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Soil Microbial Population Dynamics along a Chronosequence of Moist Evergreen Broad-leaved Forest Succession in Southwestern China

ZHU Wanze[1, *], CAI Xiaohu[2], LIU Xingliang[2], WANG Jinxi[2], CHENG Song[1], ZHANG Xiuyan[3], LI Dengyu[3], LI Maihe [1, 4*]

1 Institute of Mountain Hazards and Environment, Chinese Academy of Sciences, Chengdu 610041, China

2 Sichuan Academy of Forestry, Chengdu 610081, China

3 Sichuan Agricultural University, Yaan 625014, China

4 Swiss Federal Research Institute WSL, Zuercherstrasse 111, CH-8903 Birmensdorf, Switzerland

**Corresponding authors, e-mail: wzzhu@imde.ac.cn (ZHU Wanze), maihe.li@wsl.ch (LI Maihe)*

Abstract: Little is known about whether soil microbial population dynamics are correlated with forest succession. To test the hypotheses that (1) soil microbial composition changes over successional stages, and (2) soil microbial diversity is positively correlated with plant species diversity, we determined the soil microbial populations, community composition, and microflora diversity in evergreen broad-leaved forests along a chronosequence of vegetation succession from 5 to 300 years in southwestern China. The soil microbial community was mainly composed of bacteria (87.1-98.7% of the total microorganisms and 10 genera identified), fungi (0.3-4.0%, 7 genera), and actinomycetes (2.1-9.1%, 8 species and 1 genus). There were significant differences in soil microbial populations among different successional stages and within the four seasons. The seasonal variations of the soil microbial community may be associated with the seasonal changes in environmental conditions. The changes in soil microbial diversity (Shannon-Wiener index) with successional time followed one-humped, convex curves peaked at ~100 years since restoration, which is identical with the trends of the aboveground plant diversity. Higher plant diversity resulting in enhanced nutrient flow and root exudation may contribute to positive relationships between the soil microbial diversity and plant diversity. Hence, decreases in soil microbial diversity in the late-successional stages appear to be related to the net loss in species richness that occurs after 100 years since restoration. Our findings confirm the intermediate disturbance hypothesis that suggests diversity peaks at mid-successional stages.

Keywords: Actinomycetes; Bacteria; Fungi; Microbial diversity; Moist evergreen broad-leaved forest; Seasonal dynamics

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Introduction

Forest soils contain thousands of species of microorganisms (Staddon et al. 1996). Soil microorganisms play a crucial role in ecosystem functions (Atlas and Bartha 1993, Wardle and Giller 1996, Wardle 2002, Hackl et al. 2004, Kirk et al. 2004), and in the long-term sustainability of soil and forest ecosystems (Pankhurst et al. 1996, Staddon et al. 1998 a, b). Soil microorganisms,

consisting largely of bacteria, fungi, and actinomycetes, are important in regulating ecosystem processes such as decomposition, energy flow, carbon storage, and trace gas flues (Paul and Clark 1997). Most of the nutrient requirements of plants are provided by soil microbial processes via the mineralization of soil organic nutrients, which greatly regulates the net primary production of natural ecosystems (Paul and Clark 1997). In turn, the vegetation (plant community) is one biotic factor thought to be a major determinant of the composition of the soil microbial community since it provides the primary resource for heterotrophic growth (Nüsslein and Tiedje 1999). Forest vegetation influences the micro-environmental conditions and energy supply through their root system, and aboveground and belowground biological processes also affect soil microorganisms (Merila et al. 2002, ZHANG et al. 2005).

Many studies have demonstrated the importance of soil microbial communities for the successful establishment and growth of plants and their community development (Zak et al. 1990, St. John 1993, Zak et al. 1994, Klein et al. 1995, Bever et al. 1997, van der Heijden et al. 1998, Ruzek et al. 2001, Chabrerie et al. 2003, Antonsen and Olsson 2005). On the other hand, changes in plant diversity, composition, and production during succession (Dzwonko and Loster 1990, Zhu et al. 2009) have been found to affect the composition and diversity of soil microbial communities (Wardle et al. 1997, Bardgett and Shine 1999, Broughton and Gross 2000, Chabrerie et al. 2003) due to the bi-directional exchanges between above- and belowground communities (Bever 1994). The effects of the aboveground biomass of plants on soil microorganisms are caused by the quantity and quality of the organic matter produced by different plant species (Wedin and Tilman 1990). Hence, links between plants and soil microorganisms are essential and inevitable. However, our understanding of changes in soil microbial diversity during vegetation succession is still poor (Westover et al. 1997, Allen et al. 1999, Stephan et al. 2000, Chabrerie et al. 2001), and only a very few studies have monitored changes in soil microbial populations along vegetation successional sequences. By producing a comprehensive profile of the soil microbial community's size, functional composition, activity, and physiological status, we might be able to identify the effects of particular management practices for forest restoration.

