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Change in soil bacterial community during secondary succession depend on plant and soil characteristics

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ABSTRACT

Secondary succession has great impact on plant and soil characteristics, however, the trends of microbial patterns and the influencing factors during grassland succession without human disturbance remains unclear. Therefore, we investigated the changes of bacterial community in sloped farmlands abandoned for 0, 20, 30, and 40 years (GL-0 yr, GL-20 yr, GL-30 yr, and GL-40 yr). Additionally, plant traits (coverage, diversity, richness, evenness, biomass, and biomass carbon) and soil nutrients were also determined. The results showed that soil bacterial alpha diversity was positively and significantly correlated with the succession time, and the secondary succession greatly affected soil bacterial beta diversity, in contrast, the effects on soil bacterial beta diversity at the late succession time (GL40 and GL30) were larger than that at the early succession time (GL20). For the bacterial taxa, the dominant phyla including *Actinobacteria* (34.8%), *Proteobacteria* (26.0%), *Acidobacteria* (15.0%), *Chloroflexi* (7.5%), *Gemmatimonadetes* (8.7%), *Nitrospirae* (1.6%), *Bacteroidetes* (2.1%), *Verrucomicrobia* (1.1%), and *Planctomycetes* (1.0%) were found. Particularly, the relative abundance of *Proteobacteria* was higher at the late time (RP40), while the *Actinobacteria* was higher at the early time (RP20). Such different responses of bacterial diversity and taxa were largely explained by plant traits and soil nutrients, especially for TOC and TN. Collectively, our results indicate that plant secondary succession shifts the bacterial community structure, largely driven by changes in soil nutrients and plant diversity and composition, and also supported the growing view that soil bacterial community are the key determinants of aboveground and belowground linkages that functionally control terrestrial ecosystems.

1. Introduction

Plant-soil interactions have been widely reported during secondary succession are assumed to play vital roles in soil microbial dynamics (Lamb et al., 2011; Lloret et al., 2015; Schlatter et al., 2015; Teste et al., 2017). For example, higher plant diversity can import more nutrients into soil systems and retain higher soil moisture than lower diversity, which may affect the growths of autochthonous soil microbial communities, since these groups are associated with higher plant diversity (Thakur et al., 2015). Studies regarding the interactions between plant community traits and soil microbial communities are well documented (Legay et al., 2016; Liu et al., 2016), findings have been diverse and substantial uncertainty about the feedback plant-soil microbial. However, much is still unknown about the resolution of the uncertainties concerning the interactions of the plant community, soil properties, and the soil microbial community. Since soil microbial activity, variations in ecosystem depends on plant traits after afforestation, differential responses of plant traits and soil properties to soil microbial community diversity and composition may be caused due to changes of succession. (Zeng et al., 2016; Zhang et al., 2017). Therefore, to better understand the mechanisms of plant-soil systems, which modulate ecosystem function and sustainability, more information on plant community traits, soil properties, and microbial interactions is urgently needed.

During secondary succession, plants and soil nutrients are broadly perceived to directly influence soil bacterial taxa through the provision of carbon compounds (Bakker et al., 2010; Schlatter et al., 2015; Delgado-Baquerizo et al., 2017). Several studies show that plant traits are the primary selective factors for soil bacterial community composition (Marschner et al., 2004; Yao et al., 2014). For example, Bartelt-Ryser et al. (2005) reported that in the short term, soil carry-over

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effects on plant diversity are mediated by a general stimulation of soil microbes, whereas the longer-term effects of particular plant species are more likely due to compositional shifts in soil microbial communities, suggesting the differences of bacterial compositions under different succession time. Furthermore, several studies reported that soil bacterial diversity responded plant community depended upon the shift in resource availability (Bartelt-Ryser et al., 2005; Lian et al., 2017). For example, Yuan et al. (2014) observed that soil carbon and NH_4^+-N were the dominant environmental factors that influenced bacterial communities, but (C. Zhang et al., 2016) showed the opposite trends, suggesting that soil nutrients play significant roles as they provide inorganic and organic substrates to soil bacterial. Altogether, more recent analyses indicate that soil nutrients influence soil bacterial communities directly or indirectly (Srinivasiah et al., 2015; J. Chen et al., 2016; Orwin et al., 2016; Sardans et al., 2017; Santonja et al., 2017;), but it is uncertain whether the strength of such impacts depends on plant traits to further regulate energy and nutrient flow in terrestrial ecosystems.

