

Recovery of Collembola in *Pinus tabulaeformis* Plantations



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CHANG Liang^{1,2}, WANG Baifeng², LIU Xianghui¹, Mac A. CALLAHAM Jr.³ and GE Feng^{1,*}

¹State Key Laboratory of Integrated Management of Pest and Rodents, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101 (China)

²Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun 130102 (China)

³USDA, Forest Service, Southern Research Station, Center for Forest Disturbance Science, Athens GA 30602 (USA)

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ABSTRACT

Large areas of forest plantations have been developed in China. It is important to evaluate the soil fauna in plantations and the conditions needed for their recovery in view of the large areas of plantations in China. Three *Pinus tabulaeformis* forests, a 26-year-old plantation (P26) and a 45-year-old plantation (P45), exposed to clear-cutting before plantation, and an 80–260-year-old natural forest (N260), were chosen to study the effects of different forest ages/types on Collembola community in the litter and soil layers during 2008 and 2009. Soil conditions in P26 and P45 were significantly deteriorated when compared to N260. A higher value of soil bulk density and lower values of soil organic matter, soil N, litter depth, soil pH, and soil water content were observed in P26 and P45. Totally, the same genera of Collembola tended to occur in the forests of all ages studied; however, the Collembola community structure was significantly impacted by the differences in forest age. Both in the litter and soil layers, the density and generic richness of the Collembola were the highest in N260 and the lowest in P26. Some collembolan groups were sensitive to soil conditions in particular forest ages. N260 was associated with relatively high abundance of *Plutomurus* collembolans and P45 with relatively high abundance of *Pseudofolsomia* collembolans. The canonical correspondence analysis showed that the community structure of Collembola was mainly affected by forest age in both litter and soil layer. The ordination analysis of non-metric multidimensional scaling also found that the Collembola community did not recover to the level of natural forests in 26-year regeneration after clear-cutting. Even in 45-year regeneration after clear-cutting, the Collembola community only showed a slight recovery to the level of natural forests. Our results clearly showed that both Collembola community and soil conditions did not recover in 26- and 45-year regeneration after clear-cutting in *P. tabulaeformis* plantations; however, they might have the potential to recover in the future because the same genera of Collembola were distributed in the plantations and natural forests.

Key Words: community structure, forest age, litter layer, soil conditions, soil fauna, soil layer

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INTRODUCTION

Forest plantations are widely distributed in China, and the area occupied by plantations is increasing (Zhang, 2006). For example, plantations of *Pinus tabulaeformis* comprise 17.3% of total forest stands in Beijing (Zhang, 2006). A number of studies have suggested that monoculture plantations, especially coniferous stands, have considerable environmental costs when the land was previously occupied by deciduous forests. Specifically, the effects such as soil acidification and decreased soil fauna richness have been reported (Kazda and Pichler, 1998; Scheu and Falca, 2000; Pollierer *et al.*, 2007). In contrast, Salamon *et al.* (2008) observed that soil fauna communities did not differ strongly over different types (beech, spruce, and mixed stands) and ages (30 and 120-year-old) of stands. Moreover, popu-

lation densities of soil fauna in plantations may recover to the levels of mature forest stands in as little as 4 years (Hasegawa *et al.*, 2006). Given the variable results from previous work, the currently available evidence is insufficient to predict whether the biodiversity and physical/chemical properties of soils in monoculture plantations, in particular in *P. tabulaeformis* plantations in China, can recover to the levels found in natural mature forests.

Much of the biodiversity of forest ecosystems resides in soil (Behan-Pelletier and Newton, 1999), and the importance of the diversity of soil biota to the integrity and functioning of terrestrial ecosystems is well recognized (Wall, 1999; Osler and Sommerkorn, 2007). Collembola are one of the most abundant and ubiquitous groups of soil arthropods, and collembolan communities are structured by a number of factors, such

*Corresponding author. E-mail: gef@ioz.ac.cn.

as soil fertility (Hågvar, 1982), humus type (Cassagne *et al.*, 2003), water content (Verhoef, 1981), and biological factors (Hågvar, 1982; Addison *et al.*, 2003b). Therefore, Collembola are thought to be useful bioindicators for forest management (Cassagne *et al.*, 2006).

Many studies have employed a chronosequence approach to examine long-term changes in forest succession. Soil and soil fauna recoveries are very important to nutrient cycling and sustainable forestry (Butterfield, 1999; Johnston and Crossley, 2002). Most of these studies concerned Douglas-fir, beech, and other coniferous and deciduous forests in a number of European countries, Australia, and Japan (Addison *et al.*, 2003a, b; Hasegawa *et al.*, 2006; Salamon *et al.*, 2008). However, the responses of soil fauna community to forest succession in Chinese pine forests have not yet been adequately evaluated.

