast, due to its electrochemical properties, biochars, especially produced at high pyrolysis temperature (e.g., 700 °C), were shown to reduce soil N_2O emission (Kluepfel et al. 2014), as these biochars showed the greater electron-accepting capacities. Therefore, biochars at high pyrolysis temperatures can compete for electrons with NO_3^- during denitrification, whereas biochars produced at low pyrolysis temperatures act as electron donors and provide the electrons for NO_3^- reduction. This was also supported by the stimulated N_2O emission under supply of low-temperature biochar (e.g., 300 °C) (Dai et al. 2019) and the inhibited N_2O emission associated with the application of high-temperature biochar (e.g., 700 °C) (Harter et al. 2014, 2016). Although NO_3^- is the substrate for denitrifiers, due to the low content of NO_3^- in biochar and the negative charges in biochar surface, the NO_3^- in biochar does not significantly affect denitrification. Overall, the biochar with lower labile C content and higher electron-accepting capacity, usually produced at high pyrolysis temperatures, would induce low denitrification and N_2O emission (Fig. 4). Here, we pointed out that

the labile C of biochars mainly affected soil N_2O production while the electron-accepting capacity stimulated the conversion of N_2O to N_2, in particular in anaerobic conditions. This indicated that biochar produced at high pyrolysis temperatures decreased the N_2O/N_2 emission ratio (Harter et al. 2014, 2016; Dai et al. 2019).

5.2 Soil microbial-mediated P cycling

Microorganisms participate in soil P cycling. They can solubilize inorganic P or release enzymes to mineralize organic P, and finally increase soil P availability (Khan et al. 2014). Biochar can affect soil P cycling through (1) directly providing labile P nutrient, especially for manure biochar (Novak et al. 2014); (2) improving soil P retention capacity to reduce P leaching (Liu et al. 2019; Yang et al. 2021) and (3) affecting the activities and communities of P-solubilizing microorganisms. In this section, we discuss the effects of biochar on soil microbial communities and in turn the feedbacks of altered microbial communities to (1) soil P availability and (2) soil P fractions (Fig. 2).

Biochar can increase soil P availability via altering microbial communities, as it can provide the suitable growth condition (i.e., porous habitat and C supply as discussed above) for microorganisms (Fig. 4). For instance, the addition of rice-husk biochar enhanced soil P availability (Olsen-P) and the activities of related enzymes by enhancing the growth of P-solubilizing bacteria, such as *Thiobacillus*, *Pseudomonas*, and *Flavobacterium*, in a forest soil (Zhou et al. 2020). Leaf biochar increased the abundances of P-solubilizing bacteria, such as *Burkholderia-Paraburkholderia*, *Planctomyces*, and *Singulisphaera*, thus boosting P availability in forest soils (Zhou et al. 2020). These changes may be attributed to increased soil pH and water-holding capacity (Liu et al. 2017). Furthermore, Gao and DeLuca (2020) indicated that biochar shifted microbial communities from bacterial to fungal communities while fungi played an important role in solubilizing soil-fixed P and interactions with plant roots to enhance P acquisition. The changes in fungal communities and soil P availability were highly associated with biochar-induced pH increase (Gao and DeLuca 2020). Regardless of P status in soil, biochar can increase soil total P concentrations and dithionite-citrate-bicarbonate (DCB)-extractable P, leading to the improved growth of crops (Xu et al. 2019). Further investigation should be focused on the contribution percentages of these properties to the increase of soil P availability via changing microbial activities and communities.

Biochar can change soil P fractions and increase the labile P fraction by altering microbial communities and relevant enzyme activities (Fig. 4). For instance, a microcosm experiment revealed that manure-based biochar changed soil P fractions by increasing soil orthophosphate and pyrophosphate and decreasing those of monoesters, in additional to increasing soil P availability (Jin et al. 2016). Biochar decreased the activity of acid phosphomonoesterase but increased the activities of alkaline phosphomonoesterase (responsible for mineralization of organic P), indicating that biochar may affect related microorganisms and their released enzymes by increasing soil pH (Jin et al. 2016). Xu et al. (2018a) showed that biochar application significantly increased fractions of H_2O-soluble and NaOH-extractable inorganic P, and $NaHCO_3$-extractable organic P, but decreased the $NaHCO_3$-extractable inorganic P fraction. This indicated that biochar addition assists microorganisms to solubilize the fixed P and increases microbial P immobilization. The P immobilization is transitory and can be released after microbial mortality.

6 Conclusion and perspectives

The application of biochar to soils has great potential to influence microbial communities and relevant functional processes and hence nutrient supply and plant growth enhancement. Biochar affects soil microbial growth, activity and communities by directly providing growth promoters (e.g. substrates and porous structures) for soil biota or indirectly changing soil basic properties (e.g. pH). The porous structure, labile C, high pH and electrochemical properties of biochar dominantly affect soil microbial abundance, communities and their mediated N and P cycling processes. Due to the high variances in biochar basic properties determined by pyrolysis temperature and feedstock type, the selection and application of biochar to alter microbial communities and mediate nutrient cycling should follow the specific agricultural demands. However, some key aspects still require further investigations (Table 2).

As the rapid development of high-throughput sequencing techniques, such as 16S and ITS sequencing, a large number of literatures report the detailed changes in microbial taxonomic and phylogenetic communities caused by biochar. However, the microbial abundances are relative and only reveal the potential or dormant microbial communities. We recommend the multi-omics (combing meta-transcriptomics, meta-proteomics and meta-metabolomics) to investigate the active microbial communities. Alternatively, the improved methods of 16S sequencing (by adding an internal standard of *Aliivibrio fischeri*) (Smets et al. 2016) or an internal standard strain (ISS) HAAQ-GFP (Yang et al. 2018) that can obtain the absolute abundance of microbial taxa are recommended.

