

Functional profiles of soil microbial communities in the alpine and temperate grasslands of China

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Abstract

Grassland ecosystems in cold regions are typical of short growing seasons and limited primary productivity, rendering soil microorganisms as major ecosystem engineers in governing biogeochemical cycling. Climate warming and extensive livestock grazing have dramatically influenced soil microbial diversity and function in grassland worldwide, but it remains elusive how functional microbial communities exist and respond to global changes. Here, we present a review to highlight similarities and differences in soil functional microbial communities between alpine grasslands in the Qinghai-Tibet Plateau and temperate grasslands in the Inner Mongolian Plateau, both of which are major plateaus in China, but differ substantially in geography. We show that many specialized functional groups thrive under harsh conditions, exhibiting a high functional diversity. Their community compositions mirror the heterogeneity and complexity of grassland soils. Moreover, functional microbial responses to environmental changes have been extremely variable, with few consistent patterns across both plateaus. Because we identify a lack of technical standardization that prevents in-depth comparative studies for functional microbial communities, we conclude the review by outlining several research gaps that need to be filled in future studies.

KEYWORDS

climate changes, functional microbial communities, grassland soils, grazing, Inner Mongolian Plateau, Qinghai-Tibet Plateau

INTRODUCTION

Microorganisms are essential for soil development, elemental cycling, plant growth and health, and the global greenhouse gas balance. Microbial activity and functions strongly rely on the temperature and precipitation, projected to be continuously altering in the incoming centuries because of anthropogenic activities (Jansson & Hofmockel, 2020). Previous research has largely focused on microbial taxonomy, owing to the convenience of performing amplicon sequencing with prokaryotic 16S ribosomal RNA (rRNA) gene, eukaryotic 18S rRNA gene, or fungal ribosomal internal transcribed spacer as taxonomic biomarkers. However, taxonomy is seldom an accurate predictor of either ecological differences or functions of microorganisms because of frequent horizontal gene

transfer and convergent evolution. It is evident now that using a function-centric approach to assess and explain the ecosystem process is becoming particularly important (Escalas et al., 2019; Peay et al., 2016; Zhou et al., 2015).

Here, we dedicate this review to the fundamental question of how changing environments affect functional microbial communities, also named microbial functional groups or functional microorganisms, in the alpine and temperate grasslands, which are the main landscape type of the Qinghai-Tibet Plateau and the Inner Mongolian Plateau, respectively. We discuss (i) the geographical, climatic, and edaphic features shaping grassland ecosystems as microbial habitats with regard to global warming and livestock grazing, (ii) current understanding of functional microbial communities in grassland soils, (iii) global change

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studies on the functional microbiome, and (iv) future perspectives.

THE GRASSLANDS IN THE QINGHAI-TIBET AND INNER MONGOLIAN PLATEAUS

The Qinghai-Tibet and Inner Mongolian Plateaus have the largest natural grasslands in China, accounting for two-thirds of the country's grasslands. There are some similarities between Qinghai-Tibet and Inner Mongolian environments, including short growing seasons for plants, extreme wind speeds, high snowfall, and well-drained soils (Table 1). As plant growth is restricted by temperature, organic contents decrease with increasing altitudes, resulting in oligotrophic, severely nutrient-limited soils (Donhauser & Frey, 2018). In addition, coarse-textured, shallow soils typical in the Qinghai-Tibet and Inner Mongolian Plateaus, together with limited plant coverage and low water retention capacities, expose soil ecosystems to cope with environmental stressors such as high ultraviolet (UV) radiation and daily temperature and moisture fluctuations (Cicczazzo et al., 2014). However, geography

varies substantially in these two plateaus. The Qinghai-Tibet Plateau encompasses most of the Earth's highlands above 4 km a.s.l., whose annual average air temperature is low (Table 1). In contrast, the Inner Mongolian Plateau is characterized by a temperate continental climate, with a decreasing precipitation gradient from east to west.

Both plateaus have experienced climate warming considerably (Q. Hu et al., 2015), promoting plant growth (Z. Zhu, Piao, et al., 2016). This could turn the alpine and temperate grasslands into carbon sinks with warming, consistent with the projection of a comprehensive global study (Crowther et al., 2016) and field observations of carbon stocks in alpine grassland soils between 2002 and 2011 (L. Chen et al., 2017). For nitrogen cycling, warming has caused higher net nitrogen mineralization globally, increasing soil inorganic nitrogen pools (Bai et al., 2013). The increase of total soil nitrogen by warming has been attributed to the increased primary production in oligotrophic environments, summarized in chronosequence studies (Donhauser & Frey, 2018).

