

Rhizosphere Bacteria Exhibit Narrower Environmental Adaptation in Proso Millet Than in Foxtail Millet and Sorghum in Agricultural Fields

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Abstract

It is of great ecological significance to understand how the assembly processes of soil microbe communities respond to environmental change. However, the assembly processes of the rhizosphere bacterial communities in three minor grain crops (i.e., foxtail millet, proso millet, and sorghum) across agro-ecosystems are rarely investigated. Here, we investigated the environmental thresholds and phylogenetic signals for ecological preferences of rhizosphere bacterial communities of three minor grain crop taxa across complex environmental gradients to reflect their environmental adaptation. Additionally, we reported environmental factors affecting their community assembly processes based on a large-scale soil survey in agricultural fields across northern China using high-throughput sequencing. The results demonstrated a narrower range of environmental thresholds and weaker phylogenetic signals for the ecological traits of rhizosphere bacteria in proso millet than in foxtail millet and sorghum fields, while proso millet rhizosphere community was the most phylogenetically clustered. The null model analysis indicated that homogeneous selection belonging to deterministic processes governed the sorghum rhizosphere community, whereas dispersal limitation belonging to stochastic processes was the critical assembly process in the foxtail and proso millet. Mean annual temperature was the decisive factor for adjusting the balance between stochasticity and determinism of the foxtail millet, proso millet, and sorghum rhizosphere communities. A higher temperature resulted in stochasticity in the proso millet and sorghum communities. For the foxtail millet community, the deterministic assembly increased with an increase in temperature. These results contribute to the understanding of root-associated bacterial community assembly processes in agro-ecosystems on a large scale.

1 Introduction

Rhizosphere provides a habitat for various microorganisms in agricultural ecosystems, and complex plant-microbe interactions play a vital role in disease inhibition, decomposition rates of organic materials, and resistance to abiotic stress (Cheng, 2009; Bulgarelli et al., 2013; Reinhold-Hurek et al., 2015). The biogeographic distribution of soil bacteria has been extensively explored in natural and agricultural ecosystems (Carlson et al., 2012; Fierer and Jackson, 2006; Gumière et al., 2016; Xue et al., 2021). The rhizosphere is a biological hotspot whose biogeographic patterns, community composition, and structure are different from those of bulk soil (Zhang et al., 2018). However, only a few studies have investigated the biogeographic patterns of rhizosphere-associated bacterial communities (Fan et al., 2017).

It is common knowledge that environmental filtering, as a critical determinant of species distribution patterns and abundance, inevitably leads to a reduction in trait value range and an increase in niche overlap (Yi et al., 2019). Archaeal taxa between crops in different habitats demonstrate diverse responses to environmental changes (Jiao et al., 2019). However, the response thresholds of rhizosphere-associated bacterial communities to environmental changes have not been reported in agricultural fields.

Environmental thresholds of species represent the change in taxon distribution along the spatial or temporal environmental gradient (Baker and King, 2010). Environmental thresholds of fungi in maize and rice soils across eastern China have been estimated using the accumulated values of change points for

all the species in a given community (Zhang et al., 2021). Available environmental thresholds rarely reflect the occurrence, richness, and directionality of species-level responses, and very few studies have focused on large-scale standardized datasets of natural locations (van der Linde et al., 2018). However, the environmental thresholds for rhizosphere-associated bacteria at the species level must be identified in agricultural fields, thereby assisting calculation of the responses of different crop genotypes to environmental change. Whether foxtail millet (*Setaria italica* L.), proso millet (*Panicum miliaceum* L.), and sorghum (*Sorghum bicolor* L.) appear to have analogous thresholds for rhizosphere-associated bacterial community changes across environmental gradients is poorly understood.

Biogeography is the subject of biological distribution patterns over temporal and spatial scales (Hanson et al., 2012). Disentangling the fundamental mechanisms and ecological processes governing the diversity and assembly of microbial communities is a critical goal in microbial ecology (Nemergut et al., 2013; Zhou and Ning, 2017), which would help to better predict the response of the ecosystem to environmental change. Several studies have confirmed the biogeographic patterns of microbial communities in a wide range of habitats (Nuccio et al., 2016; Wang et al., 2017; Chen et al., 2019) at regional (Griffiths et al., 2011; Fan et al., 2017; Jiao et al., 2020), continental (Fierer and Jackson, 2006; Lauber et al., 2009) and global scales (Tedersoo et al., 2012; Delgado-Baquerizo et al., 2018). Currently, the debate on the relative quantitative contribution of deterministic (e.g., homogeneous selection) and stochastic (e.g., dispersal limitation) processes to microbial community assembly is topical (Jiao and Lu, 2019; Aguilar and Sommaruga, 2020). Deterministic processes are mainly based on the concept of the ecological niche and emphasize the major role of environmental selection imposed by adversity factors in microbial community assembly (Stegen et al., 2013; Wang et al., 2013). Conversely, stochastic processes are related to neutral theory, which holds that all organisms have the same ecological characteristics and demonstrates that community structure is largely dominated by the history of stochastic events such as death, random birth, dispersal, extinction, or speciation (Chase and Myers, 2011). Meanwhile, the distance-decay relationship (DDR) is also a biogeographic pattern, which is considered the best-documented basic law of community ecology (Nekola and White, 1999; Horner-Devine et al., 2004). It is well known that both deterministic and stochastic processes affect DDR (Hanson et al., 2012; Wang et al., 2017), but the relative contributions of both processes vary with habitats (Wang et al., 2013). When investigating microbial communities on large spatial scales, species sorting and dispersal limitation are deterministic and stochastic processes, respectively, affecting DDR (Hanson et al., 2012; Wu et al., 2018). The balance between deterministic and stochastic processes is regulated by environmental factors. For example, the variation in soil available sulfur could shift from the relative contribution of deterministic processes to the stochasticity of fungal communities (Jiao and Lu, 2020). Acidic and alkaline soils cause deterministic processes in soil bacterial communities, whereas neutral pH contributes to stochastic processes during pedogenic processes (Tripathi et al., 2018). Currently, it is still unclear how the relative contribution of stochasticity versus determinism will regulate the biogeographic patterns and what are the main environmental factors governing the dominance of rhizosphere-associated bacterial community assembly processes among three minor grain crop fields.