The effects of biochar on soil virus and protist community are poorly understood, while virus and protists affect microbial bacterial and fungal communities by top-down control (Li et al. 2019). Soil viruses influence the ecology of soil biological communities by transferring genes, cause

microbial mortality and consequently participate in soil biogeochemical cycles (Hurst et al. 1980). Soil protist communities are the predators of bacteria and fungi, and their communities are also affected by environmental perturbation. However, the interactions between communities of virus, protists, fungi and bacteria in microbial food-webs are still poorly understood. Recently, microbial network, especially the time-varying networks, has been reported to be a useful tool to capture microbial interactions during microbial community succession (Faust et al. 2015). Given the microbial key nodes in the networks, we can detect the responsive microbial keystones in biochar-amended soils and try to control the growth of these keystones. As the accurate predictions of keystones from microbial networks are still contradictory (Berry and Widder 2014; Weiss et al. 2016), combining the classic experimental validation of keystones with time-varying networks is recommended.

Most studies have focused on examining the effects of biochar on soil indigenous microbial communities, while the microbial communities, dominant taxa and their functions in biochar particles and char-sphere still require more investigations. The microorganisms that colonize on biochar particles participate in the biochar mineralization and affect biochar oxidation. They interact with soil indigenous microorganisms and consequently contribute to soil biogeochemical cycling (Dai et al. 2017a, b). The char-sphere is defined as the unique zone surrounding biochar particles with the properties, such as pH, porosity and nutrient status, differing from those of the bulk soil and the biochar particles (Pei et al. 2017; Quilliam et al. 2013). Investigation of the microbial communities and dominant taxa in biochar particles and along the char-sphere would provide a comprehensive understanding of microbial taxonomic and functional distributions from biochar particles to adjacent soils.

Previous studies have mainly focused on microbial-mediated individual nutrient cycling processes. In soil ecosystems, C, N and P cycling are usually integrated, as the C:N:P stoichiometry in microbial biomass are relatively constrained to a narrow range (Cleveland and Liptzin 2007). The environmental disturbances such as biochar addition may disrupt the coupling of microbial C, N and P cycling by changing soil nutrient statue. For example, the enrichments of C substrates may induce microbial demand for N, which leads to increased mineralization of organic N or acquirement of inorganic N from soils, or increased the mineralization of organic P (Mooshammer et al. 2014). Therefore, we point out the importance of the investigation of C, N and P coupled functional genes or processes in biochar-amended soils. This provides novel insights into soil nutrient management and plant growth after biochar amendments.

The alteration in soil microbial communities caused by biochar is linked tightly with agricultural food production. Plant rhizosphere is a special region where the complex interactions between plant root and microorganisms occur. This region provides a hotspot of microbial biomass and enzymatic activities (Mendes et al. 2013). The beneficial microorganisms including N_2-fixing bacteria, growth-promoting bacteria (PGPR) and arbuscular mycorrhiza can enhance plant defense and nutrient uptake capacity, and finally increase soil productivity (Lugtenberg 2015). However, how to build a healthy microbiome in the rhizosphere, control the pathogen and regulate the PGPR promotion or arbuscular mycorrhizal colonization still needs further investigation.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s42773-021-00099-x.

Acknowledgements This study was supported by the National Science Foundation of China (41520104001, 41807033), the Young Elite Scientists Sponsorship Program by CAST (2018QNRC001), the Serving Local Economic Development Project of Shandong (Linyi) Institute of Modern Agriculture, Zhejiang University (ZDNY-2020-FWLY01006), and the Fundamental Research Funds for the Central Universities in China.

References

Abujabhah IS, Bound SA, Doyle R, Bowman JP (2016) Effects of biochar and compost amendments on soil physico-chemical properties and the total community within a temperate agricultural soil. Appl Soil Ecol 98:243–253. https://doi.org/10.1016/j.apsoil.2015.10.021

Ameloot N, Sleutel S, Das KC, Kanagaratnam J, de Neve S (2015) Biochar amendment to soils with contrasting organic matter level: effects on N mineralization and biological soil properties. GCB Bioenergy 7:135–144. https://doi.org/10.1111/gcbb.12119

Asiloglu R, Samuel SO, Sevilir B et al (2021a) Biochar affects taxonomic and functional community composition of protists. Biol Fert Soils 57:15–29. https://doi.org/10.1007/s00374-020-01502-8

Asiloglu R, Sevilir B, Samuel SO et al (2021b) Effect of protists on rhizobacterial community composition and rice plant growth in a biochar amended soil. Biol Fert Soils 57:293–304. https://doi.org/10.1007/s00374-020-01525-1

Azeem M, Sun D, Crowley D et al (2020) Crop types have stronger effects on soil microbial communities and functionalities than biochar or fertilizer during two cycles of legume-cereal rotations of dry land. Sci Total Environ 715:136958. https://doi.org/10.1016/j.scitotenv.2020.136958

Berry D, Widder S (2014) Deciphering microbial interactions and detecting keystone species with co-occurrence networks. Front Microbiol 5:219. https://doi.org/10.3389/fmicb.2014.00219

Biederman LA, Phelps J, Ross BJ, Polzin M, Harpole WS (2017) Biochar and manure alter few aspects of prairie development: a field test. Agric Ecosyst Environ 236:78–87. https://doi.org/10.1016/j.agee.2016.11.016