The Inner Mongolian Plateau, as a water-limited ecosystem, has witnessed increasing events of heavy precipitation, projected to increase annual precipitation

TABLE 1 Important environmental attributes in the alpine grasslands of the Qinghai-Tibet Plateau and temperate grasslands in the Inner Mongolian Plateau

Environmental attributes	Qinghai-Tibet	Inner Mongolia
Average annual air temperature	−5 to 12°C	0–8°C
Average air temperature in the growing season	5–23°C	10–25°C
Growing season	May–September	May–September
Winter	December–February	December–February
Average annual precipitation	100–800 mm	100–500 mm
Average precipitation in the growing season	100–500 mm	50–400 mm
Soil moisture (V/V) (Shi et al., 2012)	20.95%*	7.29%
Soil bulk density (Shi et al., 2012)	0.95 g cm ^{−3} *	1.3 g cm ^{−3}
Ecosystem C stability (D. Liu et al., 2018)	Relatively stable upon warming	Carbon loss induced by warming
Plant root: shoot ratio (g g ^{−1}) (L. Wang et al., 2010)	0.65**	0.84
Plant leaf C (mg g ^{−1}) (Fan et al., 2016)	460.83 ^{ns}	464.86
Plant leaf N (mg g ^{−1}) (Fan et al., 2016)	17.02***	21.04
Plant leaf P (mg g ^{−1}) (Fan et al., 2016)	1.11***	1.45
Plant leaf C/N (Fan et al., 2016)	33.93***	24.19
Plant leaf N/P (Fan et al., 2016)	17.90*	16.10
Plant leaf C/P (Fan et al., 2016)	611.75***	375.28
Plant root N use efficiency (Fu et al., 2019)	108 g g ^{−1} ***	82 g g ^{−1}
Topsoil organic C content (g g ^{−1}) (Shi et al., 2012)	5.24%*	1.61%
Topsoil inorganic C content (g g ^{−1}) (Shi et al., 2012)	0.51%*	0.21%
Topsoil total N content (g g ^{−1}) (Shi et al., 2012)	0.44%	0.17%
Soil pH (Shi et al., 2012)	6.8 ^{ns}	6.9

Abbreviations: C, carbon; N, nitrogen; ns, not significant; P, phosphorus.

* $p < 0.050$, ** $p < 0.010$, *** $p < 0.001$.

intensities (Nielsen & Ball, 2015). Soil CO₂ fluxes typically increase after precipitation pulses quickly, but return to prewetting levels within 2 days or a week (S. Chen et al., 2009). A temperate semiarid steppe of Inner Mongolia was found to be a sink of CH₄ and a source of N₂O during the growing season, whose soil CH₄ uptake was decreased and N₂O emission was increased by overgrazing (W. Chen et al., 2013). Increased precipitation and nitrogen significantly stimulated ecosystem CO₂ emission by 47%–70% and N₂O emission by 65%–94%, but did not change CH₄ uptake.

Owing to excessive grazing, grasslands are among the most degraded ecosystems worldwide, with widespread soil erosion, plant diversity loss, plant productivity loss, large soil carbon loss, and ecosystem service decline (Faghihinia et al., 2020). It is estimated that between 20% (light degradation) and 65% (extreme degradation) of soil organic carbon stocks have been lost, adding up to a total loss of 0.6 Pg carbon (S. Liu et al., 2018). This huge amount of carbon loss stresses the need for timely grassland preservation efforts. As the season/annual CH₄ budgets increased with grazing intensity and the offset of CH₄ uptake by grassland soils to CH₄ emissions from sheep, sheepfolds, and feces were exponentially decreased with grazing intensity, overgrazing has shifted Chinese grasslands from a sink to a source for atmospheric CH₄ (Tang et al., 2019). Meanwhile, land uses in Inner Mongolia have also been intensified in the late half 20th century by converting grasslands to irrigated or rain-fed croplands and by overgrazing. As a result, soil desertification in Inner Mongolia was estimated to be 376 000 km² in 2010 (Hoffmann et al., 2016). The N₂O emissions increased strongly during the freezing–thawing cycles in early spring (Wolf et al., 2010), accounting for 9%–81% of annual total emissions and essential for microbial nitrogen turnover. However, grazing significantly decreased annual N₂O emissions from the semi-arid steppes (Wolf et al., 2010).

FUNCTIONAL MICROBIAL COMMUNITIES IN A CHANGING WORLD

Coldness, dry climates, and soil degradation constrain microbial life. In response, microorganisms have developed adaptive mechanisms, such as biofilm formation, to cope with harsh conditions (De Maayer et al., 2014). Delving deeper into how soil microorganisms respond to warming, livestock grazing, and restoration of degraded grasslands is critical for developing sustainable practices to maintain soil health and promote productivity (Trivedi et al., 2016). However, a vast majority of alpine and temperate grasslands are located in remote regions, imposing challenges in soil sampling and transport for microbial analyses. Despite the scarcity of scientific studies, researchers have made great efforts to analyze specific functional groups linked to ecosystem functions. For example, *nifH* gene has been used to analyze nitrogen fixers, *amoA* gene has

been used to analyze ammonia oxidizers, and *mcrA* gene has been used to analyze methanogens. Metagenomics by shotgun sequencing and functional gene arrays (e.g., GeoChip) are also powerful, enabling simultaneous detection of a large array of functional microbial communities (Tu et al., 2014; Yang, Gao, et al., 2013; Yue et al., 2015). Alternatively, 16S rRNA gene amplicon sequencing is particularly useful to reveal narrow functional groups (i.e., a function performed by a limited number of taxa), such as ammonia oxidizers and methanogens.