Previous experiments have examined changes in soil microbial communities in response to the diversity of the aboveground plant species. The published data have documented either a positive relationship between plant diversity and soil microbial diversity (e.g. Bardgett and Shine 1999, Broughton and Gross 2000) or no response of the soil microbial community to aboveground plant diversity (e.g. Wardle et al. 1997, Chabrerie et al. 2003). The present study investigated the soil microbial populations, composition, microbial flora and diversity in soils of humid evergreen broad-leaved forests along a chronosequence of secondary forest succession from 5 to 300 years in southwestern China, to test the hypotheses that (1) soil microbial populations change across successional stages, and (2) soil microbial diversity is positively correlated with plant species diversity.

1 Materials and Methods

1.1 Study area

The study was conducted in the Anzihe Nature Reserve (81.8 km^2, 103°07'-103°27' E, 30°41'-30°52' N), Sichuan, China. The reserve ranges from 960 to 3868 m a.s.l.. The climate is a northern, subtropical, humid monsoon climate. Its temperature ranges from -8 (minimum) to 32.7°C (maximum), and the annual mean temperature is 12.3°C in the centre of the reserve (Anzihe town, 103°15' E, 30°46' N, 866 m a.s.l., Weather bureau of Chongzhou city, Sichuan, China). The mean precipitation is 1300-1450 mm per year. The mean annual relative humidity is 86%. The soil types vary with altitude. The mountain yellow soil occurs in area below 2000 m a.s.l., and the mountain brown soil between 2000 and 2800 m a.s.l..

The moist evergreen broad-leaved forests occur below 2000 m a.s.l. in the reserve. These forests are secondary forests that were allowed to naturally regenerate and develop (WU 1980, LI 1997) following clear-cutting that was done from the 1950s until the end of 20th century (YANG and LI 1992). No other land use or disturbance has been conducted at these sites since the restoration

of the vegetation. The regenerated forest communities, ranging from 5 to 50 years old, are dominated by *Lithocarpus oblanceolatus* C. C. Huang & Y. T. Chang, *L. hancei* (Benth.) Rehder, *L. cleistocarpus* (Seemen) Rehder & E. H. Wilson, *Castanopsis ceratacantha* Rehder & E. H. Wilson, *Cyclobalanopsis glauca* (Thunb.) Oerst., *C. oxyodon* (Miquel) Oerst., *Nothaphoebe cavaleriei* (H. Léveillé) Yen C. Yang, and *Phoebe chinensis* Chun.

To extend the successional sequence, a second research site was selected in the Tiantai National Forest Park (103°9' E, 30°23' N), about 40 km southwest from the Anzihe site. The environmental conditions (climate, soils, vegetation, etc.) are similar to the Anzihe site. The moist evergreen broad-leaved forests at this site were 100- to 300-year-old primary forests located at altitudes of 1000 to 1800 m a.s.l.. The most common tree species are *Schima sinensis* (Hemsley & E. H. Wilson) Airy Shaw and *Symplocos botryantha* Franch.

1.2 Field sampling

Along the successional series, the sample plots were located in 5-, 20-, 30-, 40-, and 50-year-old humid evergreen broad-leaved forests between 1100 and 1700 m a.s.l. in the Anzihe Nature Reserve and in 100- and 300-year-old forests between 1200 and 1500 m a.s.l. in the Tiantai National Forest Park (Table 1). The ages of the forests were determined from tree rings or through interviews with local supervisors. All of the plots selected were similar in terms of topography and soil type. The areas of the selected forests ranged from 1.0 to 2.0 ha, and they were located >200 m apart to avoid possible edge effects of different forest types or successional stages.