The Loess Plateau in China covers approximately $62.4 \times 10^4\,km^2$ and is known for its long agricultural history and severe soil erosion (Chen et al., 2006). Abandonment of farmland with slopes > 15° to allow secondary succession is an important management practice to prevent soil erosion and recover ecological environments of this area. In recent years, numerous studies have been conducted to study the effects of succession on soil physicochemical properties and microbial dynamics (An et al., 2013; C. Zhang et al., 2016; Q. Zhang et al., 2016; Zhao et al., 2016). However, information on the relationship between soil nutrients, plant traits, and soil bacterial communities is still scarce, largely hindering our understanding of the mechanisms of plant-soil feedback following secondary succession. Therefore, the present study investigated soil nutrients, plant community traits, and soil bacterial communities at sites representing 40 years of grassland succession on abandoned farmland in the Loess Plateau. We hypothesized that plant (diversity, evenness, richness, coverage, biomass, and biomass carbon (C)) and soil organic carbon (SOC), total nitrogen (TN), nitrate nitrogen (NO_3^--N), ammonium nitrogen (NH_4^+-N), and pH structured soil bacterial abundance and composition. Our objective was to (i) evaluate changes in soil nutrients following plant succession, (ii) determine the diversity and composition of the soil bacterial community, and (iii) determine the effects of the plant community and soil nutrients on soil bacterial communities over time.

2. Material and methods

2.1. Study area

The study area was located in the Xiaocaogou watershed, which belongs to the Ansai Research Station on Soil and Water Conservation of the Chinese Academy of Sciences. It is located in the center of the Loess Plateau (109°26′-109°28′E, 36°74′-37°77′N) (Fig. 1). The site has a typical temperate continental semiarid climate with an average temperature of 8.8 °C and an average annual precipitation of 510 mm, which mainly falls from July to September. The altitude of the site is 1087.3–1290.8 m. The soil is mainly composed of Huangmian soil (Calcaric Cambisols, FAO) and is susceptible to erosion (Huang, 2014).

2.2. Soil sampling design and sampling

Four sloped farmlands abandoned for 0, 20, 30, and 40 years (GL-0 yr, GL-20 yr, GL-30 yr, and GL-40 yr) were selected as experimental sites based on their well-dated successional chronosequence. The sites had similar slope gradients, slope aspects, elevations, and previous framing practices (C. Zhang et al., 2016). With succession, the abandoned land gradually evolved into grassland with no human or animal disturbance. The plant community is a sparse, short grassland with low cover dominated by grasses such as *Artemisia sacrorum*, *Phragmites australias Trin. Stipa bungeana*, and *Cleistogenes squarrosa*.

In September 2016, for each experiment site, three independent replicates were established (20 m × 20 m each) since the distance between any two sites exceeded the spatial dependence (< 13.5 m) of most soil variables (Marriott et al., 1997). Then, we randomly selected six 1 m × 1 m quadrats in each plot for measuring plant traits. Community surveys were conducted to determine the plant coverage, plant diversity, plant richness, plant evenness, and plant biomass in each quadrat. The aboveground parts were clipped and dried to obtain aboveground biomass and to analyze biomass carbon (C). We also recorded the number of individuals for each species in each plot and the number of species was used to estimate richness (Lozano et al., 2014). Shannon's diversity index was used to assess plant diversity (Tscherko et al., 2004). Soil samples were collected from the top 0–20 cm using a soil auger (diameter 5 cm) from each of the independent replicate sites. After removing the litter layer, ten samples were collected with an “S” shape and then homogenized to provide one final soil sample per subplot (Ren et al., 2016b). The simples were sieved through a 2-mm mesh to remove the visible plant roots, stones, litter, and debris (Ren et al., 2017) and then divided into two subsamples. One subsample was immediately transported from the field to the laboratory and stored at −80 °C for DNA analysis and the other sample was kept at 4 °C for physical and chemical analyses (Li, 2014), which was processed within four weeks after collection.

2.3. Physical and chemical properties of the soil

Soil water content was determined by weighing the soil sample dried at 105 °C for 24 h (until the weight remained constant) (Ren et al., 2016b). The bulk density was determined using the cutting ring method (Xu et al., 2016). Soil pH was measured in each soil sample using an aqueous solution (1:10 w/v) with a pH meter (C. Zhang et al., 2016). Soil organic carbon (SOC) concentration ($g{\cdot}kg^{-1}$) was determined using the $K_2Cr_2O_7$ oxidation method (Zhao et al., 2016). Total nitrogen (TN) content was determined using the Kjeldahl method (Tang et al., 2011). Nitrate-N (NO_3^--N) and ammonium-N (NH_4^+-N) were measured by flow injection analysis.