Caporaso JG, Lauber CL, Walters WA et al (2012) Ultra-high-throughput microbial community analysis on the Illumina HiSeq and MiSeq platforms. ISME J 6:1621–1624. https://doi.org/10.1038/ismej.2012.8

Chen J, Liu X, Li L, Zheng J, Qu J, Zheng J, Zhang X, Pan G (2015) Consistent increase in abundance and diversity but variable change in community composition of bacteria in topsoil of rice paddy under short term biochar treatment across three sites from South China. Appl Soil Ecol 91:68–79. https://doi.org/10.1016/j.apsoil.2015.02.012

Chen J, Sun X, Li L, Liu X, Zhang B, Zheng J, Pan G (2016) Change in active microbial community structure, abundance and carbon cycling in an acid rice paddy soil with the addition of biochar. Eur J Soil Sci 67:857–867. https://doi.org/10.1111/ejss.12388

Chen J, Chen D, Xu Q et al (2019) Organic carbon quality, composition of main microbial groups, enzyme activities, and temperature sensitivity of soil respiration of an acid paddy soil treated with biochar. Biol Fert Soils 55:185–197. https://doi.org/10.1007/s00374-018-1333-2

Chen P, Liu Y, Mo C, Jiang Z, Yang J, Lin J (2020) Microbial mechanism of biochar addition on nitrogen leaching and retention in tea soils from different plantation ages. Sci Total Environ 757:143817. https://doi.org/10.1016/j.scitotenv.2020.143817

Cheng J, Lee X, Tang Y, Zhang Q (2019) Long-term effects of biochar amendment on rhizosphere and bulk soil microbial communities in a karst region, southwest China. Appl Soil Ecol 140:126–134. https://doi.org/10.1016/j.apsoil.2019.04.017

Cleveland CC, Liptzin D (2007) C : N : P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? Biogeochemistry 85:235–252. https://doi.org/10.1007/s10533-007-9132-0

Cobb AB, Wilson GWT, Goad CL, Grusak MA (2018) Influence of alternative soil amendments on mycorrhizal fungi and cowpea production. Heliyon 4:e00704. https://doi.org/10.1016/j.heliyon.2018.e00704

Cross A, Sohi SP (2011) The priming potential of biochar products in relation to labile carbon contents and soil organic matter status. Soil Biol Biochem 43:2127–2134. https://doi.org/10.1016/j.soilbio.2011.06.016

Dai Z, Meng J, Muhammad N, Liu X, Wang H, He Y, Brookes PC, Xu J (2013) The potential feasibility for soil improvement, based on the properties of biochars pyrolyzed from different feedstocks. J Soil Sediment 13:989–1000. https://doi.org/10.1007/s11368-013-0698-y

Dai Z, Hu J, Xu X, Zhang L, Brookes PC, He Y, Xu J (2016a) Sensitive responders among bacterial and fungal microbiome to pyrogenic organic matter (biochar) addition differed greatly between rhizosphere and bulk soils. Sci Rep 6:36101. https://doi.org/10.1038/srep36101

Dai Z, Meng J, Shi Q, Xu B, Lian Z, Brookes PC, Xu JM (2016b) Effects of manure- and lignocellulose-derived biochars on adsorption and desorption of zinc by acidic types of soil with different properties. Eur J Soil Sci 67:40–50. https://doi.org/10.1111/ejss.12290

Dai Z, Barberan A, Li Y, Brookes PC, Xu J (2017a) Bacterial community composition associated with pyrogenic organic matter (biochar) varies with pyrolysis temperature and colonization environment. mSphere 2:e00085–17. https://doi.org/10.1128/mSphere.00085-17

Dai Z, Zhang X, Tang C, Muhammad N, Wu J, Brookes PC, Xu J (2017b) Potential role of biochars in decreasing soil acidification-a critical review. Sci Total Environ 581:601–611. https://doi.org/10.1016/j.scitotenv.2016.12.169

Dai Z, Enders A, Rodrigues JLM, Hanley KL, Brookes PC, Xu J, Lehmann J (2018a) Soil fungal taxonomic and functional community composition as affected by biochar properties. Soil Biol Biochem 126:159–167. https://doi.org/10.1016/j.soilbio.2018.09.001

Dai Z, Su W, Chen H et al (2018b) Long-term nitrogen fertilization decreases bacterial diversity and favors the growth of Actinobacteria and Proteobacteria in agro-ecosystems across the globe. Glob Chang Biol 24:3452–3461. https://doi.org/10.1111/gcb.14163

Dai Z, Li Y, Zhang X, Wu J, Luo Y, Kuzyakov Y, Brookes PC, Xu J (2019) Easily mineralizable carbon in manure-based biochar added to a soil influences N_2O emissions and microbial-N cycling genes. Land Degrad Dev 30:406–416. https://doi.org/10.1002/ldr.3230

Dai Z, Liu G, Chen H et al (2020) Long-term nutrient inputs shift soil microbial functional profiles of phosphorus cycling in diverse agroecosystems. ISME J 14:757–770. https://doi.org/10.1038/s41396-019-0567-9

DeForest JL, Otuya RK (2020) Soil nitrification increases with elevated phosphorus or soil pH in an acidic mixed mesophytic deciduous forest. Soil Biol Biochem 142:107716. https://doi.org/10.1016/j.soilbio.2020.107716