The composite sampling method was used to collect samples for the characterization of the structure of the microbial community in each forest (Leckie et al. 2004). For each successional stage, three 20 × 20 m plots were selected for plant diversity research (ZHU et al. 2009) and soil sampling. We sampled soil from each plot in April, July, and October 2003, and January 2004, representing the spring, summer, autumn, and winter, respectively. Soil samples (top soil, 0 - 20 cm) were collected from 10 different points by the S-type or diagonal-mixing sampling method at each plot using a steel cylinder (5 cm in diameter × 20 cm in length). The 10 sampled soil cores were then mixed and homogenized and hand-sieved to remove large particles and organic material (≥ 2 mm in length). Samples were transported to the laboratory and stored at 4°C. Some basic properties of the soils are listed in Table 1.

1.3 Determination of soil microbial populations and its flora

The populations of bacteria, fungi, and actinomycetes were estimated by the dilution plate counting technique (Soil Research Institute of Chinese Academy of Science 1985). This approach

Table 1 Characteristics of the plots and soils sampled

Recovery time (years)	Elevation (m a.s.l.)	Community types	pH	Organic matter ($g \cdot kg^{-1}$)	Available nitrogen ($g \cdot kg^{-1}$)	Available phosphorus ($g \cdot kg^{-1}$)	Available potassium ($g \cdot kg^{-1}$)
5	1620-1650	Shrubbery	6.27	9.58	275.10	1.17	143.35
20	1240-1300	*Lindera limprichtii* +*Cunninghamia lanceolata*	6.86	22.90	540.11	1.34	206.91
30	1360-1400	*Lindera limprichtii*	5.52	36.90	543.17	1.12	323.33
40	1250-1300	*Lindera limprichtii*	7.29	37.82	564.75	1.79	337.21
50	1140-1300	*Juglans cathyensis*+ *Machilus pingii*	7.42	29.62	674.14	2.01	336.00
100	1260-1300	*Symplocos botryatha*	4.43	47.58	770.00	3.09	409.50
300	1400-1450	*Schima sinensis*	4.91	28.04	610.50	3.27	432.20

can provide quantitative yields and specific information on the active, heterotrophic component and biodiversity of microbial populations from soil habitats (Torsvik et al. 1990, Liesack et al. 1997, Kirk et al. 2004), although only a small fraction of the total bacterial population has been found to be cultivable on standard media (Fagri et al. 1977, Ward et al. 1990).

The soil samples were serially diluted, and 0.1 ml suspensions were spread, in duplicate, on the following selective media: beef peptone agar for the enumeration of bacteria; Rose Bengal agar for fungi; and modified Gause No 1 for actinomycetes. Total colony counts were determined after incubating samples for 3 days at 28 - 30 °C for bacteria, 3 - 4 days at 25 °C for fungi, and 7 - 10 days at 28 - 30 °C for actinomycetes.

The soil bacteria (ZHANG 1983), fungi (Barnett and Hunter 1998, Wei 1979) and actinomycetes taxa (The classification department of streptomyces taxonomy of Institute of Microbiology, Chinese Academy of Sciences 1975, Jiang et al. 1995) were identified by microscopic morphology. Bacteria and fungi were identified to the genus level and actinomycetes to the species or genus level.

1.4 Calculation of soil microbial diversity

The soil bacteria, fungi, and actinomycetes communities were identified only to the level of genus due to the difficulties in isolation. Studies have shown that using the genus or family as the measuring unit can reflect the characteristics of microbial diversity (YU and ZHOU 1996). We calculated the Shannon-Wiener index (H') at the genus level in the present study (Ma and Liu 1994).

$$H' = -\sum P_i \ln P_i ,$$

where P_i is the proportional abundance of the ith genus in a plot ($P_i = n_i / N$, n_i was the number of strains of the ith genus for the bacteria, fungi or actinomycetes in a plot; $N=\sum n_i$, N is the sum of the number of strains of all genera).

1.5 Data analysis

Analyses were carried out using the triplicate samples, and the mean values with their standard error (SE) are presented after statistical analyses. The significance of the main effects for soil microbial populations (microbial composition, successional stage, season) was evaluated by one-way ANOVAs. The soil microbial Shannon-Wiener diversity index was calculated for each soil sample using the above-mentioned formula, and the least significant ranges (LSR) test was used to detect differences between pairs of diversity data. Pearson correlation analysis was used to test for correlations between the soil microbial Shannon-Wiener index and the plant species diversity. The SPSS (version 13) statistical software (SPSS Inc. Chicago, USA) and SigmaPlot 8.0 software (Aspire Software International, Leesburg, USA) were used to perform the analyses.