Foxtail millet, proso millet, and sorghum are one of the traditional minor grain crops with drought-tolerant crops in northern China, making it possible to sample in a wide range of geographical locations and environmental factors. Meanwhile, the development of broomcorn millet industry plays an irreplaceable role in the adjustment of agricultural structure in arid and semi-arid areas of northern China. In this study, We addressed these questions using high-throughput 16S ribosomal RNA (rRNA) gene Illumina sequencing of rhizosphere bacteria along with nine environmental variables in adjacent pairs of foxtail millet, proso millet, and sorghum-cultivated fields across northern China. We attempted to examine the following hypotheses: (i) rhizosphere-associated bacteria in the three minor grain crops exhibit different biogeographic patterns, (ii) environmental thresholds and phylogenetic signals are different among the three minor grain crops, and (iii) relative contributions of community assembly processes vary among the three minor grain crops. Our findings could improve the understanding of the generation and maintenance of rhizosphere bacterial diversity, and facilitate the prediction of bacterial responses to global change in agricultural ecosystems.

2 Materials And Methods

2.1. Sample collection

Rhizosphere samples were collected from foxtail millet (*c.v.* Datong No. 26), proso millet (*c.v.* Yumi No. 2), and sorghum (*c.v.* Longza No. 18) fields during July–August 2020, which corresponded to the flowering stage of the crops in all fields. Samples were obtained at nine paired sites across the main cultivation areas of the minor grain crops in China (36.17–45.60 ° N and 106.23–122.82 ° E), which ranged from 145 to 1,821 km (Fig. S1, Table S1). At each site, three 20-m² plots were selected, compound fertilizer (600 kg·hm⁻²) was applied as basal fertilizer before sowing, and no herbicide spraying during the whole crop growth stage. The rhizosphere was obtained from 10–15 randomly selected healthy plants from each plot using a spade. The roots were shaken violently to remove large chunks of soil, loose soil attached to the roots was then carefully collected and merged into one sample. The rhizosphere collected were grouped into one sample per plot and placed in a sterile ziplock bag. All rhizosphere samples were sieved through < 2-mm sieve, transported to the laboratory on ice, and stored at – 80°C before physiochemical analysis and DNA extraction.

Edaphic variables, including pH, organic matter (OM), total nitrogen (TN), available potassium (AK), available phosphorus (AP), nitrate (NO₃), and ammonium (NH₄), were measured using standard soil testing procedures (Ma et al., 2016; Shi et al., 2018). Additionally, climatic variables, including mean annual temperature (MAT) and mean annual precipitation (MAP), were obtained from the China Meteorological Data Service Centre (<http://data.cma.cn/>). Microbial diversity was analyzed using high-throughput sequencing of the V3–V4 regions of the 16S rRNA genes of bacteria in rhizosphere samples, and the gene regions were amplified using the universal prokaryotic primer sets 338F (5'-ACTCCTACGGGAGGCAGCA-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') on a genome analyzer (Illumina Miseq PE300; Illumina, Inc., CA, USA). Sequences were filtered for quality control, split into

operational taxonomic units (OTUs) using a 97% similarity cut-off, and assigned to taxonomic groups (Yang et al., 2020).

2.2 Data analysis

All statistical analyses were performed using R (v4.0.3; <http://www.r-project.org/>). To avoid random influence on the recognition of rare taxa, OTUs with less than 20 reads were discarded. To determine the phylogenetic clustering among the three minor grain crop taxa, the nearest taxon index (NTI) was estimated using the “ses.mntd” function in “picante” package (Kembel et al. 2010). The pairwise phylogenetic turnover between communities was evaluated using the beta mean nearest taxon distance (β MNTD) metric in the “comdisnt” function (abundance.weighted = TRUE) in the same package. The β -diversity for bacterial communities (β MNTD metric) among foxtail millet, proso millet, and sorghum rhizosphere was determined using Wilcoxon rank-sum tests, performed using the “wilcox.test” function in the “stats” R package (Field et al., 2012). The distance-decay relationships (DDRs) were estimated as the slopes of linear least-squares regression for the relationships between geographic distances and community similarities (1 – β MNTD metric). The geographical distances between the sampling sites were calculated from the sampling coordinates.

Global non-metric multidimensional scaling ordinations were used to investigate and visualize the major variables affecting the bacterial community composition. The edaphic and climatic variables were fitted to the ordination plots using the “envfit” function of the “vegan” package (Oksanen and Blanchet, 2015). Threshold values among the three minor grain crop taxa in response to each environmental variable were estimated using threshold indicator taxa analysis (Baker and King, 2010). The sums of indicator taxa scores for bacterial OTUs were used to determine the lower and upper thresholds of change among the three minor grain crop communities based on the environmental variables. Blomberg's K was calculated using the “multiPhylosignal” function in the “picante” package (Kembel et al., 2010). The K -value describes the correlation between taxon and phylogeny in the strength of phylogenetic signals based on Brownian motion (Blomberg et al., 2003). K values closer to zero indicate a random or convergent evolution pattern, whereas K values greater than 1 indicate strong phylogenetic signals and trait conservatism.