Forest stands with three ages, representing 2 stand types (plantations after clear-cutting and natural forests), were chosen to analyze the differences of the Collembola community in their litter and soil layers. The specific objectives of the present study were as follows: i) to estimate the recovery of soil properties in the replanted pine forests plantations, ii) to estimate the recovery of soil Collembola community in pine forest plantations when compared to natural mature forests, and iii) to sift some local indicative groups for different forest ages.

MATERIALS AND METHODS

Study site and experimental design

The study area was located in the Jundu Mountain in the Yanshan Mountains of northern Beijing, China (40°19' N, 115°30' E). The mean annual air temperature is 8.5 °C, and the mean annual precipitation is approximately 600 mm. The original forests were dominated by *Pinus tabulaeformis*, and *Populus davidiana*, *Quercus mongolica* and *Juglans mandshurica* were sparsely distributed in this area. Most of the forests were cut in 1950s–1960s and pine trees were replanted in 1963 and 1982. Three forests with different ages were selected in this study: an 80–260-year-old natural forest (N260), where all the trees were more than 80 years old and over 80% of the trees were ≥ 260 years old; a 45-year-old plantation (P45), where monospecific *P. tabulaeformis* pine trees were replanted in 1964 after clear-cutting; and a 26-year-old plantation (P26), where monospecific *P. tabulaeformis* pine trees were replanted in 1982 after clear-cutting. In total, 12 sites with the area more than 100 m \times 100 m were located in 3 forested fields, with intervals of 20 km between

each site. In Field I, one N260 site, one P45 site, and two P26 sites were located; in Field II, one N260 site, two P45 sites, and one P26 site were located; and in Field III, two N260 sites, one P45 site, and one P26 site were located. Four replicate sites were chosen for each forest age. Sampling for the study was conducted in 2008–2009. All the forest fields had typical dark brown forest soil.

Collembola sampling and identification

Collembolans in the litter layer were sampled on May 30, July 30, and September 30 in 2008 and 2009. On each sampling date, three litter samples (10 cm \times 10 cm) were taken from each site. Litter depths were recorded at each sampling location on each sampling date during 2008. Collembolans in the soil layer were sampled monthly from April 30 to October 10 during 2008 and 2009. On each sampling date, three soil cores (height of 52 mm, diameter of 70 mm) were taken per site. Frost and snow cover prevented litter and soil sampling for the remaining months during 2008 and 2009. The collembolans were extracted using the method of Macfadyen (1961). The extracted organisms were preserved in 75% (volume:volume) ethanol for subsequent identification. The collembolans were identified to genus with the keys in Yin (1998) and Christiansen and Bellinger (1980).

Soil sampling and analysis

Soil samples were collected to determine soil main physicochemical characteristics on the same dates as litter and collembolan sampling in 2008. Two soil cores (height of 52 mm, diameter of 70 mm) per site were collected. One soil core was weighed to determine soil bulk density. Another soil core was prepared to determine some other soil properties using the following methods. Approximately 20 g of soil was oven-dried at 110 °C for 48 h and reweighed to determine soil water content. Soil pH was measured in 1 mol L⁻¹ KCl, soil organic matter (SOM) was determined by wet oxidation with K₂Cr₂O₇, and soil N content was assayed using automated KjeltecTM N analysis (Model 2100, FOSS, Denmark).

Data analyses

The individual number of Collembola was $\log(n+1)$ transformed to obtain a normal distribution. Differences in the composition of Collembola among the different forest stands were analyzed using canonical correspondence analysis (CCA). Only the genera of collembolans present in at least three independent samples were included in the analysis.

To obviate phenological differences of sampling dates, cumulative genus abundances of all the sampling dates were combined. A one-way analysis of variance was performed to analyze the influence of different forest stands on soil properties, density and generic richness of Collembola. SPSS 13.0 for Windows and CANOCO version 4.5 were used for data analysis. Non-metric multidimensional scaling (NMDS) was computed using Bray-Curtis similarity matrix to visualize the relationships between all the samples at 12 sites, based on the $\log(n + 1)$ transformed data of cumulative genus abundances. The optimal number of dimensions was determined by the NMDS ordination with the minimum stress.

RESULTS

Soil properties

Forest age had a significant effect on main soil physicochemical properties and litter depth (Table I). Soil bulk density in N260 was less than that in P45 and P26. The SOM and soil pH were greater in N260 than in P45 and P26. Litter depth and soil water content were less in P45 than in N260 and P26. Soil N was the highest in N260 and the lowest in P26.

Collembola composition

A total of 26 648 collembolans, involving 25 genera of Collembola (Tables II and III), were identified in the litter and soil layers of the three different forest stands (P26, P45, and N260). Over the two years of sampling nearly all the genera were found in each forest. The only exception was the genus *Folsomia*, which was not found in P45 at any sampling date.