2.4. Soil DNA extraction, PCR amplification, and illumina sequencing

Microbial DNA was extracted from 0.5 g of fresh soil three times (for a total of 1.5 g of soil) with E.Z.N.A soil DNA (OMEGA, USA), following the manufacturer's instructions (Ren et al., 2016b; C. Zhang et al., 2016). The concentration and quality of the DNA were assessed using a NanoDrop2000 spectrophotometer (Thermo Scientific, Wilmington, DE, USA). PCR amplification of bacterial 16S rRNA targeting the V4 region was conducted by using primers 515F (5′-GTGCCAGCMGCCG CGG-3′) (Gunnarsdóttir et al., 2011). This primer set provides comprehensive coverage with the highest taxonomical accuracy for bacterial sequences. The PCR protocols that were used to amplify the 16S rRNA gene were described previously (Ren et al., 2016a). Finally, an equal amount of PCR product from each sample was put in a single tube, and sent to Illumina's MiSeq platform at the Major Biological Institute in Shanghai, China.

Reads were demultiplexed, quality-filtered, and processed using QIIME according to the following three criterions (Suleiman et al., 2013). Sequence analysis was performed using the USEARCH v5.2.32 to filter and eliminate noise from the data by clustering similar sequences with < 3% dissimilarity. Microbial Ecology pipeline software was used to select 16S rRNA operational taxonomic units from combining reads of clustered operational taxonomic units with 97% similarity. Finally, the complete dataset was sent to the Sequence Read Archive (SRA) database of the National Center for Biotechnology Information (NCBI) under the accession number of SRP150907.

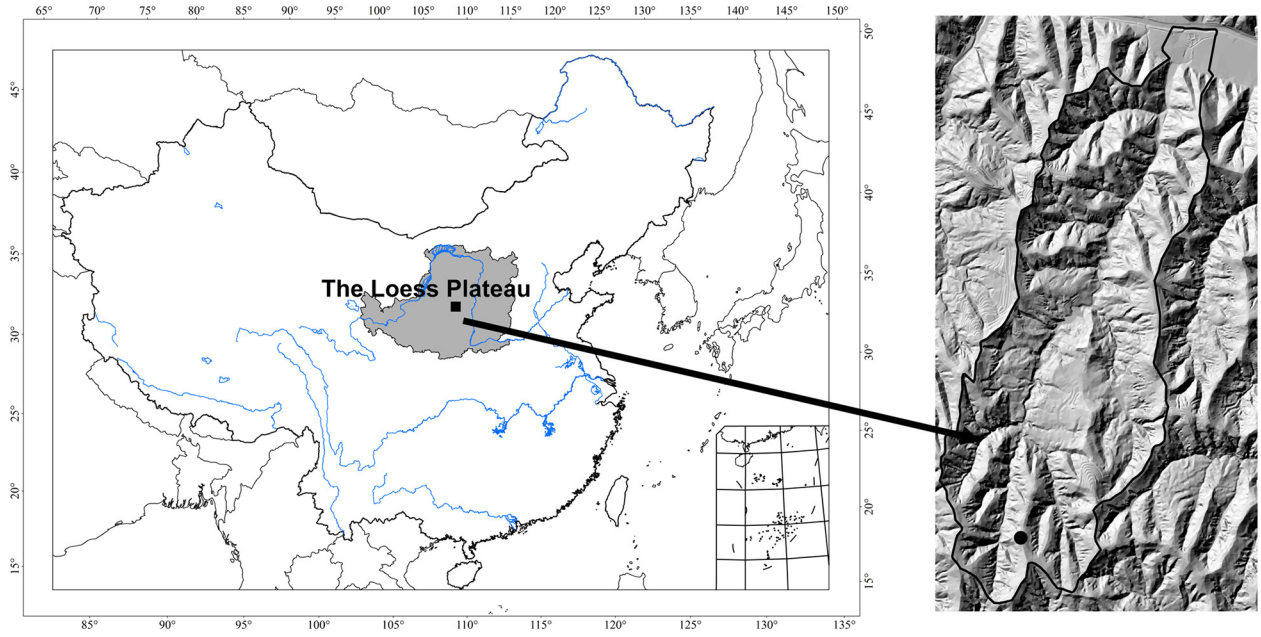

Fig. 1. Location of the Loess Plateau and the study site.