Null model analysis was used to estimate the assembly processes among the three minor grain crop taxa (Stegen et al., 2013). The variation between phylogenetic diversity and taxonomic diversity was measured using null model-based phylogenetic and taxonomic β -diversity matrices, namely, beta nearest taxon index (β NTI) and Bray–Curtis-based Raup–Crick (RC_{bray}). Briefly, $|\beta\text{NTI}| > 2$ indicates the dominance of deterministic processes, with significantly more (i.e., variable selection; $\beta\text{NTI} > 2$) or less (i.e., homogeneous selection; $\beta\text{NTI} < -2$) phylogenetic turnover than expected. $|\beta\text{NTI}| < 2$, $RC_{\text{bray}} > 0.95$, and $RC_{\text{bray}} < -0.95$ represents the relative effects of dispersal limitation and homogeneous dispersal, respectively, and $|RC_{\text{bray}}| < 0.95$ indicates the effect of the “non-dominant” fraction (Zhou and Ning, 2017; Tripathi et al., 2018). To examine the relative importance of species sorting and dispersal limitation among three minor grain crop rhizosphere, we calculated the ratio of species sorting to dispersal

limitation effect (SDER) using the percentage of pairwise communities controlled by species sorting divided by the percentage of pairwise communities controlled by dispersal limitation. The percentage of species sorting was calculated as the sum of the variable and homogeneous selection. Additionally, we also used the “niche.width” function in the “spaa” package (Zhang and Zhang, 2013) to assess the Levins’ niche breadth (B) index (Levins, 1968) for the members of the microbial group according to the formula:

$$B_j = 1/\sum_{i=1}^N P_{ij}^2$$

where, B_j represents the habitat niche breadth of OTU j in a metacommunity, N is the total number of communities in each metacommunity, and P_{ij} is the fraction of OTU j in community i (Pandit et al., 2009; Wu et al., 2018). A higher B-value for a given OTU indicates a wider habitat niche breadth. The community-level B-value (B_{com}) was calculated as the average of the B values from all taxa occurring in one community (Wu et al., 2018). We predicted a microbial group with a wider niche breadth to be more flexible in metabolism at the community level (Pandit et al., 2009; Wu et al., 2018).

To estimate the contribution of stochastic processes to microbial community assembly, a neutral community model was fitted to the three minor grain crop taxa by predicting the relationship between the frequency of taxonomic occurrence and abundance (Sloan et al., 2006). In the model, the estimated migration rate is a parameter used to evaluate whether a random loss of an individual in a local community would be replaced by dispersal from the meta-community. Therefore, it is a measure of the dispersal limitations. R^2 indicates the fit of the neutral community model. Higher m values indicate that microbial communities are less dispersed (Sloan et al., 2006; Burns et al., 2016).

We investigated the main variables affecting the assembly processes among the three minor grain crop communities. The “mantel” function of the “ecodist” package was used to evaluate the changes in the gradient of environmental variables along the community assembly process, and β NTI values were compared with the Euclidean distance matrix of each environmental variable. The partial Mantel test was used to estimate the relationship between phylogenetic turnover and the derived environmental variables after controlling for spatial or other environmental variables (Goslee and Urban, 2007).

3 Results

3.1 Bacterial community structure and biogeographic patterns of three minor grain crops rhizosphere

In general, we obtained a total of 4 482 922 high-quality sequences, which were separated into 11 477 OTUs based on 97% similarity. Actinobacteria (27.54%), Proteobacteria (22.11%), Acidobacteria (14.05%), Chloroflexi (13.55%), Firmicutes (6.36%), and Gemmatimonadota (3.54%) contained the largest proportion of sequences in the rhizosphere of the three minor grain crops (Fig. S2). The relative

abundances of bacterial phyla at each sample site were evaluated for the three minor crops (Table S2). ANOVA indicated significant differences in the top 10 most abundant taxa of rhizosphere at the phylum level among the three minor crops in the nine regions. Among the different crop types, Actinobacteria, Firmicutes, Gemmatimonadota, Myxococcota, Nitrospirota, and Methylophilum reached a significant level. The relative abundance of Firmicutes in sorghum was 14.71% higher than that in foxtail millet ($P < 0.05$).

We also evaluated the DDRs of bacterial communities in the rhizosphere of foxtail millet, proso millet, and sorghum within a geographic distance of 1821 km of the minor grain crop cultivation area in China (Fig. 1). The Pearson's correlation coefficient between geographic distance and phylogenetic β diversity (β MNTD matrix) had a significant negative correlation in the rhizosphere of foxtail millet, proso millet, and sorghum. The slope of proso millet rhizosphere (slope = -0.080, $P < 0.001$, Fig. 1B) was steeper than that of foxtail millet (slope = -0.076, $P < 0.001$, Fig. 1A) and sorghum rhizosphere (slope = -0.077, $P < 0.001$, Fig. 1C). Additionally, proso millet rhizosphere displayed significantly lower β diversity than foxtail millet and sorghum rhizosphere (Fig. 1D). Meanwhile, the mean values of NTI were highest for the proso millet than for the foxtail millet and sorghum taxa (Fig. S3).

3.2 Environmental responses of three minor crop rhizosphere bacteria

We observed that there were obvious differences in soil physicochemical properties and climate factors among different crops (Table S3). The environmental threshold of the response of bacterial community change to each environmental variable was determined by accumulating Z - and Z + change points using TITAN2 (Fig. S4-S6). Environmental variables were fitted with global non-metric multidimensional scaling ordinations to determine the variables that had the most influence on the bacterial community distribution in foxtail millet, proso millet, and sorghum rhizosphere (Table S4, Fig. S7). Seven major variables were determined for subsequent analysis: soil pH, OM, TN, NH_4 , and MAT for the three minor grain crop rhizosphere; NO_3 and AK for foxtail millet rhizosphere; and AP for proso millet rhizosphere soils. The environmental threshold range of the proso millet rhizosphere was narrower than that of the foxtail millet and sorghum rhizosphere for almost all environmental variables, except for OM, TN, and MAP (Fig. 2A). Furthermore, the strength of the relationship between phylogeny and environmental preference was investigated to identify whether ecological characteristics could predict the phylogeny level. The Blomberg's K values demonstrated that the proso millet rhizosphere demonstrated weaker phylogenetic signals for almost all variables than the foxtail millet and sorghum rhizosphere, excluding for AP and NH_4 (Fig. 2B).