Despite harsh environmental conditions, recent studies have shown that soils in the alpine and temperate grasslands harbor a high microbial diversity (X. Ma et al., 2017; X. Ma et al., 2019; Suyal et al., 2021; Yang et al., 2014). For example, soil bacterial communities inhabiting high altitudes are among the most multifaceted and diverse assemblies of microorganisms (Suyal et al., 2021). Functional α -diversity, β -diversity, and gene abundance were shown to vary by site. Soil pH, temperature, moisture, NH₄⁺, NO₃[−], plant diversity, and plant coverage accounted for 83.1% of functional microbial community variations along the altitudinal gradient of an alpine meadow (Yang et al., 2014), showing much higher explanatory power than those commonly observed elsewhere. This suggests that functional community composition is highly sensitive to soil and vegetation conditions. The mutual influence between soil microorganisms and plants is pronounced in alpine ecosystems, which might be stressed by climatic restriction and nutrient paucity (Ciccazzo et al., 2014). Likewise, soil depth and seasonal variation could affect functional microbial communities considerably (Y. Yuan et al., 2015).

Overall microbial functional α -diversity, measured by Shannon or Simpson index, in the alpine grasslands was significantly reduced by warming (Yue et al., 2015). As warming in cold regions ameliorates stressful environmental conditions and thereby makes it more similar to environments at lower altitudes, the diversity of microbial niches would be reduced. Consequently, warming could lead to a considerable loss of microbial α -diversity, in tandem with lower plant α -diversity in cold environments with warming. Although functional redundancy, buffering ecosystem functioning against species loss (Allison & Martiny, 2008), has been widely observed (Louca et al., 2016; Talbot et al., 2014), the observation of concurrent reduction of both microbial taxonomic and functional α -diversities (Yue et al., 2015) implies that functional redundancy might be minor in cold environments. In contrast, microbial functional α -diversity was reduced when plant α -diversity decreased in a long-term experiment conducted in a semiarid temperate steppe located in Xilingol River Basin, Inner Mongolia, while microbial taxonomic α -diversity remained unchanged (X. Zhang, Johnston, Barberan, et al., 2017). The main reason was attributed to lower plant productivity caused by the loss of plant α -diversity, since lower plant productivity reduced fresh, labile carbon supply for soil microorganisms. The selection pressure from nutrient limitation would favor microbial functional groups

closely involved in energy production at the expense of other functional groups.

In a typical steppe of Inner Mongolia, experimental warming, increased precipitation, and their combination had higher functional α -diversity than their controls, reflecting more complex communities (X. Zhang, Johnston, Li, et al., 2017). Although very light grazing imposed no effect on the microbial taxonomic compositions, it changed the overall microbial functional compositions without affecting functional α -diversity (X. Ma et al., 2019). These results demonstrated that the shifts in community functional gene profiles by grazing were more readily detectable than the shifts in microbial taxonomy. Grazing increased functional α -diversity at some sites, but decreased it at other sites of Temperate grasslands. Grazing also reduced microbial functional α -diversity in the alpine grasslands, imposing similar compositional changes in functional microbial communities despite geographic differences (Chu et al., 2014; Yang, Wu, et al., 2013). Despite exceptions, a general conclusion based on current results is that functional microbial communities are highly variable between the alpine and temperate grasslands. A comparison of representative data is shown in Table 2 and presented in detail below.

Nitrogen cycle-related microorganisms

The *amoA* gene encoding ammonia monooxygenase subunit A is the biomarker gene of nitrification, as ammonia monooxygenase catalyzes the oxidation of ammonium into nitrite and then nitrate in a subsequent reaction. The relative abundance of *amoA* gene was decreased with increasing altitudes in the Qinghai-Tibet Plateau (Yang et al., 2014), consistent with lower amounts of soil ammonium. Conversely, the relative abundances of functional genes associated with denitrification, which reduces nitrate into nitrite, nitrous oxide and dinitrogen, were increased with altitudes, concomitant with the increase of soil nitrate contents. When *amoA* was assigned to archaeal and bacterial domains, relative abundances of archaeal *amoA* decreased at higher altitudes in the topsoil, but were unchanged in deeper soils along a transect between 4400 m and 5200 m a.s.l. in the Qinghai-Tibet Plateau (Y. Yuan et al., 2015). In contrast, bacterial *amoA* increased with altitudes across all soil depths. Precipitation and soil pH were major environmental factors that explain patterns of *amoA* abundance and community composition, highlighting the importance of soil geochemical properties in shaping microbial functional guilds.