2.5. Statistical analysis

Differences in plant traits, soil properties, bacterial diversity, and relative abundance of bacterial taxa along the successional stages were evaluated using general linear models. One-way analysis of variation (ANOVA) and least significant difference (LSD) multiple comparison ($P < 0.05$) were used to assess the significance of effects of successional age on the plant traits (coverage, biomass, plant diversity, plant evenness, and species richness), soil properties, and bacterial composition and diversity (C. Zhang et al., 2016). Linear regression analysis and Redundancy analysis (RDA) was used to identify the relationship between the soil properties and microbial populations. We used RDA because the RDA plots provide a representation of relations between dependent and independent variables. The RDA plots were interpreted in terms of the Euclidean distances between centroids, and between centroids and individual objects. The angles of the vectors plotted in the plane of the first two RDA axes, which explain the largest proportion of the variation represent, show the strength of correlation between response and explanatory variables (a narrow angle indicates a strong correlation). Soil bacterial community comparisons were made by non-metric multidimensional scaling (NMDS) plots based on Bray-Curtis dissimilarity following succession. The RDA and NMDS analyses were performed using the Canoco 4.5 software package.

3. Results

3.1. Effects of secondary succession on plant and soil properties

Floristic composition at different sites showed differences in plant traits and the differences are shown in Table 1. Plant traits, such as plant coverage, plant diversity, plant richness, plant evenness, plant biomass, and plant biomass C greatly increased with succession time. Particularly, plant coverage, richness, and plant biomass C in the GL-40 yr site was higher by > 47.13%, 41.19%, and 11.85%, respectively. The variation in soil nutrients at different sites was remarkable (Table 2), and significant differences occurred among the four sites ($P < 0.01$), including soil organic carbon (SOC), total nitrogen (TN), and nitrate nitrogen (NO_3^--N). Our results show that SOC, TN, NO_3^--N, and NH_4^+-N contents in the GL-20 yr, GL-30 yr, GL-40 yr sites were higher than those in the GL-0 yr site, especially for GL-40 yr, which was higher by 252.04%, 435.00%, 64.38%, and 23.57%, respectively. However, soil pH, C/N, and BD had no significant difference in these sites compared with GL-0 yr.

3.2. Effects of secondary succession on bacterial community diversity

A total of 496,656 quality sequences, ranging from 34,162 to 49,290 sequences per sample for bacteria, respectively, were obtained from the 12 samples (an average of 41,388 sequences per sample). For the downstream analysis of bacteria, datasets were rarefied to 34,100 sequences. The alpha diversity of bacteria (Shannon index) significantly increased with succession time (Fig. 2). Similarly, in the two-dimensional NMDS plot visualized, Bray-Curtis analysis showed segregation among sample points (the three replicates at each of the four succession sites) (Fig. 3). Our results showed that the GL-30 yr and GL-40 yr sites are very different from the GL-0 yr site, especially the 40-yr sites.

Table 1
Characteristics of the vegetation during the succession.

Abandoned site	Plant coverage (%)	Plant richness	Plant diversity	Plant evenness	Biomass (kg m^{-2})	Biomass C (g m^{-2})
GL-0 yr	–	–	–	–	–	–
GL-20 yr	46.4 ± 0.702b	2.84 ± 0.255b	3.06 ± 0.224a	1.04 ± 0.081a	0.11 ± 0.012b	463.99 ± 21.26a
GL-30 yr	47.53 ± 2.219b	3.12 ± 0.056b	3.27 ± 0.194a	1.15 ± 0.033a	0.11 ± 0.006b	505.80 ± 21.793a
GL-40 yr	68.27 ± 0.267a	4.01 ± 0.255a	3.47 ± 0.027a	1.09 ± 0.029a	0.17 ± 0.009a	518.98 ± 53.74a

Values are means ± standard error (n = 3). Different letters indicate significant differences ($P < 0.05$) among soils for the individual variables based on a one-way ANOVA followed by an LSD test.

Table 2
Soil physicochemical properties during the succession.

Abandoned sites	Organic C (g kg^{-1})	Total N (g kg^{-1})	C/N	NO_3-N (mg kg^{-1})	NH_4^+-N (mg kg^{-1})	pH	Bulk density (mg cm^{-3})
GL-0 yr	3.19 ± 0.133c	0.20 ± 0.020b	15.79 ± 1.118a	0.73 ± 0.026b	4.20 ± 0.871a	8.55 ± 0.112a	108.23 ± 3.199a
GL-20 yr	4.05 ± 0.305c	0.32 ± 0.070b	13.60 ± 2.464a	0.808 ± 0.030b	3.63 ± 0.031a	8.62 ± 0.015a	108.63 ± 3.973a
GL-30 yr	6.94 ± 0.289b	0.83 ± 0.088a	8.53 ± 1.007b	1.851 ± 0.280a	4.42 ± 0.154a	8.56 ± 0.037a	107.96 ± 6.023a
GL-40 yr	11.23 ± 0.578a	1.07 ± 0.144a	10.88 ± 1.385a	1.20 ± 0.108b	5.19 ± 0.180a	8.58 ± 0.051a	102.25 ± 1.187a

Values are means ± standard error (n = 3). NS: not significant. Different letters indicate significant differences ($P < 0.05$) among soils for the individual variables based on a one-way ANOVA followed by an LSD test.