3.3 Assembly processes in rhizosphere bacterial communities

Environmental variables– β NTI relationships were estimated to investigate the relative effects of deterministic and stochastic assembly processes. Mantel tests revealed that MAT was the most

significant environmental variable for explaining the assembly processes in the rhizospheric of foxtail millet and proso millet but not in sorghum (Table 1). Additionally, the partial mantel test confirmed that the relationships were still significant after controlling for spatial distance and other measured environmental variables (Table S5). Pearson correlation analysis indicated a significant and positive correlation between β NTI and differences in MAT in the rhizosphere for foxtail millet and proso millet, whereas a significant and negative correlation was observed in the rhizosphere of sorghum (Fig. 3). Within the difference in MAT, the community assembly processes of the rhizosphere for foxtail millet and proso millet belonged to stochasticity, whereas an increasing difference in MAT caused a shift from stochasticity to homogeneous selection in the community assembly process of the sorghum rhizosphere. To further investigate the relationship between MAT and phylogenetic turnover (β NTI), samples were separated into subgroups based on the MAT; with an increase in MAT, the relative contributions of stochasticity first decreased and then increased in the proso millet and sorghum communities, whereas it decreased in the foxtail millet community (Fig. S8).

Table 1
Mantel tests of environmental variables against the phylogenetic turnover (β -nearest taxon index) of the rhizosphere soils among three minor grain crops

	Foxtail millet	Proso millet	Sorghum
Geographic distance	-0.062	0.004	-0.167
pH	-0.081	0.176	0.063
OM	-0.115	0.198	0.105
TN	-0.075	0.125	0.015
AP	-0.070	-0.151	-0.019
AK	-0.038	0.032	-0.055
NH ₄	-0.084	0.011	0.004
NO ₃	-0.018	-0.089	0.079
MAT	0.289**	0.350*	-0.328
MAP	0.022	-0.009	-0.034

Through the quantitative analysis of the deviation of phylogenetic turnover, we found that the foxtail millet (64.1%) and proso millet (76.3%) communities were mainly stochastic assemblies, while the deterministic combination (50.7%) mainly controlled the sorghum community (Fig. 4A). The results demonstrated that homogeneous selection contained the largest proportion of the sorghum community. Dispersal limitation affected the foxtail millet (42.5%) and proso millet communities (44.2%) more than it

did the sorghum community (28.5%). The null model analysis demonstrated that the SDERs of bacterial communities in proso millet rhizosphere were significantly lower than those in sorghum rhizosphere (Fig. 4B). This suggests that the relative influence of stochasticity processes (dispersal limitation) was greater in proso millet rhizosphere than in sorghum rhizosphere, which was mainly governed by deterministic processes (homogeneous selection) (Fig. 4A-4B). Furthermore, the bacterial communities of the rhizosphere among the three minor grain crops fit the neutral community model, which explained a higher proportion of variation in the proso millet rhizosphere ($R^2 = 0.78$) than in the sorghum rhizosphere ($R^2 = 0.75$, Table S6). Meanwhile, the migration rates of the proso millet community were higher than those of sorghum community (Table S4), indicating that the bacterial communities were less limited by dispersal in the proso millet rhizosphere. The habitat niche breadths (*Bcom*) at the community level were evaluated to illustrate the contributions of species sorting and dispersal limitation to bacterial community assembly. The mean *Bcom* values of proso millet rhizosphere were significantly higher than those of foxtail millet and sorghum rhizosphere (Fig. 4C).

4 Discussion

4.1 Different biogeographic patterns of bacterial communities among three minor grain crops

Microbial biogeography and community assemblage mechanisms are major issues in microbial ecology (Nemergut et al., 2013). Variations in microbial taxa in space are essential for understanding their ecological diversity. The DDRs illustrates how community similarity changes with geographic distance. The DDRs of the bacterial communities in the rhizosphere of the three minor grain crops exhibited a significantly negative correlation. The steepest slope was observed in the rhizosphere of the proso millet. This demonstrated that the rhizosphere bacteria of the proso millet were non-random clusters, and their members were distributed in a narrow biogeographic region. These results not only confirm my first hypothesis, but are also consistent with previous observations of field crops such as soybeans, wheat, rice, and maize in terrestrial agro-ecosystems (Fan et al., 2017; Shi et al., 2018; Zhang et al., 2018; Feng et al., 2019; Zhao et al., 2019). The higher turnover rate of proso millet taxa may have resulted from the limited dispersal or environmental selection of the proso millet species in contrast to the foxtail millet and sorghum species (Hou et al., 2020).

4.2 Narrower environmental adaptations of proso millet bacterial taxa

Environmental variation regulates microbial diversity and affects related ecosystem functioning (Smith et al., 2016). Several studies have investigated the effects of various environmental variables on the bacterial community composition of several plant hosts (Wang et al., 2018; Cheng et al., 2020; Hou et al., 2020), and few studies have explored whether the environmental adaptation of rhizosphere bacteria varies among three minor grain crops across agro-ecosystems at regional scales. The potential environmental adaptation was mirrored from two measures: (a) the breadth of environmental thresholds

using TITAN analysis (Baker and King, 2010; van der Linde et al., 2018), and (b) the strength of phylogenetic signals to ecological preferences using Blomberg's K statistic (Blomberg et al., 2003; Martiny et al., 2015).