2 Results

2.1 Soil microbial populations and composition across successional stages

The total soil microbial plate counts within each season were significantly different among successional stages (F=1265.908, p<0.001 for spring; F=16891.367, p<0.001 for summer; F=5902.677, p<0.001 for autumn; F=873.213, p<0.001 for winter) (Figure 1a). The total counts for all of the microbial populations tended to increase with recovery time for the first 40 years after vegetation restoration, except for during the summer (Figure 1a). After 40 years of succession, the total microbial populations tended to decrease with recovery time (Figure 1a). The counts of the bacterial (Figure 1b), fungal (Figure 1c), and actinomycetes populations (Figure 1d) also varied among the successional stages of vegetation. The pattern of the bacterial populations across successional stages was similar to that of the total microbial populations (Figure 1b vs. Figure 1a), whereas the fungal and actinomycetes populations had patterns similar to each other (Figure 1c, d). The bacterial and actinomycetes populations had their maximum counts in soils of 40-year-old forests (after restoration) (Figure 1b, d), whereas the fungal populations reached the maximum values in soils of 100-year-old vegetation (Figure 1c). There were more fungal populations in the

later successional stages (100-300 years) than in the earlier stages (before 50 years).

The composition of the soil microbial community was similar across the successional stages. In the earlier successional stages (<50 years), the bacterial populations occupied 89.7-98.7% of the total soil microbial counts, followed by actinomycetes (2.1-9.1%), and fungal populations (0.3-4.1%). The fraction that the bacterial population contributed to the total abundance of microorganisms decreased to 87.1% in the soils under the 100-year-old secondary forests, while the contribution of the fungal populations increased to 8.2%.

2.2 Seasonal variations of soil microbial populations across successional stages

The seasonal variations of the total soil microbial populations were similar among the successional stages (Figure 1a). The total abundance of the microbial populations in summer was significantly greater than in the other 3 seasons (p<0.001) at each successional stage (Figure 1a). The differences in the total abundance of microbial populations between any two seasons were significant (p<0.001), except that there was no difference between autumn and spring (F=2.825, p>0.05) at each recovery time.

The counts of bacterial populations in the soils of early successional stages (<30 years) followed a seasonal variation of summer > spring > autumn > winter, while those in forest soils with >30 years restoration time showed an order of summer > autumn > spring > winter (Figure 1b). The seasonal variations in the counts of soil fungi populations tended to be similar to those of bacterial populations (Figure 1c), while the actinomycetes had the highest population abundances in the autumn, followed by the summer, spring, and winter (Figure 1d). The fraction of bacteria in the total microbial population was higher in summer, while those of the fungi and actinomycetes were higher in the autumn. The seasonal variations in the abundance of the total soil microbial population were mainly determined by the differences in the bacterial population due to its