Elmer WH, Pignatello JJ (2011) Effect of Biochar amendments on mycorrhizal associations and fusarium crown and root rot of asparagus in replant soils. Plant Dis 95:960–966. https://doi.org/10.1094/pdis-10-10-0741

Elzobair KA, Stromberger ME, Ippolito JA, Lentz RD (2016) Contrasting effects of biochar versus manure on soil microbial communities and enzyme activities in an Aridisol. Chemosphere 142:145–152. https://doi.org/10.1016/j.chemosphere.2015.06.044

Enders A, Hanley K, Whitman T, Joseph S, Lehmann J (2012) Characterization of biochars to evaluate recalcitrance and agronomic performance. Bioresour Technol 114:644–653. https://doi.org/10.1016/j.biortech.2012.03.022

Faust K, Lahti L, Gonze D, de Vos WM, Raes J (2015) Metagenomics meets time series analysis: unraveling microbial community dynamics. Curr Opin Microbiol 25:56–66. https://doi.org/10.1016/j.mib.2015.04.004

Feng Z, Sheng Y, Cai F, Wang W, Zhu L (2018) Separated pathways for biochar to affect soil N_2O emission under different moisture contents. Sci Total Environ 645:887–894. https://doi.org/10.1016/j.scitotenv.2018.07.224

Fierer N (2017) Embracing the unknown: disentangling the complexities of the soil microbiome. Nat Rev Microbiol 15:579–590. https://doi.org/10.1038/nrmicro.2017.87

Freddo A, Cai C, Reid BJ (2012) Environmental contextualisation of potential toxic elements and polycyclic aromatic hydrocarbons in biochar. Environ Pollut 171:18–24. https://doi.org/10.1016/j.envPol.2012.07.009

Gao S, DeLuca TH (2020) Biochar alters nitrogen and phosphorus dynamics in a western rangeland ecosystem. Soil Biol Biochem 148:107868. https://doi.org/10.1016/j.soilbio.2020.107868

Geisen S, Mitchell EAD, Adl S et al (2018) Soil protists: a fertile frontier in soil biology research. FEMS Microbiol Rev 42:293–323. https://doi.org/10.1093/femsre/fuy006

Graber ER, Harel YM, Kolton M et al (2010) Biochar impact on development and productivity of pepper and tomato grown in fertigated soilless media. Plant Soil 337:481–496. https://doi.org/10.1007/s11104-010-0544-6

Gray M, Johnson MG, Dragila MI, Kleber M (2014) Water uptake in biochars: the roles of porosity and hydrophobicity. Biomass Bioenergy 61:196–205. https://doi.org/10.1016/j.biombioe.2013.12.010

Guo K, Zhao Y, Liu Y et al (2020) Pyrolysis temperature of biochar affects ecoenzymatic stoichiometry and microbial nutrient-use efficiency in a bamboo forest soil. Geoderma 363:114162. https://doi.org/10.1016/j.geoderma.2019.114162

Han Y, Douds DD Jr, Boateng AA (2016) Effect of biochar soil-amendments on Allium porrum growth and arbuscular mycorrhizal fungus colonization. J Plant Nutr 39:1654–1662. https://doi.org/10.1080/01904167.2015.1089903

Han G, Lan J, Chen Q, Yu C, Bie S (2017) Response of soil microbial community to application of biochar in cotton soils with different continuous cropping years. Sci Rep 7:10184. https://doi.org/10.1038/s41598-017-10427-6

Hansen V, Müller-Stöver D, Imparato V, Krogh PH, Jensen LS, Dolmer A, Hauggaard-Nielsen H (2017) The effects of straw or straw-derived gasification biochar applications on soil quality and crop productivity: a farm case study. J Environ Manage 186:88–95. https://doi.org/10.1016/j.jenvman.2016.10.041

Harter J, Krause HM, Schuettler S, Ruser R, Fromme M, Scholten T, Kappler A, Behrens S (2014) Linking N_2O emissions from biochar-amended soil to the structure and function of the N-cycling microbial community. ISME J 8:660–674. https://doi.org/10.1038/ismej.2013.160

Harter J, Weigold P, El-Hadidi M, Huson DH, Kappler A, Behrens S (2016) Soil biochar amendment shapes the composition of N_2O-reducing microbial communities. Sci Total Environ 562:379–390. https://doi.org/10.1016/j.scitotenv.2016.03.220

Herrmann L, Lesueur D, Robin A, Robain H, Wiriyakitnateekul W, Bräu L (2019) Impact of biochar application dose on soil microbial communities associated with rubber trees in North East Thailand. Sci Total Environ 689:970–979. https://doi.org/10.1016/j.scitotenv.2019.06.441

Hu B, Liu S, Wang W et al (2014) pH-dominated niche segregation of ammonia-oxidising microorganisms in Chinese agricultural soils. FEMS Microbiol Ecol 90:290–299. https://doi.org/10.1111/1574-6941.12391

Huang DL, Liu LS, Zeng GM, Xu P, Huang C, Deng LJ, Wang RZ, Wan J (2017) The effects of rice straw biochar on indigenous microbial community and enzymes activity in heavy metal-contaminated sediment. Chemosphere 174:545–553. https://doi.org/10.1016/j.chemosphere.2017.01.130

Hurst CJ, Gerba CP, Cech I (1980) Effects of environmental variables and soil characteristics on virus survival in soil. Appl Environ Microbiol 40:1067–1079. https://doi.org/10.1128/aem.40.6.1067-1079.1980