The breadth of the environmental thresholds for the microbial community could reveal the niche breadths of the species. In the present study, we confirmed strong evidence that the proso millet rhizosphere bacteria exhibited narrower response thresholds to most environmental factors than the foxtail millet and sorghum rhizosphere bacteria. Similar phenomena were reported by (Zhang et al., 2021), who observed that soil fungi exhibited narrower environmental thresholds in maize fields than those in rice fields. From a new perspective, our results support the view that proso millet rhizosphere bacterial species adapt to a smaller environmental gradient range (Table S3), thereby occupy a narrower environmental threshold breadths (Barberán et al., 2014; Zhang et al., 2021). As a critical ecosystem assessment tool, environmental threshold analysis has been widely applied in aquatic, forest, and farmland ecosystems at a large spatial scale (van der Linde et al., 2018; Jiao and Lu, 2020; Wan et al., 2021). The application of environmental threshold analysis to determine the environmental breadth of microbial communities is an attractive method, but the impact of the actual situation may be controversial. Therefore, it is necessary to implement experimental verification when employing these statistical results to formulate environmental policies. Nevertheless, our region-scale results provide robust evidence for the narrower environmental breadths for proso millet rhizosphere bacterial communities than foxtail millet and sorghum rhizosphere bacterial communities in agricultural fields. To our knowledge, these results are unprecedented and novel.

Phylogenetic signals could offer predictions for the evolutionary adaptation of species in response to environmental changes. We observed that the rhizosphere bacterial taxa of foxtail millet and sorghum exhibited stronger phylogenetic signals for the ecological preferences than that of proso millet based on Blomberg's K statistic. The results suggested that closely related species in foxtail millet and sorghum rhizosphere communities demonstrated more similar ecological preferences and conservatism of traits on environmental thresholds. Prior studies have confirmed that the traits derived from the ecological preferences of an organism rely on its evolutionary history (Amend et al., 2016; Saladin et al., 2019). For instance, bacterial traits in forest ecosystems are more restricted by evolutionary history than environmental heterogeneity (Morrissey et al., 2019). Furthermore, pH and temperature preference traits were strongly conserved in methane-oxidizing bacteria (Krause et al., 2014). In this study, the stronger phylogenetic signals and conservation of traits of foxtail millet and sorghum rhizosphere bacteria for their ecological preferences may explain their broader environmental breadths and more distinct distribution patterns than that of proso millet bacteria. In summary, these two results revealed that the foxtail millet and sorghum millet rhizosphere bacterial communities had a broader environmental breadth and stronger phylogenetic signal for the ecological preferences than that of proso millet across different environmental conditions in agricultural fields.

4.3 Distinct assembly processes among three minor grain crop bacterial communities

The spatial turnover of microorganisms is potentially regulated by different ecological mechanisms; therefore, it is crucial to identify the principal contributions of deterministic and stochastic processes to the microbial community assembly (Bahram et al., 2016; Martin et al., 2018). In the present study, the null model analysis indicated that deterministic processes (e.g., homogeneous selection) mainly controlled the sorghum rhizosphere community, and stochastic assembly (e.g., dispersal limitation) was primary in the proso millet and foxtail millet rhizosphere bacterial communities in agricultural fields. It is difficult to assess the relative contributions of species sorting and dispersal limitation using their absolute values (Wu et al., 2018; Jiao et al., 2020). We further estimated the community assembly processes by applying the ratios of species sorting and dispersal limitations. Our findings demonstrated that lower sorting/dispersal effect ratios for rhizosphere bacterial communities were observed in proso millet fields, suggesting that the proso millet rhizosphere bacterial community was less limited by the environment than foxtail millet and sorghum communities. This is demonstrated by the results of the neutral community model. Furthermore, the proso millet rhizosphere bacterial community exhibited significantly wider niche breadths than foxtail millet and sorghum community, using community-level habitat niche breadth analysis. This result is consistent with findings that habitat generalists with wider niche breadths are less affected by environmental variables (Pandit et al., 2009; Jiao et al., 2020). The visible discrepancy in distinct ecological assembly processes among proso millet, foxtail millet, and sorghum rhizosphere bacterial communities may be due to habitat specificity, environmental heterogeneity, and the individual ability of the taxon to cope with environmental changes (Wang et al., 2017; Wan et al., 2021). Our findings also confirmed that stochastic processes may surpass the deterministic processes in systems with minimal environmental variation in proso millet taxa at the regional scale (Wang et al., 2013).

To gain a more advanced understanding of microbial community assembly mechanisms, it is necessary to uncover the environmental variables influencing the relative contributions of stochastic and deterministic assembly processes of microbial communities (Tripathi et al., 2018; Jiao and Lu, 2019). Several studies have reported that soil pH, temperature, and dissolved oxygen are critical variables affecting the bacterial community assembly processes in various environments (Fan et al., 2018; Jiao and Lu, 2019; Wan et al., 2021). However, only a few studies have emphasized the environmental variables influencing the relative contributions of stochastic and deterministic processes that govern the assembly of rhizosphere bacterial communities for minor grain crops in agro-ecosystems. We observed that β NTI of both foxtail and proso millet rhizosphere bacterial communities is more strongly associated (mantel and partial mantel coefficient) with MAT than other factors based on the null model analysis. This may indicate that MAT was the critical variable adjusting the dynamic balance between stochastic and deterministic assembly processes for foxtail and proso millet rhizosphere bacterial communities in agro-ecosystems.