TABLE 2 Responses of functional microbial communities to experimental disturbance

Experimental treatments	Functional microorganisms	Qinghai-Tibet	Inner Mongolia
Warming	Functional α -diversity	Decreased	Increased
	<i>nirK/S</i>	Unchanged	Decreased
	<i>norBC</i>	N/A	Decreased
	<i>nosZ</i>	Unchanged	Decreased
	<i>narG</i>	N/A	Increased
	<i>pcc</i>	Increased	N/A
	<i>xylA</i>	Increased	N/A
Grazing	Functional α -diversity	Decreased	Increased, decreased, or unchanged
	AOA	Increased	Increased
	AOB	Increased	Increased
	<i>nifH</i>	N/A	Increased
	<i>nirK/S</i>	Decreased	N/A
	<i>amyA</i>	Decreased	Increased or decreased
Nutrient amendment	AOA	Decreased	Decreased
	AOB	Increased	Increased
	<i>nirK/S</i>	Unchanged	Increased
	<i>nosZ</i>	N/A	Increased
	<i>narG</i>	Unchanged	Increased
	<i>mcrA</i>	Decreased	N/A
	AMF	Decreased	Decreased

Abbreviation: N/A, not available.

The majority of nitrogen cycling genes in an alpine grassland were decreased or unchanged in relative abundances by experimental warming, except *narG* encoding nitrate reductase and *ureC* encoding urease (Yue et al., 2015). The increase of *ureC* with a concurrent decrease of *gdh* could accelerate nitrogen mineralization from organic matter, concomitant with a substantial increase of total organic carbon content, total nitrogen content, ammonia, and vegetation biomass upon warming. A closer examination showed that the relative abundance of the bacterial *amoA* gene increased upon warming (Zheng, Yang, et al., 2014), while that of the archaeal *amoA* gene was less affected. In contrast, the relative abundance of denitrification genes *nirK* encoding nitrite reductase K, *nosZ* encoding nitrous oxide reductase Z, and *nirS* encoding nitrite reductase S were unaffected. Collectively, those results suggest the enhanced nitrification but no changes in denitrification upon warming in the alpine grassland.

In a typical steppe in Inner Mongolia, functional genes involved in the uptake and biosynthesis of nitrogen were increased in relative abundances by simulated warming, while the relative abundances of denitrification genes, such as *nirK/S*, *norBC*, and *nosZ*, were decreased (X. Zhang, Johnston, Li, et al., 2017). In addition, a field experiment focusing on soil erosion and sand deposition prevalent in temperate grasslands showed that almost all functional genes associated with nitrogen cycling decreased or remained unaltered at both eroded and deposited sites, which held true across bacteria, archaea, and fungi (X. Ma et al., 2017). Specifically, nitrification genes (*amoA* and *hao*) decreased at the eroded site, and the ammonification gene (*ureC*) decreased at the deposited site. The decrease of nitrogen cycling genes implicated the possible limitation of available nitrogen at eroded and deposited sites. In contrast, nitrogen amendment stimulated relative abundances of most nitrogen-cycling genes, including *narG*, *nirK*, *nirS*, and *nosZ*, in a temperate meadow steppe (Xiao et al., 2021).

Livestock grazing induced a soil microbiome closely linked to soil organic carbon-to-nitrogen ratio and $\text{NH}_4^+\text{-N}$ in an alpine grassland (Yang, Wu, et al., 2013). Since urine deposition by livestock provides a unique nitrogen source to grazed sites, the relative abundance of *gdh* encoding glutamate dehydrogenase was decreased while that of *ureC* encoding urease was increased, shifting the balance of urea metabolism toward urea ammonification and hence increasing nitrogen mineralization potential. The *amoA* genes derived from ammonia-oxidizing bacteria (AOB) and ammonia-oxidizing archaea (AOA) were increased, whose relative abundances were positively correlated with N_2O emission. In contrast, relative abundances of denitrification and dissimilatory and assimilatory nitrogen reduction genes were decreased by grazing. Among them, relative abundances of denitrification genes *nirS*, *nirK*, and *nosZ* were negatively correlated with N_2O emission. Therefore, N_2O emission was mainly attributed to nitrification instead of denitrification. In contrast, nitrogen amendment did not significantly change the relative abundances of

nitrogen-cycling genes, such as *hao*, *narG*, *napA*, *nirS*, and *nirK*, in an alpine steppe (Y. Hu et al., 2021).