Irfan M, Hussain Q, Khan KS et al (2019) Response of soil microbial biomass and enzymatic activity to biochar amendment in the organic carbon deficient arid soil: a 2-year field study. Arab J Geosci 12:95. https://doi.org/10.1007/s12517-019-4239-x

Jaiswal AK, Elad Y, Graber ER, Frenkel O (2014) Rhizoctonia solani suppression and plant growth promotion in cucumber as affected by biochar pyrolysis temperature, feedstock and concentration. Soil Biol Biochem 69:110–118. https://doi.org/10.1016/j.soilbio.2013.10.051

Jin Y, Liang X, He M, Liu Y, Tian G, Shi J (2016) Manure biochar influence upon soil properties, phosphorus distribution and phosphatase activities: a microcosm incubation study. Chemosphere 142:128–135. https://doi.org/10.1016/j.chemosphere.2015.07.015

Kappler A, Wuestner ML, Ruecker A, Harter J, Halama M, Behrens S (2014) Biochar as an electron shuttle between bacteria and Fe(III) minerals. Environ Sci Tech Let 1:339–344. https://doi.org/10.1021/ez5002209

Khadem A, Raiesi F (2017) Responses of microbial performance and community to corn biochar in calcareous sandy and clayey soils. Appl Soil Ecol 114:16–27. https://doi.org/10.1016/j.apsoil.2017.02.018

Khan MS, Zaidi A, Musarrat J (2014) Phosphate solubilizing microorganisms: principles and application of microphos technology. Springer, Cham

Kluepfel L, Keiluweit M, Kleber M, Sander M (2014) Redox properties of plant biomass-derived black carbon (biochar). Environ Sci Technol 48:5601–5611. https://doi.org/10.1021/es500906d

Lehmann J, Joseph S (2012) Biochar for environmental management: science and technology. Routledge

Lehmann J, Joseph S (2015) Biochar for Environmental Management: Science, Technology and Implementation, vol 1. Routledge, New York

Lehmann J, Rillig MC, Thies J, Masiello CA, Hockaday WC, Crowley D (2011) Biochar effects on soil biota—a review. Soil Biol Biochem 43:1812–1836. https://doi.org/10.1016/j.soilbio.2011.04.022

Li Y, Li Y, Chang SX et al (2018) Biochar reduces soil heterotrophic respiration in a subtropical plantation through increasing soil organic carbon recalcitrancy and decreasing carbon degrading microbial activity. Soil Biol Biochem 122:173–185. https://doi.org/10.1016/j.soilbio.2018.04.019

Li Y, Liu H, Pan H et al (2019) T4-type viruses: Important impacts on shaping bacterial community along a chronosequence of 2000-year old paddy soils. Soil Biol Biochem 128:89–99. https://doi.org/10.1016/j.soilbio.2018.10.007

Li X, Wang T, Chang SX, Jiang X, Song Y (2020) Biochar increases soil microbial biomass but has variable effects on microbial diversity: a meta-analysis. Sci Total Environ 749:141593. https://doi.org/10.1016/j.scitotenv.2020.141593

Lin Y, Ding W, Liu D, He T, Yoo G, Yuan J, Chen Z, Fan J (2017) Wheat straw-derived biochar amendment stimulated N_2O emissions from rice paddy soils by regulating the amoA genes of ammonia-oxidizing bacteria. Soil Biol Biochem 113:89–98. https://doi.org/10.1016/j.soilbio.2017.06.001

Liu J, Sui Y, Yu Z, Shi Y, Chu H, Jin J, Liu X, Wang G (2015) Soil carbon content drives the biogeographical distribution of fungal communities in the black soil zone of northeast China. Soil Biol Biochem 83:29–39. https://doi.org/10.1016/j.soilbio.2015.01.009

Liu S, Meng J, Jiang L, Yang X, Lan Y, Cheng X, Chen W (2017) Rice husk biochar impacts soil phosphorous availability, phosphatase activities and bacterial community characteristics in three different soil types. Appl Soil Ecol 116:12–22. https://doi.org/10.1016/j.apsoil.2017.03.020

Liu X, Li J, Yu L et al (2018) Simultaneous measurement of bacterial abundance and composition in response to biochar in soybean field soil using 16S rRNA gene sequencing. Land Degrad Dev 29:2172–2182. https://doi.org/10.1002/ldr.2838

Liu L, Tan Z, Gong H, Huang Q (2019) Migration and transformation mechanisms of nutrient elements (N, P, K) within biochar in straw-biochar-soil-plant systems: a review. ACS Sustain Chem Eng 7:22–32. https://doi.org/10.1021/acssuschemeng.8b04253

Liu T, Yang L, Hu Z et al (2020a) Biochar exerts negative effects on soil fauna across multiple trophic levels in a cultivated acidic soil. Biol Fert Soils 56:597–606. https://doi.org/10.1007/s00374-020-01436-1

Liu X, Zhang D, Li H et al (2020b) Soil nematode community and crop productivity in response to 5-year biochar and manure addition to yellow cinnamon soil. BMC Ecol 20:39. https://doi.org/10.1186/s12898-020-00304-8

Lugtenberg B (2015) Principles of plant-microbe interactions: microbes for sustainable agriculture. Princ Plant-Microbe Interact Microbes Sustain Agric. Springer, Cham

Luo Y, Durenkamp M, De Nobili M, Lin Q, Brookes PC (2011) Short term soil priming effects and the mineralisation of biochar following its incorporation to soils of different pH. Soil Biol Biochem 43:2304–2314. https://doi.org/10.1016/j.soilbio.2011.07.020