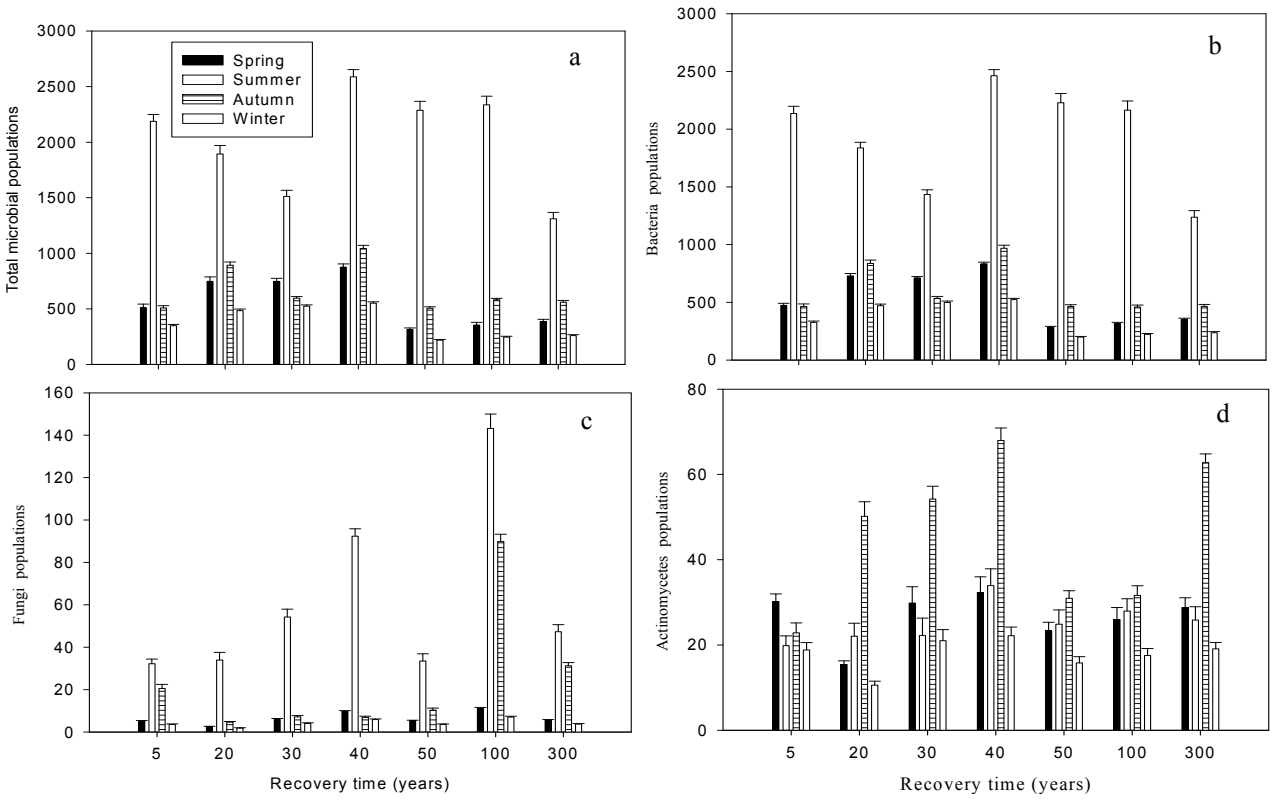

Figure 1 Composition and seasonal variations of soil microbial populations (mean ±SE, $\times 10^3$ CFU g^{-1} dry soil) over the successional stages. (a) Total microorganism, (b) Bacteria, (c) Fungi, and (d) Actinomycetes

great proportion.

2.3 Soil bacterial flora among successional stages

Ten genera of soil bacteria were isolated from the study sites, and the dominant genera varied among the successional stages (Table 2). *Achromobater*, *Brevibacterium*, and *Bacillus* occurred the most frequently among the successional stages (Table 2). The abundance of *Achromobater* was higher in the late- successional stages than in the early-successional stages, with 30.98% in the 100-year-old forest soils and 20.71% in the 300-year-old forest soils, respectively. *Conynebacterium* and *Plavobacterium* only appeared in the early-successional stages (before 50 years) with their maximum abundances in the 30-year-old and the 20-year-old successional stages respectively (Table 2). *Micrococcus* and *Arthrobacterium* only occurred in the 100- and 300-year-old community forest soils (Table 2).

2.4 Soil fungi flora among successional stages

A total of 7 fungal genera mainly belonging to the Deuteromycetes and Zygomycetes were identified along the chronosequence of vegetation restoration (Table 3). *Geoglossun* only occurred in the 100- and 300-year-old communities, and the other 6 genera were present in each successional stage (Table 3). The abundance of *Absidia* increased gradually with recovery time during the early-successional stages (< 50 years) and showed a decreasing trend after 50 years (Table 3). The dominant fungal genera varied among successional stages; for example, *Pythium* and *Mncor* dominated in the 5-year-old shrub soil, *Trichoderm* in the 20- and 30-year-old forest soil, *Pythium* in the 40-year-old forest soil, and *Absidia* in the 50-year-old forest soil (Table 3).