In a typical steppe located in Duolun, Inner Mongolia, the relative abundance and composition of *nifH* encoding nitrogenase reductase, the biomarker gene of nitrogen fixation, were changed by light grazing (X. Ma et al., 2019). In addition, the community compositions of both *amoA*-AOA and *amoA*-AOB genes were affected. The total abundance of *Nitrospira*, a major genus of AOA, was increased by grazing. Grazing and nitrogen amendment affected both AOA and AOB, while phosphorus amendment only affected AOB abundance (Y.-L. Chen, Hu, et al., 2014). Long-term nitrogen amendment affected the community compositions of AOB and denitrifiers represented by *nosZ* gene, while increased precipitation only affected the community composition of AOA (C.-J. Zhang et al., 2018). Similarly, nitrogen amendment affected AOA and AOB abundances differentially, decreasing AOA but increasing AOB in an alpine steppe (Y. Hu et al., 2021). In contrast, grazing imposed little effect on the community composition of nitrogen-cycling genes in the temperate steppe (C.-J. Zhang et al., 2018). By systematically analyzing various treatments of long-term nitrogen amendment, phosphorus amendment, warming, wetting, plant biodiversity loss, grazing, and their combinations, AOB was found to be the most responsive to various experimental treatments (X. Zhang et al., 2013). In addition, all microbial functional groups associated with nitrogen cycling (i.e., nitrogen fixation, mineralization, nitrification, and denitrification) were affected by nitrogen amendment.

Carbon fixation and degradation-related microorganisms

Several studies detected more phototrophs with increasing altitudes in the Qinghai-Tibet Plateau (Donhauser & Frey, 2018; Janatková et al., 2013). In accordance, the relative abundances of carbon-fixing Rubisco gene encoding a ribulose-1,5-bisphosphate carboxylase/oxygenase and several genes associated with labile carbon degradation increased with higher altitudes in the Qinghai-Tibet Plateau (Yang et al., 2014), suggesting that autotrophic CO_2 fixation by microorganisms has an essential role in carbon cycling of alpine environments limited in plant photosynthesis. Also, Rubisco enzyme activity and relative abundance of *cbbL* gene encoding ribulose bisphosphate carboxylase large chain increased with higher altitudes (Guo et al., 2015). The *cbbL* community composition varied by altitudes, which are mostly autotrophs belonging to Actinomycetales, Rhizobiales, and Burkholderiales.

In a simulated warming experiment conducted in an alpine meadow, relative abundances of functional genes associated with recalcitrant carbon degradation, for example, genes encoding exochitinase and endochitinase, were decreased by warming, while that of carbon fixation gene *pcc* encoding a propionyl-CoA carboxylase was increased (Yue et al., 2015). Therefore, the alpine meadows harbor a feedback mechanism to stabilize soil

carbon pool upon warming, owing to reduced degradation of organic matter and elevated CO₂ uptake from the atmosphere. This was supported by in situ measurements of carbon stocks in the alpine grasslands (Yue et al., 2015). When soils from an alpine meadow were incubated in microcosms, microbial communities were examined in a 10°C–40°C temperature gradient (J. Wu et al., 2015). Shifts in bacterial community compositions occurred in a gradual manner over time, concomitant with changes in carbon-utilization patterns using Eco-plate. Changes in bacterial communities and carbon-utilization patterns were pronounced after 28 days. As global warming is occurring on a century-scale, current warming studies have suggested that functional microbial communities in the alpine grasslands might react significantly to global warming.

The relative abundance and α -diversity of genes associated with labile carbon decomposition were decreased in a simulated cooling experiment in the Qinghai-Tibet Plateau (L. Wu et al., 2017). These genes included *apu*, *cda*, and *glucoamylase* genes for starch decomposition, *xylA* and *mannanase* genes for hemicellulose decomposition, and *pectinase* genes for pectin decomposition. In contrast, functional genes responsible for the decomposition of recalcitrant carbon (e.g., lignin and aromatics), accounting for about 95% of topsoil organic carbon in the alpine grasslands (G. Wang et al., 2002), were unchanged in relative abundances (L. Wu et al., 2017). Therefore, degradation of recalcitrant carbon by functional microbial communities persisted under climate cooling scenarios, resulting in soil carbon loss.

In sharp contrast to observations in the alpine grasslands, warming, increased precipitation, and their combination increased the relative abundances of functional genes associated with the degradation of recalcitrant substrates in a typical steppe of the Inner Mongolian Plateau (X. Zhang, Johnston, Li, et al., 2017). Plant growth and labile soil organic matter content were also increased by those experimental treatments, offsetting the substantial loss of soil organic matter induced by microbial functional groups.