Luo Y, Durenkamp M, De Nobili M, Lin Q, Devonshire BJ, Brookes PC (2013) Microbial biomass growth, following incorporation of biochars produced at 350 ℃ or 700 ℃, in a silty-clay loam soil of high and low pH. Soil Biol Biochem 57:513–523. https://doi.org/10.1016/j.soilbio.2012.10.033

Luo Y, Zang H, Yu Z et al (2017) Priming effects in biochar enriched soils using a three-source-partitioning approach: 14C labelling and 13C natural abundance. Soil Biol Biochem 106:28–35. https://doi.org/10.1016/j.soilbio.2016.12.006

Madigan MT, Martinko JM, Dunlap PV, Clark DP (2008) Brock Biology of Microorganisms, 12th edn. Int Microbiol 11:65–73

Maestrini B, Herrmann AM, Nannipieri P, Schmidt MWI, Abiven S (2014) Ryegrass-derived pyrogenic organic matter changes organic carbon and nitrogen mineralization in a temperate forest soil. Soil Biol Biochem 69:291–301. https://doi.org/10.1016/j.soilbio.2013.11.013

Matsubara Y, Hasegawa N, Fukui H (2002) Incidence of Fusarium root rot in asparagus seedlings infected with arbuscular mycorrhizal fungus as affected by several soil amendments. J Jpn Soc Hortic Sci 71:370–374. https://doi.org/10.2503/jjshs.71.370

Mendes R, Garbeva P, Raaijmakers JM (2013) The rhizosphere microbiome: significance of plant beneficial, plant pathogenic, and human pathogenic microorganisms. FEMS Microbiol Rev 37:634–663. https://doi.org/10.1111/1574-6976.12028

Mooshammer M, Wanek W, Hämmerle I et al (2014) Adjustment of microbial nitrogen use efficiency to carbon: Nitrogen imbalances regulates soil nitrogen cycling. Nat Commun 5:3694. https://doi.org/10.1038/ncomms4694

Muhammad N, Dai Z, Xiao K et al (2014) Changes in microbial community structure due to biochars generated from different feedstocks and their relationships with soil chemical properties. Geoderma 226:270–278. https://doi.org/10.1016/j.geoderma.2014.01.023

Nguyen BT, Koide RT, Dell C, Drohan P, Skinner H, Adler PR, Nord A (2014) Turnover of soil carbon following addition of switchgrass-derived biochar to four soils. Soil Sci Soc Am J 78:531–537. https://doi.org/10.2136/sssaj2013.07.0258

Nguyen TTN, Wallace HM, Xu CY et al (2018) The effects of short term, long term and reapplication of biochar on soil bacteria. Sci Total Environ 636:142–151. https://doi.org/10.1016/j.scitotenv.2018.04.278

Nicol GW, Leininger S, Schleper C, Prosser JI (2008) The influence of soil pH on the diversity, abundance and transcriptional activity of ammonia oxidizing archaea and bacteria. Environ Microbiol 10:2966–2978. https://doi.org/10.1111/j.1462-2920.2008.01701.x

Novak JM, Cantrell KB, Watts DW, Busscher WJ, Johnson MG (2014) Designing relevant biochars as soil amendments using lignocellulosic-based and manure-based feedstocks. J Soil Sediment 14:330–343. https://doi.org/10.1007/s11368-013-0680-8

Noyce GL, Winsborough C, Fulthorpe R, Basiliko N (2016) The microbiomes and metagenomes of forest biochars. Sci Rep 6:26425. https://doi.org/10.1038/srep26425

Oliverio AM, Geisen S, Delgado-Baquerizo M, Maestre FT, Turner BL, Fierer N (2020) The global-scale distributions of soil protists and their contributions to belowground systems. Sci Adv 6:eaax8787. https://doi.org/10.1126/sciadv.aax8787

Palansooriya KN, Wong JTF, Hashimoto Y et al (2019) Response of microbial communities to biochar-amended soils: a critical review. Biochar 1:3–22. https://doi.org/10.1007/s42773-019-00009-2

Pei J, Zhuang S, Cui J, Li J, Li B, Wu J, Fang C (2017) Biochar decreased the temperature sensitivity of soil carbon decomposition in a paddy field. Agric Ecosyst Environ 249:156–164. https://doi.org/10.1016/j.agee.2017.08.029

Philippot L, Raaijmakers JM, Lemanceau P, van der Putten WH (2013) Going back to the roots: the microbial ecology of the rhizosphere. Nat Rev Microbiol 11:789–799. https://doi.org/10.1038/nrmicro3109

Pokharel P, Ma Z, Chang SX (2020) Biochar increases soil microbial biomass with changes in extra-and intracellular enzyme activities: a global meta-analysis. Biochar 2:65–79. https://doi.org/10.1007/s42773-020-00039-1

Quilliam RS, Glanville HC, Wade SC, Jones DL (2013) Life in the 'charosphere'—does biochar in agricultural soil provide a significant habitat for microorganisms? Soil Biol Biochem 65:287–293. https://doi.org/10.1016/j.soilbio.2013.06.004

Rousk J, Brookes PC, Baath E (2009) Contrasting Soil pH effects on fungal and bacterial growth suggest functional redundancy in carbon mineralization. Appl Environ Microbiol 75:1589–1596. https://doi.org/10.1128/aem.02775-08

Rousk J, Baath E, Brookes PC, Lauber CL, Lozupone C, Caporaso JG, Knight R, Fierer N (2010) Soil bacterial and fungal communities across a pH gradient in an arable soil. ISME J 4:1340–1351. https://doi.org/10.1038/ismej.2010.58