2.5 Soil actinomycetes flora among successional stages

A total of 9 soil actinomycetes species were isolated along the chronosequence of forest succession (Table 4). Among them, 8 species belong to *Streptomyces* and 1 genus to *Micromonospora*. *S. albosporus* and *S. griseofuscus* were found across all of the successional stages, and *S. aureus* and *Micromonospora* (genera) were present in 6 out of 7 vegetation succession stages (Table 4). *S. griseorubroviolaceus* only occurred in soils of the early successional stages (< 50 years), while *S. uiridis* existed only in the late-successional stages (after 100 years) (Table 4). *S. lavendulae* occurred only in the 100-year-old forest sites at a low abundance (4.91%) (Table 4). The dominant actinomycetes were *Micromonospora* in the 5-

Table 2 Soil bacterial flora among successional stages (mean abundance, %)

Genus	Recovery time (years)						
	5	20	30	40	50	100	300
Achromobater	20.07	2.28	19.14	3.07	10.98	30.98	20.71
Corynebacterium	32.67	27.35	33.61	10.65	21.32	—	—
Brevibacterium	14.30	30.08	4.35	36.64	40.24	21.51	11.29
Cellulomonas	—	—	16.20	—	—	—	—
Bacillus	2.04	9.92	1.86	14.04	4.33	7.79	7.04
Plavobacterium	2.21	11.53	5.71	4.15	5.23	—	—
Pseudomonas	—	—	—	16.92	2.65	—	—
Micrococcus	—	—	—	—	—	10.49	4.69
Arthrobacterium	—	—	—	—	—	12.40	37.73
Chromobacterium	13.09	—	—	—	—	—	—
Others	15.61	18.84	19.13	14.54	15.25	16.84	18.54

"—" indicates that no distribution was found.

Table 3 Soil fungi flora among successional stages (mean abundance, %)

Genus	Recovery time (years)						
	5	20	30	40	50	100	300
Penicillium	12.56	5.82	6.87	5.27	13.06	13.49	8.18
Trichoderma	10.47	43.02	46.64	15.15	14.29	8.62	4.44
Geotrichum	—	14.84	11.69	4.38	11.98	7.43	—
Geoglossun	—	—	—	—	—	13.50	9.19
Mncor	22.95	4.41	6.02	13.83	3.68	6.90	6.43
Absidia	3.30	5.48	6.84	12.40	30.98	18.95	25.06
Pythium	40.29	21.88	10.81	44.58	13.07	21.81	42.26
Others	10.43	4.55	11.14	4.39	12.93	9.30	4.44

"—" indicates that no distribution was found.

Table 4 Soil actinomycetes flora among the successional stages (mean abundance, %)

Species or Genus	Recovery time (years)						
	5	20	30	40	50	100	300
Streptomyces Griseorubroviolaceus	8.69	26.87	14.59	8.51	8.54	—	—
S. Uiridis	—	—	—	—	—	6.81	5.64
S. Aureus	4.35	—	4.49	17.01	33.68	22.11	34.16
S. Glaucus	—	—	16.83	2.16	5.12	22.74	4.72
S. Roseosporus	6.53	—	—	4.25	10.25	5.42	—
S. Griseofuscus	8.69	25.53	9.35	21.27	3.11	19.86	6.54
S. Lavendulae	—	—	—	—	—	4.91	—
S. Albosporus	6.53	25.53	12.35	29.78	20.50	5.50	8.93
Micromonospora	52.18	16.85	31.53	—	11.96	3.61	32.68
Others	13.04	5.22	10.86	17.01	6.84	9.04	7.33

"—" indicates that no distribution was found.

year-old forest soil; *S. griseorubroviolaceus*, *S. albosporus* and *S. griseofuscus* in the 20-year-old forest soil; *Micromonospora* in the 30-year-old forest soils; *S. albosporus* and *S. griseofuscus* in the 40-year-old forest soil; and *S. aurens* in the 50-year-old forest soil (Table 4). In the 100-year-old forest, soil actinomycetes were dominated by *S. aureus*, *S. glaucus* and *S. griseofuscus* (Table 4). The absolutely dominant actinomycetes in the soils of the latest successional stage, 300-year-old forests, were *S. aureus* and *Micromonospora* (Table 4).

2.6 Soil microbial diversity among successional stages

The diversity of soil microbial communities significantly varied among successional stages (Table 5). The trends in the Shannon-Wiener diversity indices through the recovery times for the total microbial community and each component (bacteria, fungi, actinomycetes) showed one-humped, convex curves with a turning point at 100 years since vegetation restoration, except for that the bacteria reached its maximum H' between 40

Table 5 The Shannon-Wiener indices (mean values ± SE) of soil microorganisms across a forest successional series