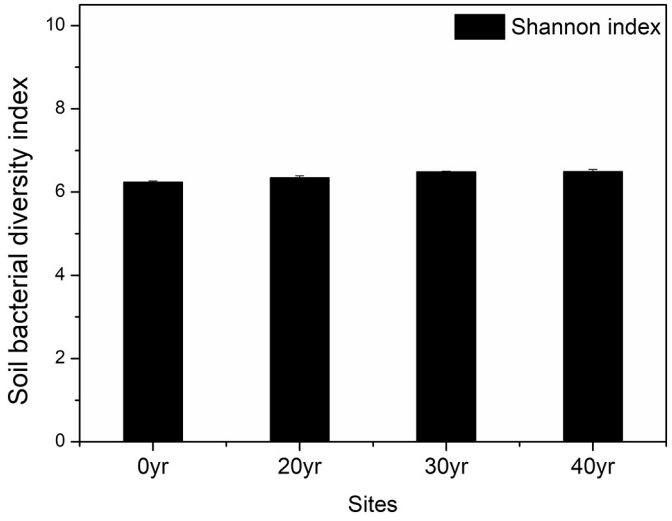

Fig. 2. Impact of succession on alpha diversity (Shannon index) of soil bacterial diversity.

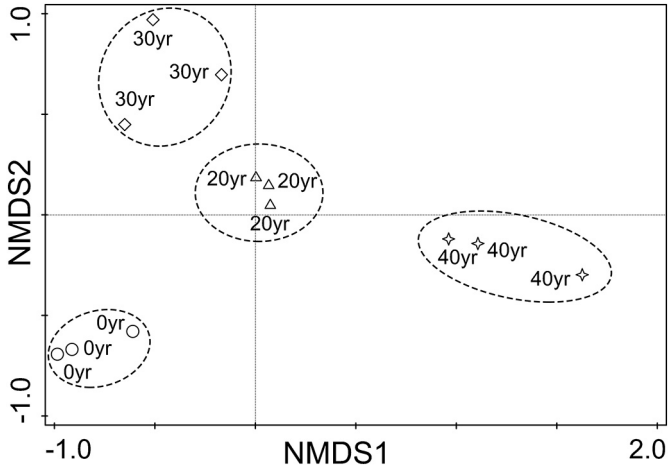

Fig. 3. Soil bacterial community comparisons by NMDS plots based on Bray-Curtis dissimilarity during secondary succession.

3.3. Effects of secondary succession on bacterial community composition

The dominant bacterial phyla with a relative abundance of > 1% were Actinobacteria (34.8%), Proteobacteria (26.0%), Acidobacteria (15.0%), Chloroflexi (7.5%), Gemmatimonadetes (8.7%), Nitrospirae (1.6%), Bacteroidetes (2.1%), Verrucomicrobia (1.1%), and Planctomycetes (1.0%) (Figs. 4 and S1). Notably, the relative abundance of the bacterial phylum Actinobacteria was higher in GL-0 yr, while that of Proteobacteria was higher in the GL-20 yr, GL-30 yr, and GL-40 yr sites.

3.4. Relationships among plant communities, soil properties, and bacterial communities

Linear regression analysis showed that changes in soil bacterial diversity (alpha diversity) were significantly correlated with plant traits (plant biomass, plant diversity, plant richness, plant evenness, plant biomass C and plant coverage) and soil characteristics (SOC, TN and NH_4^+-N) (Table 3). The relationship between environmental variables (dominant bacterial phyla taxa), soil nutrients (SOC, TN, NO_3^--N, pH, BD and NH_4^+-N), and plant traits (plant coverage, plant diversity, plant richness, plant evenness, plant biomass, and plant biomass C) was examined based on redundancy analysis (Fig. 5 and Table S1). The relative abundance of Actinobacteria, Proteobacteria, Acidobacteria, Chloroflexi, Gemmatimonadetes, Nitrospirae, Bacteroidetes, Verrucomicrobia, and Planctomycetes was significantly correlated with SOC, TN, NO_3^--N, NH_4^+-N, plant coverage, plant diversity, plant richness, plant evenness, plant biomass, and plant biomass C. Our result indicates that soil properties and plant traits were influential factors driving the changes in composition of the bacterial communities.