The major role of MAT in mediating the assembly processes of foxtail and proso millet rhizosphere bacterial communities may be attributed to the soil microbial community being sensitive to temperature changes (Jurburg et al., 2017; Zheng et al., 2019; Zhang et al., 2020). Climate warming could accelerate the kinetics of biological processes (e.g., adaptive evolution, speciation, metabolic activity, and rates of

reproduction), temporal turnover, and divergent succession of microbial communities, thereby resulting in apparent changes in microbial community biodiversity (Allen et al., 2002; Zhou et al., 2016; Guo et al., 2019; Zhang et al., 2020). We also found that MAT regulated the assembly processes of the three minor grain crop communities, which were dominated by the stochasticity of proso millet communities in high MAT regions and stochasticity of the foxtail millet community in low MAT regions. The dominance of stochastic assembly in high MAT regions indicates that proso millet and sorghum communities are more sensitive to hot environments. In contrast, the dominance of stochastic assembly in low MAT regions indicates that weaker niche-based exclusion of foxtail millet taxa lineages may dominate in cold regions (Jiao and Lu, 2019).

5 Conclusions

In summary, the turnover rate of proso millet rhizosphere taxa was higher across space, so the distribution of proso millet rhizosphere species is more restricted by geography or environment than foxtail millet and sorghum taxa. Furthermore, we also constructed a conceptual framework describing the environmental adaptation and assembly processes of foxtail millet, proso millet, and sorghum rhizosphere bacterial communities in agricultural ecosystems. Foxtail millet and sorghum rhizosphere communities demonstrated broader environmental breadths and stronger phylogenetic signals of ecological preference than proso millet. Meanwhile, the proso millet rhizosphere community was more closely clustered phylogenetically than the foxtail millet and sorghum rhizosphere communities. Stochastic processes governed the proso and foxtail millet rhizosphere community assembly, whereas the sorghum rhizosphere community displayed the opposite trend. MAT was the critical factor governing the balance between the assembly processes of the foxtail millet, proso millet, and sorghum rhizosphere communities. In the proso millet and sorghum rhizosphere communities, the higher MAT regions cause an increase in stochastic assembly, whereas in the foxtail millet rhizosphere community, increased MAT results in an increase in deterministic assembly. In the present study, the findings are of great significance for explaining the generation and maintenance of rhizosphere bacterial diversity, which is crucial for promoting the prognostication of bacterial responses to global environmental changes in agro-ecosystems. Considering the consequences of soil rhizosphere bacterial communities on ecosystem function, experimental verification of the model should be implemented in a wider range of ecosystems.

Declarations

Declaration of Competing Interest

The authors declare that they have no current or conflict completing financial interests.

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Data avail ability statement

The raw sequence data reported in this paper are available in the NCBI Sequence Read Archive under BioProject PRJNA715590.

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Figures

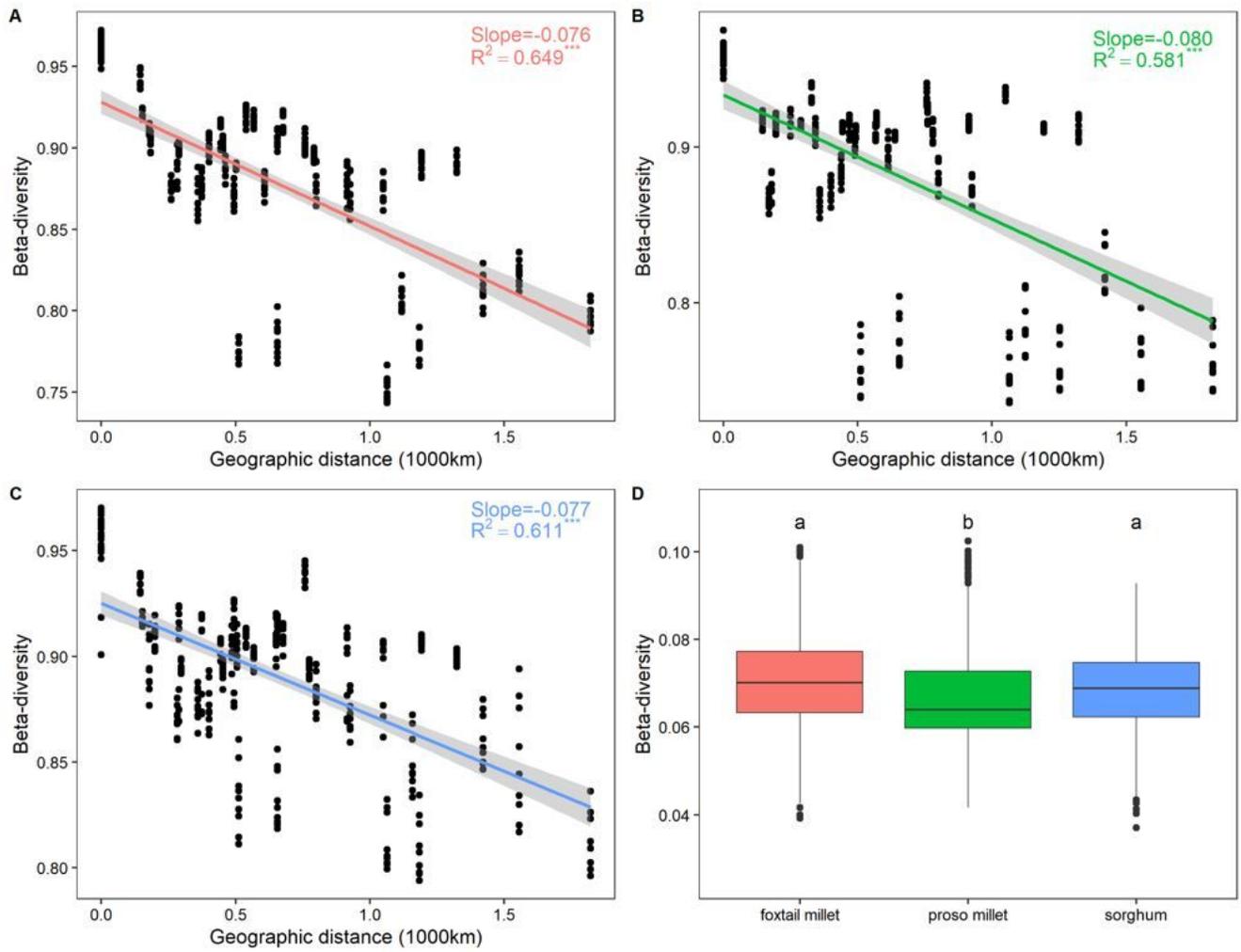


Figure 1

General patterns of microbial beta-diversity in soil samples from the rhizosphere soils of three minor grain crops.