Saquing JM, Yu Y-H, Chiu PC (2016) Wood-derived black carbon (biochar) as a microbial electron donor and acceptor. Environ Sci Tech Let 3:62–66. https://doi.org/10.1021/acs.estlett.5b00354

Smets W, Leff JW, Bradford MA, McCulley RL, Lebeer S, Fierer N (2016) A method for simultaneous measurement of soil bacterial abundances and community composition via 16S rRNA gene sequencing. Soil Biol Biochem 96:145–151. https://doi.org/10.1016/j.soilbio.2016.02.003

Spokas KA (2010) Review of the stability of biochar in soils: predictability of O: C molar ratios. Carbon Manage 1:289–303. https://doi.org/10.4155/cmt.10.32

Subedi R, Taupe N, Pelissetti S, Petruzzelli L, Bertora C, Leahy JJ, Grignani C (2016) Greenhouse gas emissions and soil properties following amendment with manure-derived biochars: influence of pyrolysis temperature and feedstock type. J Environ Manage 166:73–83. https://doi.org/10.1016/j.jenvman.2015.10.007

Suliman W, Harsh JB, Abu-Lail NI, Fortuna AM, Dallmeyer I, Garcia-Perez M (2017) The role of biochar porosity and surface functionality in augmenting hydrologic properties of a sandy soil. Sci Total Environ 574:139–147. https://doi.org/10.1016/j.scitotenv.2016.09.025

Sun T, Levin BDA, Guzman JJL, Enders A, Muller DA, Angenent LT, Lehmann J (2017) Rapid electron transfer by the carbon matrix in natural pyrogenic carbon. Nat Commun 8:14873. https://doi.org/10.1038/ncomms14873

Sun T, Levin BDA, Schmidt MP et al (2018) Simultaneous quantification of electron transfer by carbon matrices and functional groups in pyrogenic carbon. Environ Sci Technol 52:8538–8547. https://doi.org/10.1021/acs.est.8b02340

Tsai WT, Liu SC, Chen HR, Chang YM, Tsai YL (2012) Textural and chemical properties of swine-manure-derived biochar pertinent to its potential use as a soil amendment. Chemosphere 89:198–203. https://doi.org/10.1016/j.chemosphere.2012.05.085

Wang Z, Zong H, Zheng H, Liu G, Chen L, Xing B (2015) Reduced nitrification and abundance of ammonia-oxidizing bacteria in acidic soil amended with biochar. Chemosphere 138:576–583. https://doi.org/10.1016/j.chemosphere.2015.06.084

Wang Y, Zheng J, Liu X, Yun Q, Hu Y (2020) Short-term impact of fire-deposited charcoal on soil microbial community abundance and composition in a subtropical plantation in China. Geoderma 359:113992. https://doi.org/10.1016/j.geoderma.2019.113992

Watzinger A, Feichtmair S, Kitzler B, Zehetner F, Kloss S, Wimmer B, Zechmeister-Boltenstern S, Soja G (2014) Soil microbial communities responded to biochar application in temperate soils and slowly metabolized C-13-labelled biochar as revealed by C-13 PLFA analyses: results from a short-term incubation and pot experiment. Eur J Soil Sci 65:40–51. https://doi.org/10.1111/ejss.12100

Weiss S, Van Treuren W, Lozupone C et al (2016) Correlation detection strategies in microbial data sets vary widely in sensitivity and precision. ISME J 10:1669–1681. https://doi.org/10.1038/ismej.2015.235

Woolet J, Whitman T (2020) Pyrogenic organic matter effects on soil bacterial community composition. Soil Biol Biochem 141:107678. https://doi.org/10.1016/j.soilbio.2019.107678

Wu D, Senbayram M, Zang H et al (2018) Effect of biochar origin and soil pH on greenhouse gas emissions from sandy and clay soils. Appl Soil Ecol 129:121–127. https://doi.org/10.1016/j.apsoil.2018.05.009

Xiao Z, Rasmann S, Yue L, Lian F, Zou H, Wang Z (2019) The effect of biochar amendment on N-cycling genes in soils: a meta-analysis. Sci Total Environ 696:133984. https://doi.org/10.1016/j.scitotenv.2019.133984

Xiong W, Jousset A, Guo S et al (2018) Soil protist communities form a dynamic hub in the soil microbiome. ISME J 12:634–638. https://doi.org/10.1038/ismej.2017.171

Xu G, Shao H, Zhang Y, Junna S (2018a) Nonadditive effects of biochar amendments on soil phosphorus fractions in two contrasting soils. Land Degrad Dev 29:2720–2727. https://doi.org/10.1002/ldr.3029

Xu Y, Seshadri B, Sarkar B et al (2018b) Biochar modulates heavy metal toxicity and improves microbial carbon use efficiency in soil. Sci Total Environ 621:148–159. https://doi.org/10.1016/j.scitotenv.2017.11.214

Xu M, Gao P, Yang Z et al (2019) Biochar impacts on phosphorus cycling in rice ecosystem. Chemosphere 225:311–319. https://doi.org/10.1016/j.chemosphere.2019.03.069

Yang F, Cao X, Gao B, Zhao L, Li F (2015) Short-term effects of rice straw biochar on sorption, emission, and transformation of soil NH_4^+-N. Environ Sci Pollut R 22:9184–9192. https://doi.org/10.1007/s11356-014-4067-1

Yang L, Lou J, Wang H, Wu L, Xu J (2018) Use of an improved high-throughput absolute abundance quantification method to characterize soil bacterial community and dynamics. Sci Total Environ 633:360–371. https://doi.org/10.1016/j.scitotenv.2018.03.201