4. Discussion

Plant secondary succession without human or animal disturbance has commonly been shown to directly alter plant growth and productivity (Chen, 2016; Li et al., 2004; Liu et al., 2012), and such changes in turn affect biogeochemical cycling in the above- and belowground systems in degraded environments. It was found in our study that changes in soil properties, such as SOC, TN, and NH_4^+-N, parallel changes in plant characteristics including plant biomass and plant diversity (Tables 1 and 2, Figs. S1 and S2). Possible explanations can be ascribed to either input from the number of plant species or changes in plant floristic composition. This is also suggested by previous studies showing that the quantity and quality of plant biomass and its chemical composition can influence substrate availability, thereby controlling soil conditions across different scales (Schlatter et al., 2015; Sun, 2017). Moreover, we also found that soil nutrients (SOC, TN, and NH_4^+-N) and plant characteristics (biomass, evenness, coverage, and diversity) increased following plant secondary succession and peaked at the 40-yr site (Tables 1 and 2). Not surprisingly, it is likely that soil properties increased with plant succession due to increased plant biomass. This reason is also supported by previous studies which showed plant secondary succession could enhance plant biomass, ultimately increasing the concentration of SOC, TN, and NH_4^+-N (L.F. Chen et al., 2016; Chen, 2016; Millard and Singh, 2009). Altogether, these results support our first hypothesis that the interaction between plants and soil can be affected by plant secondary succession, and further clarify that plant secondary succession time can be considered when assessing soil conditions and plant productivity in degraded environments.

In addition to the effects of plant secondary succession time, the interactions between plants and soil properties, caused by plant secondary succession, are also accompanied by microbial processes (Bartelt-Ryser et al., 2005; Na, 2017). Evidence is mounting in support of the notion that identifying changes in the soil microbial community can reveal how the ecosystem functionally responds to human-induced environmental change (Pennanen, 2001; Xue, 2007). Our findings add

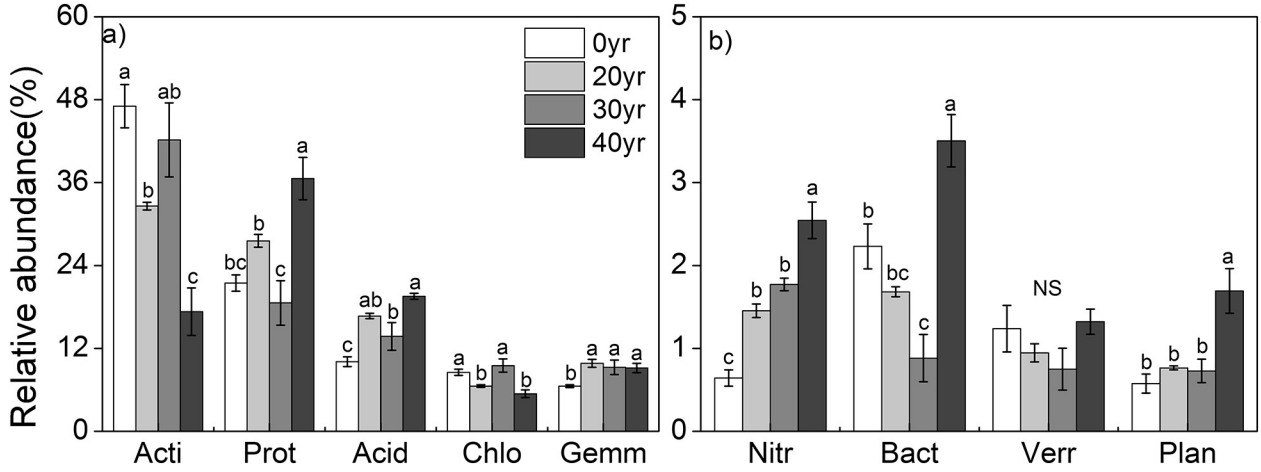

Fig. 4. Relative abundance of the soil bacterial communities at the phylum level. The data for the average relative abundances from three replicates were calculated as the ratio between the abundance of the sequence type and the total number of sequences. All calculations used normalized data. Values are means ± standard error (n = 3). Different letters indicate significant differences ($P < 0.05$) among the successional stages. Actinobacteria (Acti), Proteobacteria (Prot), Acidobacteria (Acid), Chloroflexi (Chlo), Gemmatimonadetes (Gemm), Nitrospirae (Nitr), Bacteroidetes (Bact), Verrucomicrobia (Verr), Planctomycetes (Plan).