The abundances of most carbon fixation and degradation genes were either reduced or unchanged by grazing in an alpine meadow (Yang, Wu, et al., 2013), suggesting that the soil carbon cycling potential was inhibited. CO₂ emission was decreased but soil total organic carbon was increased, likely due to changes in microbial functional potentials. A multitude of genes was sensitive to grazing since they became undetectable at the grazed sites compared to the control sites, including *amyA* genes derived from *Psychromonas ingrahamii* (37), *Cellvibrio japonicus* (Ueda107), *Thermoanaerobacter mathranii* subsp. *mathranii* (str. A3), *Vibrio orientalis* (CIP102891), and *Erythrobacter litoralis* (HTCC2594). In contrast, very light grazing in a temperate grassland changed the relative abundances of *amyA* encoding α -amylase associated with starch degradation, chitinase, and acetylglucosaminidase genes associated with chitin degradation and cellobiose gene associated with cellulose degradation (X. Ma et al., 2019).

Most of the microbial functional genes associated with carbon fixation were decreased or remained unchanged in relative abundances at eroded and deposited sites in a typical steppe of the Inner Mongolian Plateau (X. Ma et al., 2017). In particular, there were decreases in genes associated with dicarboxylate/4-hydroxybutyrate and reductive tricarboxylic acid cycles, including 4-hydroxybutyryl-CoA dehydratase gene and *frdA*. Similarly, most of the carbon degradation genes were decreased or remained unchanged by soil erosion and deposition, consistent with a decrease in soil respiration at the field sites. Decreased genes included those associated with labile carbon degradation (e.g., *apu*, *cda*, glucoamylase, isopullulanase, *pulA*, pectate-lyase, pectinase, *pme*, *rgh*, and *rgl*) and recalcitrant carbon degradation (e.g., *camDCBA*, endochitinase, and cutinase). There was a striking exception in *amyA*, which was specifically increased at the deposited sites. The relative abundances of *amyA* genes were positively correlated to dissolved organic carbon, which likely explained the increase of dissolved organic carbon at those sites.

Methane cycle-related microorganisms

The *mcrA* gene encodes an enzyme that is considered a diagnostic indicator of methanogenesis (Luton et al., 2002), while *pmoA* and *mmoX* encode for the two methane monooxygenases indicative of methanotrophs. The relative abundance of methanotrophic gene *pmoA* encoding particulate methane monooxygenase subunit A and the potential CH₄ oxidation increased upon warming in an alpine meadow, with the relative abundance of *pmoA* was negatively correlated with moisture and ammonium content (Zheng et al., 2012). Those results suggest that enhanced methane oxidation could offset the warming-induced increase in CH₄ emission. However, warming did not affect methanotrophic community compositions. When alpine grasslands were subjected to livestock grazing, relative abundances of *mcrA* and *mmoX* were decreased, while that of *pmoA* remained unchanged (Yang, Wu, et al., 2013). A number of *mcrA* genes, mainly derived from uncultured methanogenic archaea, appeared to be sensitive to grazing as they were reduced at grazed sites (Qi et al., 2017; Yang, Wu, et al., 2013). Nitrogen amendment decreased the relative abundance of *mcrA*, but did not affect that of *pmoA* in an alpine steppe (Y. Hu et al., 2021).

The temperate grassland is a CH₄ sink (Geng et al., 2010). Consistently, methanotrophs are highly abundant in the temperate grasslands, with 10⁷–10⁸ *pmoA* gene copies per gram of soil and USC- γ as the main methanotrophic cluster (T. Ma et al., 2015). Methanotrophic abundance increased with lower soil moisture content, which facilitates more CH₄ and O₂ diffusion into soil amenable for the proliferation of methanotrophs. Conversely, methanogen abundance increased with higher soil moisture content.

Antibiotic resistome

A variety of antibiotics are applied in livestock husbandry to treat animal diseases or as a prevention measure. Long-term animal excretion application would introduce antibiotic-resistant genes that confer resistance to different antibiotics, collectively called antibiotics resistome, into the soils. In accordance, a field experiment in the alpine meadow showed that antibiotic-resistant genes were more abundant at the grazed site (Yang, Wu, et al., 2013). The most increased genes by grazing were *van* conferring resistance to vancomycin, *tet* conferring resistance to tetracycline and *B lactamase* conferring resistance to β -lactam antibiotics. Those genes were derived from a variety of bacterial phyla such as Actinobacteria, Firmicutes, Verrucomicrobia, and Proteobacteria. Similarly, virulence genes, many of which were derived from Clostridia prevalent in the animal gut, were more abundant at the grazed site.

The desert and typical grasslands of the Inner Mongolian Plateau are important reservoirs of antibiotic resistome (Burke et al., 2011). In sharp contrast with observations in the alpine meadow, the number of detected antibiotic-resistant genes decreased with increasing grazing intensity in the desert steppe, and relative abundances of antibiotic-resistant genes in grazed sites were lower than those in ungrazed sites. No significant changes in the numbers and relative abundances of antibiotic-resistant genes were detected between grazed and ungrazed sites in the typical steppe. It is likely that the selective pressure exerted by antibiotic residue from animal excreta is not strong enough to induce the soil resistome in those sites.