Recovery time (years)	Shannon-Wiener index			
	Community	Bacteria	Fungi	Actinomycete
5	4.22±0.06a	1.15±0.04a	1.55±0.05a	1.52±0.04a
20	4.28±0.05a	1.20±0.04a	1.58±0.04a	1.50±0.02ae
30	4.62±0.05b	1.19±0.03a	1.63±0.04a	1.81±0.05b
40	4.75±0.07c	1.43±0.05b	1.61±0.04a	1.72±0.07c
50	4.97±0.06d	1.33±0.04cd	1.81±0.06b	1.83±0.04b
100	5.36±0.08e	1.39±0.03bc	2.00±0.05c	1.98±0.07d
300	4.32±0.06a	1.30±0.04d	1.59±0.04a	1.43±0.03e

Differences in diversity between recovery times were tested with *LSR* (least significant ranges). Different letters indicate significant differences in means ($p < 0.05$) between recovery times within each category.

and 100 years (Table 5). The diversity indices did not change across successional stages for the first 20 years of restoration for the total soil microbial community and actinomycetes community, and within the first 30 years for bacterial and fungal communities (Table 5).

3 Discussion

3.1 Composition of soil microbial community

In line with our hypothesis 1 (see Introduction), soil microbial composition was found to change across the successional stages (Figure 1, Tables 2, 3, 4, and 5). Previous studies have expected that changes in plant composition or vegetation type along a successional series determine soil microbial community composition (Mason et al. 1983, Widden 1986, Johnson et al. 1991, Visser 1995, Grayston et al. 2001, Marschner et al. 2001, XUE et al. 2006). Not only the complexity of soil microbial communities but also the absolute quantities of microorganisms or microbial biomass have been found to increase with time from the early stages to the late stages of succession (Singh et al. 2001, Merila et al. 2002 ZHU 2005). In the present study, the total abundance of soil microorganisms, and the bacteria and actinomycetes populations in the 40-year-old forest soils increased by 1.72-4.51, 1.75-4.57, and 1.07-2.97 folds, respectively, compared to those found at the 5-year-old sites. The fungal populations increased by 2.11-4.45 folds in the 100-year-old forest soils compared to those in the soils of the 5-years-old sites.

The soil microbial composition and variability reflect the adaptability of microorganisms to soil environments (Harris 2003). As plant succession proceeded, the ratio of fungi to bacteria increased and reached a maximum value of 0.035 to 0.195 (depending on seasons) in the 100-year-old forest community. Soil bacteria have been found to be dominant in microbial communities during the early successional stages, and fungi gradually became predominant with further succession (c.f. Ohtonen et al. 1999, Bardgett et al. 1999a). Ohtonen et al. (1999) have found that the ratio of fungi to bacteria increased in soils along a glacial successional sequence. Similarly, Bardgett et al. (1999a) have reported an increase in the fungi-bacteria ratio in an experiment that simulated plant succession.

However, our results did not coincide with Frankland's (1998) demonstration of greater fungal richness in mid-successional coastal dunes. In the present study, the initial increase in the abundance of microbial populations at the early stages of succession coincided with inputs of fresh organic matter. This rapid increase reflects the ubiquity of heterotrophic microorganisms and their rapid growth rates once carbon resources became available. During the late stages of succession (100 - 300 years), the evergreen broad-leaved trees such as *S. sinensis* and *S. botryatha* that dominate the forest community create a shady, wet, and acidic environment (pH 4-5) that is unfavourable for the

propagation of bacteria but favourable to fungi, leading to decreases in the total microbial and bacterial populations but increases in the fungal populations.

3.2 Relationships between soil microbial diversity and plant diversity

The Shannon-Wiener diversity of soil microbial populations was found to vary among the successional stages (Table 5). XUE et al. (2006) have found that microbial community diversity increased with time in 8- to 50-year-old tea orchards and then decreased with time in 50- to 90-year-old tea orchards. In a previous study carried out at the same plots as the present study, we found that the plant composition and diversity also changed with time since vegetation restoration (ZHU et al. 2009). In line with our hypothesis 2 (see Introduction), correlations analysis revealed that the Shannon-Wiener diversity indices of the overall soil microbial community, and the bacterial, fungal, and actinomycetes communities were significantly positively correlated with the diversity index of the aboveground plant community ($p<0.01$ for each) and of the shrub species ($p<0.05$ for each) (Table 6). The diversity of trees significantly positively affected the bacterial diversity ($p<0.05$), while the diversity of the herbaceous vegetation significantly positively influenced the fungal diversity ($p<0.01$) and the total soil microbial diversity ($p<0.01$) (Table 6). Significant effects of plant diversity on soil microbial diversity have already been reported (Hedlund et al. 2003, Carney and Matson 2005, Goberna et al. 2005, Carney and Matson 2006). Stephan et al. (2000) have found that the diversity of soil bacteria increased linearly with the number of plant species and plant functional groups in experimental grassland ecosystems. These positive effects of plant diversity on soil microbial diversity may be caused by an increase in the quality and quantity of organic material and energy flow into soils (Klein et al. 1988, Grayston et al. 1998, Merbach et al. 1999, Stephan et al. 2000). A higher litter diversity and decomposability resulting from a greater diversity of plant species (Sulkava and Huhta 1998, Hansen 2000) may result in a higher number of micro-niches available for soil microorganisms. These, consequently, might promote the coexistence of microbial species and stimulate their diversity (Wardle and Giller 1996, Ettema and Wardle 2002).