Table 3
Spearman's rank correlation coefficients (R) between soil bacterial diversity (i.e., alpha diversity: Shannon index; beta diversity: NMDS1) and the plant and soil characteristics.

Spearman	Shannon index	NMDS1	NMDS2
Plant coverage	0.723**	0.787**	0.293
Plant richness	0.709**	0.755**	0.339
Plant diversity	0.690*	0.704*	0.472
Plant evenness	0.528	0.331	0.838**
Plant biomass	0.638*	0.769**	0.335
Plant biomass C	0.387	0.472	0.704*
Organic C(SOC)	0.783**	0.706*	0.35
Total N(TN)	0.783**	0.622*	0.399
C/N	−0.769**	−0.322	−0.531
NO_3^--N	0.816**	0.378	0.673*
NH_4^+-N	0.413	0.364	0.021
pH	0.48	0.172	0.259
Bulk density(BD)	−0.469	−0.469	0.112

* Significant at 0.05.
** Significant at 0.01.

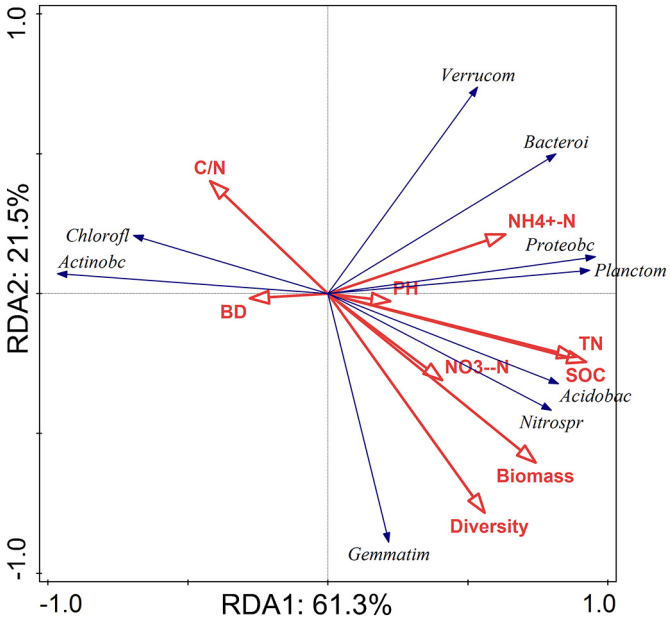

Fig. 5. Ordination plots of the results from the redundancy analysis (RDA) to identify the relationships between the abundance of bacterial taxa (Blue arrows) and environment variable (Red arrows). The plant coverage, plant richness, plant evenness and plant biomass C are highly correlated with plant diversity and biomass (Spearman R = 0.712, R = 0.687, R = 0.786, R = 0.776 respectively for plant diversity; Spearman R = 0.697, R = 0.713, R = 0.806, R = 0.782 respectively for biomass) thus are removed from this analysis. SOC: soil organic C, TN: total N, BD: bulk density, NO_4^+-N: ammonium nitrogen, NO_3^--N: nitrate nitrogen, C/N: C:N ratio, diversity: plant diversity, biomass: plant biomass. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

to the evidence that changes in plant diversity and biomass can support positive responses of soil bacterial alpha diversity during plant secondary succession (Table 3). This result suggests that plant diversity was positively related to soil bacterial diversity in unaffected grasslands (Lloret et al., 2015; Zeng et al., 2016; Ren et al., 2017). A possible explanation is the ability of plant species to provide different niches for bacteria. We also found that plant biomass and plant biomass C were significantly correlated with soil bacterial diversity (Fig. S5a, e). This indicates that higher plant biomass C should lead to stronger plant-soil relationships due to increased substrate availability for decomposers. And the modifications in plant composition that resulted from afforestation greatly affected soil properties such as pH and organic inputs. This result agrees with Zak (2003), who also found a positive effect of plant biomass C on the soil microbial community. Apart from the aboveground plant community, soil nutrients, such as SOC, TN, and NH_4^+-N and control key processes that influence soil bacterial community diversity (Jeanbille, 2015). Our result showed that SOC, TN, and NH_4^+-N positively correlated with soil bacterial alpha diversity (Table 3). The results suggest the importance of soil C and N to the formation of bacterial communities. This result is supported by previous studies (e.g. Yuan et al., 2014) that found that changes in bacterial community composition are sensitive to changes in soil NH_4^+-N after afforestation in topsoil depth along altitudinal gradients. Lian et al. (2017) reported that bacterial diversity in residue treatments was significantly associated with soil characteristics, especially C content, in coarse particulate organic carbon (POC) and microbial biomass carbon (MBC) fractions. However, there is conflicting evidence reported by C. Zhang et al. (2016), who found that NH_4^+-N content was not closely correlated with the relative abundances of the bacterial communities, but that NO_3^--N did have a significant influence. A possible reason for this might be part of N fractions contributing to variation in the bacterial communities during secondary successions (C. Zhang et al.,