Arbuscular mycorrhizal fungi (AMF)

AMF are symbiotic root-associated soil biota, which plays a key role in maintaining plant productivity, sustaining above- and below-ground biodiversity, and improving soil attributes vital for plant growth (Faghihinia et al., 2020). Obligate AMF relies on their host plants for photosynthetic carbon. In return, they provide a wide range of *beneficial* services for their hosts (Powell & Rillig, 2018). Grazing-caused defoliation reduces plant's photosynthetic capacity and below-ground carbon allocation, resulting in a reduction of the AMF abundance (Gehring & Whitham, 2002). Similarly, loss of plant diversity reduces root types and root exudates, consequently decreasing the resource variability for AMF (Ba et al., 2012). However, AMF species are different. Some species are better at defending the hosts against plant pathogens, whereas others are better at improving plant growth through nutrient uptake (Faghihinia et al., 2020). Plant-AMF associations that respond positively to grazing would be favored.

The α -diversity of AMF decreased at higher altitudes (4149–5033 m a.s.l.) in the Qinghai-Tibet Plateau, China (L. Liu et al., 2015). The reason is that dark septate endophytes (i.e., fungal symbionts colonizing plant roots in high elevations (Urcelay et al., 2011) can replace

AMF at extreme elevations above 4000 m a.s.l. to help plants acquire nutrients and act as surrogate mycorrhizae (Kotlínek et al., 2017). The cell walls of dark septate endophytes are rich in melanin, which slows carbon decomposition and thus improves soil carbon stability at high elevations.

In a typical grassland in Duolun, Inner Mongolia, nitrogen amendment decreased AMF extraradical hyphal density and altered AMF community composition (Kim et al., 2015). Similar effects of nitrogen amendment were observed in an alpine meadow (Zheng, Kim, et al., 2014). High nitrogen amendment reduced AMF colonization and biomass, resulting from acidification induced by nitrogen inputs. In contrast, phosphorus amendment reduced mycorrhizal colonization rate, arbuscular colonization, and hyphal length density, affecting AMF abundance (Y.-L. Chen, Zhang, et al., 2014). Driven by a stronger influence from stochastic processes, increased precipitation reduced AMF α -diversity and increased β -diversity (Gao et al., 2016), which overrode the warming effects that increased AMF α -diversity and spore density (Kim et al., 2015). Increased precipitation also showed stronger effects on AMF communities than nitrogen amendment (Li et al., 2015).

FUTURE DIRECTIONS

Functional microbial communities play a pivotal role in regulating the biogeochemical processes of grassland ecosystems. Warming accelerates carbon and nitrogen cycling, causing net nutrient losses in many cold regions (Dawes et al., 2017; Feng et al., 2020; Tao et al., 2020). However, the alpine grassland soils possess a feedback mechanism counteracting the mineralization of organic matters upon warming, ultimately keeping carbon and nitrogen stocks stable. Such contrasting results may arise from various co-occurring changes in vegetation types, soil properties, soil nutrient status and quality, and biotic interactions. Since warming increases microbial activity in cold regions, microorganisms are likely to facilitate plant expansion to higher altitudes and latitudes, stimulating primary productivity and biogeochemical cycling.

Current research on functional microbial communities is extremely scarce in the alpine and temperate grasslands, making it unlikely to draw reliable conclusions about regional-scale ecological patterns and biogeochemical cycles. Considering high heterogeneity in topography, climate, soil, and vegetation, it is important to generate large data sets with a fine spatiotemporal resolution to make alpine and temperate grasslands comparable. This kind of comprehensive interdisciplinary study will allow us to identify the key drivers of functional microbial communities by disentangling the covarying variables. Standardized experimental or bio-informatics technologies will be vital in achieving this goal. For example, the application of shotgun DNA sequencing, GeoChip, and metatranscriptomics technologies could identify functional microorganisms important for ecosystem processes, establishing the links