In forest soils, a greater diversity of litter types can support a greater fungal diversity (Widden 1986). Myers et al. (2001) have stated that the distinct composition of microbial communities in different forest types is likely a result of the content of labile and recalcitrant compounds released during litter decomposition. Furthermore, plant species can regulate the development of beneficial rhizobacteria through the release of specific sugars and amino acids into the root zone (Burr and Caesar 1984, Kowalchuk et al. 2002). Hence, higher plant diversity may produce a higher biochemical diversity of root exudates and, therefore, select for more diverse microbial communities (Lavelle et al. 1995). Annual herbaceous plants exude more of their assimilated carbon into the soil than trees (Leyval and Berthelin 1993, Grayston et al. 1996) and also exude a different spectrum of compounds (Grayston et al. 1996) for various soil microorganisms, leading to a higher correlation between the total soil microbial community and herbaceous species diversity (Table 6).

Table 6 Correlative coefficient between the Shannon-Wiener indices of plant species and the indices of the soil microbial community. *R-values* are given. $^{*}p<0.05$, $^{**}p<0.01$.

Soil microbial diversity	Aboveground plant diversity			
	Community	Arbor stratum	Shrub stratum	Herbage stratum
Community	0.7331**	0.4128	0.6757*	0.7512**
Becteria	0.6658**	0.5254*	0.7352**	0.2775
Fungi	0.6529**	0.2594	0.5703**	0.5915**
Actinomycetes	0.6018**	0.3482	0.5183*	0.3314

Note data of plant diversity were published in ZHU et al. (2009).

3.3 Seasonal dynamics of soil microorganisms

The present study found that the total abundance of soil microorganisms and the bacterial and fungal populations were highest in summer and lowest in winter, while the actinomycetes population was highest in autumn and lowest in winter (Figure 1). Similar seasonal variations in soil microorganisms have already been reported by studies carried out in different ecosystems (e.g. Rahno et al. 1978, Gilmanov and Bogoev 1984, Golovchenko and Polyanskaya 1996, Bossio et al. 1998, Bardgett et al. 1999b, Alekhina et al. 2002, Cleveland et al. 2006). Consistent with our findings, those studies have also shown that the microbial populations were highest in summer or autumn. Such seasonal variation could be associated with variations in microclimate and resource availability that occur at the same time scale. Seasonal variations in temperature, soil moisture, flushes of resource inputs from litter, and root exudates affect microbial activity and may suppress or promote the development of populations (Clarholm and Rosswall 1980, Torsvik and Øvreås 2002). Buckley and Schmidt (2003) have also stated that microbial community composition and populations in soil can vary dramatically at spatial and temporal scales associated with environmental conditions.

In conclusion, the seasonal variations of the soil microbial community (Figure 1) are associated with the seasonal changes in environmental conditions. Changes in soil microbial diversity (Shannon-Wiener index) with successional time followed one-humped, convex curves peaked at ~100 years since restoration (Table 5), which is identical with the trends of the aboveground plant diversity (Table 6, ZHU et al. 2009). Higher plant species diversity leading to enhanced flux of nutrients and root exudates may contribute to positive relationships between plant diversity and soil microbial diversity. Hence, decreases in soil microbial diversity in the late-successional stages (Table 5) appear to be related to a net loss in plant species richness that occurs after 100 years since restoration (Table 6, ZHU et al. 2009). Our findings confirm the intermediate disturbance hypothesis that suggests diversity peaks at the mid-successional stages.

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