2016). Therefore, the profound effect of soil nutrients on soil bacterial communities may be largely indirect (Schlatter et al., 2015).

The positive response of soil bacterial diversity to plant secondary succession and the response to plant and soil characteristics have been discussed above; however, do such responses represent a community-wide response or are they accompanied by changes in certain bacterial taxa? Through further analysis, we determined the functions of specific phyla within the bacterial community, thus revealing their significance to plant and soil characteristics during plant secondary succession. We found a significant correlation between the relative abundance of Actinobacteria, Proteobacteria, Acidobacteria, Chloroflexi, Gemmatimonadetes, Nitrospirae, and Planctomycetes with plant biomass C (Fig. S3), plant biomass (Figs. 5 and S4), plant coverage (Fig. S5) and plant diversity (Figs. 5 and S6). This illustrates the role of plants and plant-microbe interactions in determining the composition of the bacterial community, and bacterial communities dominated by Proteobacteria and Acidobacteria likely play a functional role in plant-soil systems during plant secondary succession. Our present study also found that the phyla Proteobacteria, Acidobacteria, Nitrospirae, Bacteroidetes, and Planctomycetes responded differently to plant secondary succession and correlated to SOC (Fig. S7), TN (Fig. S8), and NH_4^+-N (Fig. S9). Particularly, the Actinobacteria and Proteobacteria were the most abundant bacterial phyla, regardless of successional time. Generally, soil Proteobacteria are favored in copiotrophic environments when labile substrates are available (Goldfarb et al., 2011; Li et al., 2014). The Proteobacteria communities in our study increased during the 40 years of succession, suggesting that soil conditions recovered during plant succession because the rapid growth of Proteobacteria may need large amounts of RNA for high rates of cell division. Jangid et al. (2013) also reported an increasing number of Proteobacteria with increasing age during vegetation succession along the Franz Josef chronosequence in New Zealand. Meanwhile, Proteobacteria, which include the Rhizobiales, are rhizospheric plant growth-promoting symbiotic bacteria (Trivedi, 2016). It is reported that increasing Proteobacteria abundance can also contribute to N accumulation, thereby affecting NO_3^--N and NH_4^+-N contents (Ren et al., 2016b; Wang, 2016; Yao et al., 2017).Thus, these results suggested that the soil bacterial community composition changed during plant secondary succession, and reflected the changes in plant biomass and soil conditions in the changing environment.

Altogether, plant community diversity, soil nutrients, and microbial interactions can significantly affect soil bacterial communities during plant succession. Feedbacks between plant and soil bacterial communities through soil nutrients control ecosystem productivity and maintain ecosystem stability (Goberna, 2016). Our results suggested that converting farmland to grassland results in secondary succession characterized by changes in plant composition, soil properties, and soil bacterial community composition. Such shifts in the bacterial community structure are underpinned, in part, by shifts in plant diversity and composition, and are largely driven by changes in soil nutrients in response to plant succession. Our results provide mechanistic insights disentangling the role of plant and soil parameters in the variation of ecosystem properties associated with plant secondary succession. Finally, our results point toward the important role of plant diversity traits, soil properties, and microbial interactions, supporting the growing view that they are key determinants of aboveground and belowground linkages controlling the functioning of terrestrial ecosystems.

5. Conclusions

The results showed that changes in soil bacterial abundance and diversity were significantly correlated with soil properties and plant traits. We conclude that soil properties and plant traits were the influential factors driving changes in the composition of the bacterial communities following plant secondary succession. Thus, this study can act as a framework that provides insight into the close relationship between plants and soil, which may help us to better understand ecological C cycling in ecosystems. Future studies are required to illustrate how particular taxa respond to the plant-soil system and how these changes, in turn, affect microbial decomposition.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.catena.2018.10.024.

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