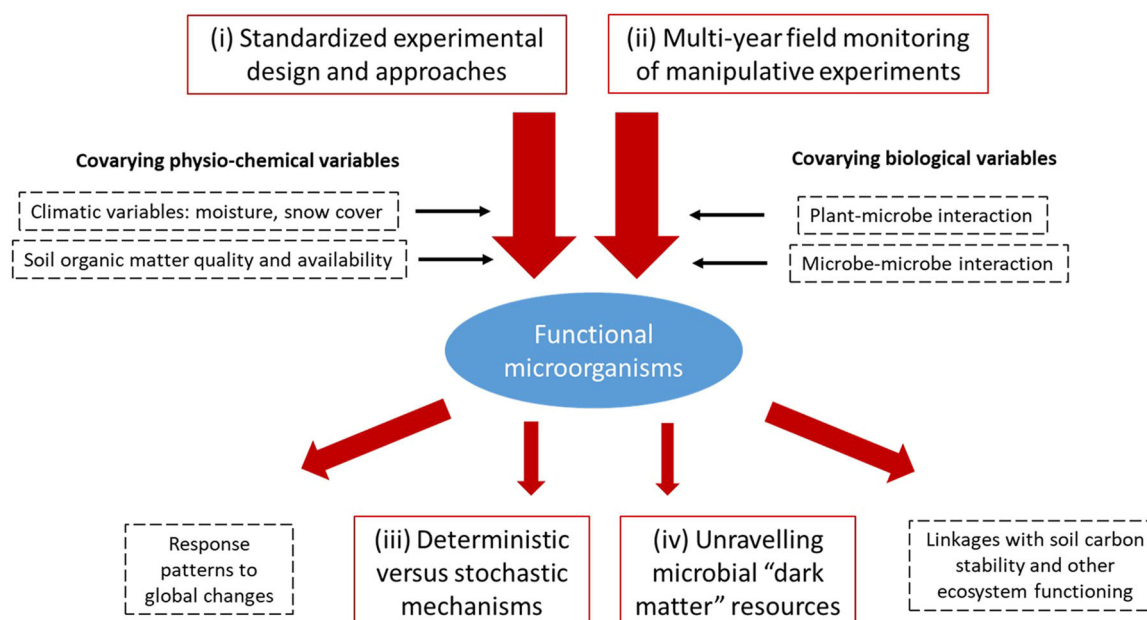


FIGURE 1 Future research needs for functional microbial communities of grassland soils. Four research needs are indicated in red boxes.

between biogeochemical cycling and microbial functional capacities (Zhao et al., 2014). Recently, the rapid development of computational algorithms to analyze cooccurrence patterns has facilitated the investigation of ecological relationships among microbial members within a community, yielding a more mechanistic understanding of microbial interactions (Yang et al., 2009; M. M. Yuan et al., 2021).

We recommend several key topics for future research on functional microbial communities (Figure 1). First, our review solely relies on existing results in the literature, so it is neither comprehensive nor comparable across different data sets. Standardize experimental design, sampling, and sequencing techniques are highly desired, which allow for quantitative analyses and comparison of multiple data sets (Zhou et al., 2015). Second, the impact of interannual changes on ecosystems is often higher than those of global changes, such as warming and nutrient amendment (K. Zhu, Chiariello, et al., 2016). Therefore, it is necessary to offset interannual changes through multi-year, continuous field experiments. Although it has become a prevalent practice in plant ecology, it remains rare in soil microbiology. Third, intensive efforts are needed to identify and quantify abiotic and biotic drivers underlying the turnover in microbial functional diversity, composition, and specific functional groups. This effort would help elucidate how functional microbial communities affect ecosystem processes and how environmental changes play a role in between. In general, arid grasslands are limited in soil moisture, while alpine grasslands are more limited in temperature. Finally, high functional diversity in cold environments is a potential resource for biotechnological purposes that need to be tapped. Psychrophilic microorganisms or cold-adapted enzymes require low thermal energy but have similar performance to mesophilic enzymes in catalyzing biochemical reactions. Efforts have been

made to isolate psychrophilic methanogens from RuorGai wetlands in the Qinghai-Tibet Plateau, aiming to uncover environmentally friendly, energy-saving solutions for biogas production. As the world faces a shortage of new antibiotics, researchers have looked into the Qinghai-Tibet and Inner Mongolian Plateaus as important reservoirs of substances with potential pharmaceutical applications. The Qinghai-Tibet and Inner Mongolian Plateaus are also typical of high levels of UV radiation, it is thus valuable to investigate the protective mechanisms of microorganisms, with biomolecule applications to protect human skin from UV damage or be used for future interstellar travel (Karsten & Holzinger, 2014).

In summary, recognition of the importance of functional microbial communities in the alpine and temperate grasslands has just emerged. Currently, our knowledge remains severely limited. It is thus important to initiate large-scale sampling campaigns and develop novel tools to achieve a comprehensive understanding of microbial ecology in those regions. There have been several plateau-wide soil sampling efforts in the past decades, such as the Matter Fluxes of Grasslands in Inner Mongolia as Affected by Grazing Project, the Second Tibetan Plateau Scientific Expedition and Research Program, and the Strategic Priority Research Program of the Chinese Academy of Sciences in Soil Microbiology. Therefore, we are optimistic that large data sets related to functional microbial communities will be publicly available in the near future, which could be helpful for effective socioeconomic decision-making on sustainable and productive use of China's grassland ecosystems.

AUTHOR CONTRIBUTIONS

Yunfeng Yang: Conceptualization; funding acquisition; writing—original draft. **Jizhong Zhou:** Writing—review and editing. **Xue Guo:** Writing—review and editing.

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no data sets were generated or analyzed during the current study.

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