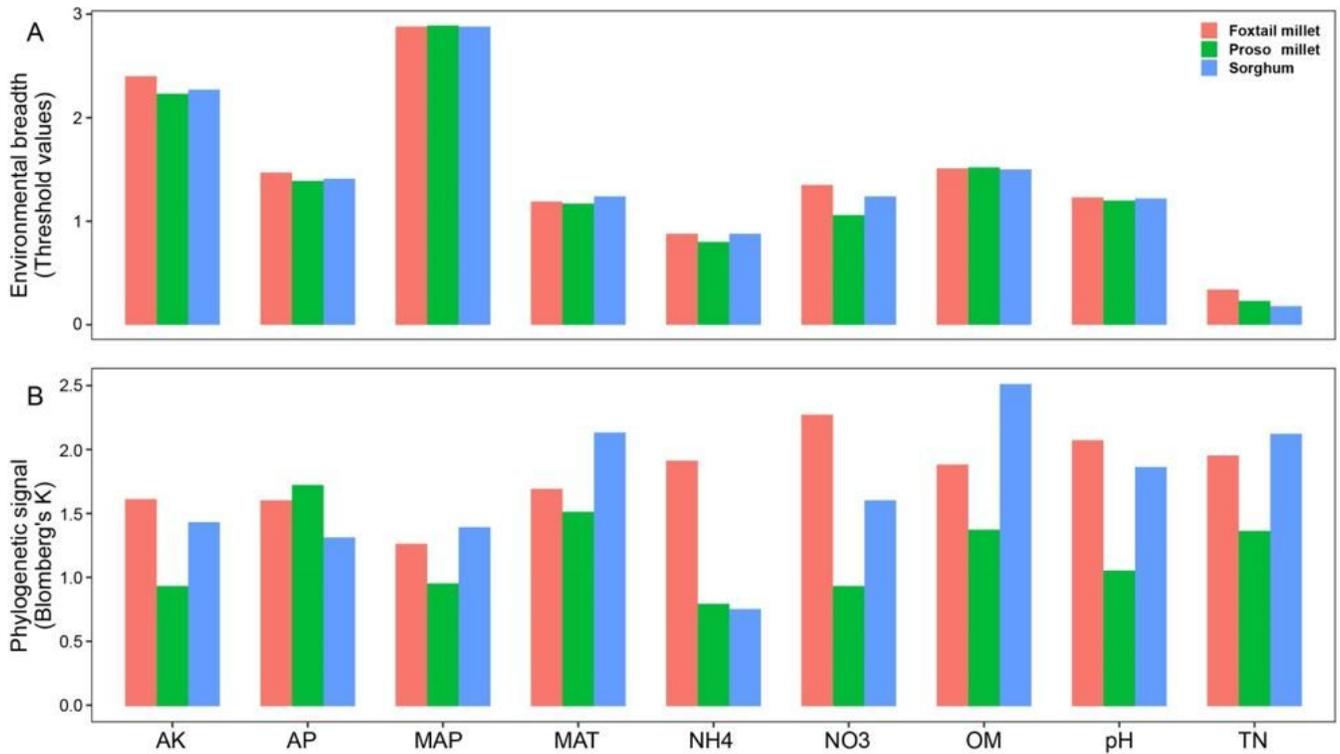


Figure 2

Environmental adaptation of bacteria taxa in the rhizosphere soils among three minor grain crops.

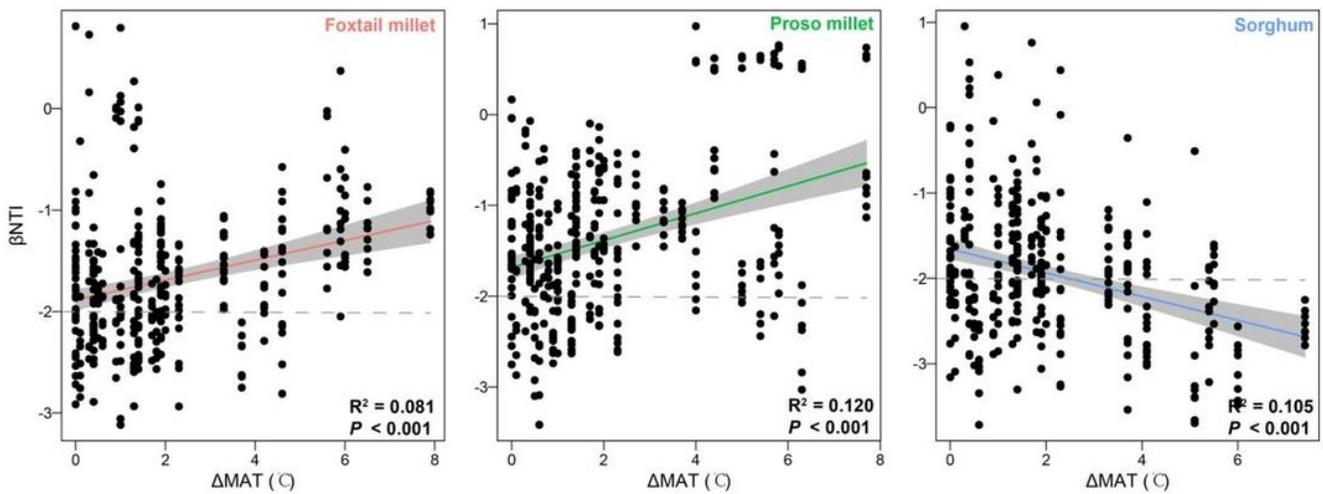


Figure 3

The effects of deterministic and stochastic assembly processes in shaping bacteria communities in the rhizosphere soils among three minor grain crops.