Yang Q, Ravnskov S, Andersen MN (2020) Nutrient uptake and growth of potato: Arbuscular mycorrhiza symbiosis interacts with quality and quantity of amended biochars. J Soil Sci Plant Nut 183:220–232. https://doi.org/10.1002/jpln.201900205

Yang L, Wu Y, Wang Y, An W, Jin J, Sun K, Wang X (2021) Effects of biochar addition on the abundance, speciation, availability, and leaching loss of soil phosphorus. Sci Total Environ 758:143657. https://doi.org/10.1016/j.scitotenv.2020.143657

Yao Q, Liu J, Yu Z, Li Y, Jin J, Liu X, Wang G (2017) Three years of biochar amendment alters soil physiochemical properties and fungal community composition in a black soil of northeast China. Soil Biol Biochem 110:56–67. https://doi.org/10.1016/j.soilbio.2017.03.005

Ying J, Li X, Wang N, Lan Z, He J, Bai Y (2017) Contrasting effects of nitrogen forms and soil pH on ammonia oxidizing microorganisms and their responses to long-term nitrogen fertilization in a typical steppe ecosystem. Soil Biol Biochem 107:10–18. https://doi.org/10.1016/j.soilbio.2016.12.023

Yu L, Yuan Y, Tang J, Wang Y, Zhou S (2015) Biochar as an electron shuttle for reductive dechlorination of pentachlorophenol by Geobacter sulfurreducens. Sci Rep 5:16221. https://doi.org/10.1038/srep16221

Yu L, Yu M, Lu X, Tang C, Liu X, Brookes PC, Xu J (2018a) Combined application of biochar and nitrogen fertilizer benefits nitrogen retention in the rhizosphere of soybean by increasing microbial biomass but not altering microbial community structure. Sci Total Environ 640:1221–1230. https://doi.org/10.1016/j.scitotenv.2018.06.018

Yu Z, Chen L, Pan S, Li Y, Kuzyakov Y, Xu J, Brookes PC, Luo Y (2018b) Feedstock determines biochar-induced soil priming effects by stimulating the activity of specific microorganisms. Eur J Soil Sci 69:521–534. https://doi.org/10.1111/ejss.12542

Yu M, Meng J, Yu L et al (2019) Changes in nitrogen related functional genes along soil pH, C and nutrient gradients in the charosphere. Sci Total Environ 650:626–632. https://doi.org/10.1016/j.scitotenv.2018.08.372

Yu Z, Ling L, Singh BP, Luo Y, Xu J (2020) Gain in carbon: Deciphering the abiotic and biotic mechanisms of biochar-induced negative priming effects in contrasting soils. Sci Total Environ 746:141057. https://doi.org/10.1016/j.scitotenv.2020.141057

Yu M, Liang S, Dai Z, Li Y, Luo Y, Tang C, Xu J (2021) Plant material and its biochar differ in their effects on nitrogen mineralization and nitrification in a subtropical forest soil. Sci Total Environ 763:143048. https://doi.org/10.1016/j.scitotenv.2020.143048

Yuan JH, Xu RK, Zhang H (2011) The forms of alkalis in the biochar produced from crop residues at different temperatures. Bioresour Technol 102:3488–3497. https://doi.org/10.1016/j.biortech.2010.11.018

Yuan H, Zhang Z, Li M et al (2019) Biochar's role as an electron shuttle for mediating soil N_2O emissions. Soil Biol Biochem 133:94–96. https://doi.org/10.1016/j.soilbio.2019.03.002

Zackrisson O, Nilsson MC, Wardle DA (1996) Key ecological function of charcoal from wildfire in the Boreal forest. Oikos 77:10–19. https://doi.org/10.2307/3545580

Zhang M, Cheng G, Feng H et al (2017) Effects of straw and biochar amendments on aggregate stability, soil organic carbon, and enzyme activities in the Loess Plateau, China. Environ Sci Pollut R 24:10108–10120. https://doi.org/10.1007/s11356-017-8505-8

Zhang L, Xiang Y, Jing Y, Zhang R (2019) Biochar amendment effects on the activities of soil carbon, nitrogen, and phosphorus hydrolytic enzymes: a meta-analysis. Environ Sci Pollut R 26:22990–23001. https://doi.org/10.1007/s11356-019-05604-1

Zhang L, Ma B, Tang C, Yu H, Lv X, Mazza Rodrigues JL, Dahlgren RA, Xu J (2021) Habitat heterogeneity induced by pyrogenic organic matter in wildfire-perturbed soils mediates bacterial community assembly processes. ISME J. https://doi.org/10.1038/s41396-021-00896-z

Zhou GY, Zhou XH, Zhang T et al (2017) Biochar increased soil respiration in temperate forests but had no effects in subtropical forests. Forest Ecol Manag 405:339–349. https://doi.org/10.1016/j.foreco.2017.09.038

Zhou C, Heal K, Tigabu M, Xia L, Hu H, Yin D, Ma X (2020) Biochar addition to forest plantation soil enhances phosphorus availability and soil bacterial community diversity (vol 455, 117635, 2020). Forest Ecol Manag 455:117857. https://doi.org/10.1016/j.foreco.2019.117857

Zwart DC, Kim S-H (2012) Biochar amendment increases resistance to stem lesions caused byphytophthora spp. in tree seedlings. HortScience 47:1736–1740. https://doi.org/10.21273/hortsci.47.12.1736