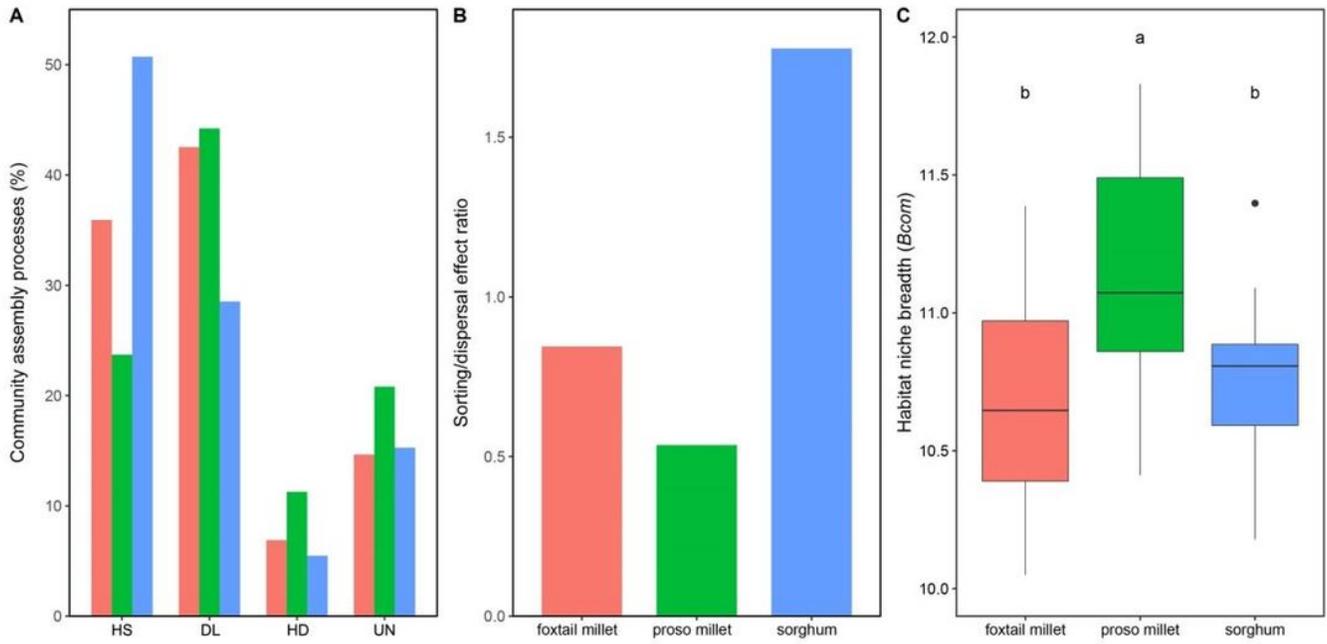


Figure 4

Comparison of community assembly and niche breadths in the rhizosphere soils among three minor grain crops.

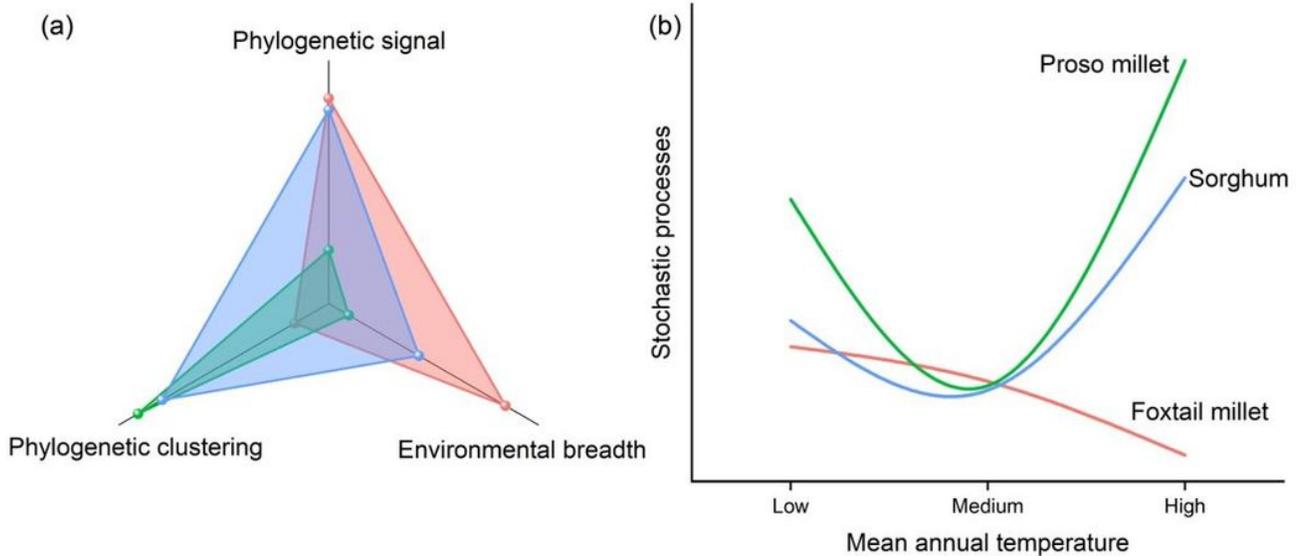


Figure 5

A conceptual paradigm showing (a) environmental adaptation and (b) stochastic processes in the assembly of three minor grain crop communities under the influence of mean annual temperature in

agricultural ecosystems.

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