In the litter layer, forest age significantly ($P < 0.05$) influenced the community structure of Collembola

(Table IV) and it explained 11.0% of the total variance. The litter depth and C/N significantly affected the variation of the Collembola community composition and they explained 7.3% and 3.2%, respectively, of the total variance. From the NMDS ordination of the 36 litter samples at 12 sites (stress = 17.18), there was a clear transition from P26 to N260 sites. The P45 sites were generally intermediate, although a few of the P45 sites overlapped the N260 sites in the ordination space. Dispersion of cluster points was the highest in P26 and the lowest in N260 (Fig. 1).

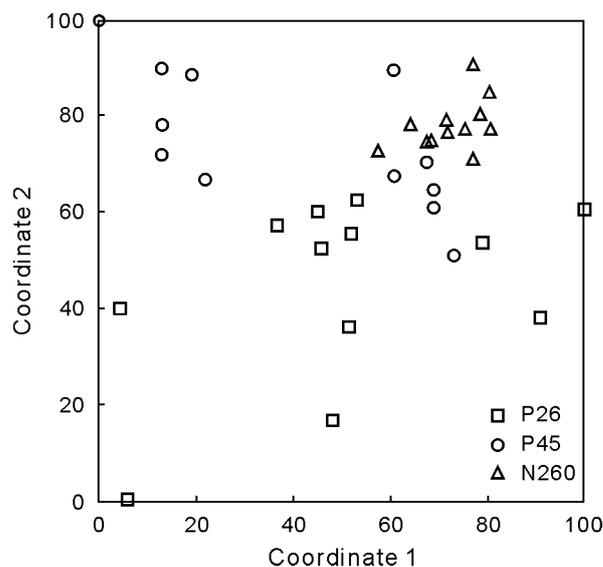


Fig. 1 Non-metric multidimensional scaling plot based on Bray-Curtis dissimilarity matrix derived from the $\log(n + 1)$ transformed data of cumulative genus abundances of Collembola in the litter layer of the 26-year-old plantation (P26), 45-year-old plantation (P45), and 80–260-year-old natural forest (N260) in the Jundu Mountain of Beijing, China in 2008 and 2009.

In the soil layer, forest age (P26, P45, and N260) significantly ($P < 0.05$) altered the community structure of Collembola (Fig. 2) and it explained 7.0% of

TABLE I

Main soil physicochemical properties and litter depth in the 26-year-old plantation (P26), 45-year-old plantation (P45), and 80–260-year-old natural forest (N260) in the Jundu Mountain of Beijing, China

Forest	Soil N	SOM ^{a)}	Soil pH	Soil water content	Soil bulk density	Litter depth
	g kg ⁻¹			g kg ⁻¹	g cm ⁻³	mm
P26	2.56 ± 0.35 ^{b)c)}	166.17 ± 10.53b	5.34 ± 0.18b	2.1 ± 0.1a	1.00 ± 0.02a	54.42 ± 1.61b
P45	3.59 ± 0.19a	169.85 ± 4.58b	5.34 ± 0.08b	1.7 ± 0.1b	1.00 ± 0.02a	53.58 ± 1.43b
N260	3.99 ± 0.24a	206.15 ± 9.05a	6.23 ± 0.17a	2.2 ± 0.1a	0.73 ± 0.03b	70.33 ± 0.67a
P value	0.009**	0.007**	< 0.001***	0.04*	< 0.001***	< 0.001***

*, **, ***Significant at $P < 0.05$, $P < 0.01$, and $P < 0.001$, respectively.

^{a)}Soil organic matter.

^{b)}Means ± standard errors ($n = 12$).

^{c)}Means followed by the same letter within each column are not significantly different by the least significant difference test at $P < 0.05$.

TABLE II

Densities of Collembola in the litter layer of the 26-year-old plantation (P26), 45-year-old plantation (P45), and 80–260-year-old natural forest (N260) in the Jundu Mountain of Beijing, China in 2008 and 2009

Family	Genus (abbreviation)	2008			2009		
		P26	P45	N260	P26	P45	N260
		individuals m ⁻²					
Arrhopalitidae	<i>Arrhopalites</i> (AR.ar)	4	0	118	419	309	748
Bourletiellidae	<i>Bourletiella</i> (BO.bo)	0	0	8	71	94	161
Brachystomellidae	<i>Setanodosa</i> (BR.se)	43	121	90	67	114	125
Entomobryidae	<i>Entomobrya</i> (EN.en)	39	8	74	349	251	678
	<i>Lepidocyrtus</i> (EN.le)	12	0	39	82	71	121
	<i>Margimobrya</i> (EN.ma)	4	0	71	67	12	231
	<i>Sinella</i> (EN.si)	12	20	71	74	125	208
Hypogastruridae	<i>Acherongia</i> (HY.ac)	43	43	172	129	106	270
	<i>Hypogastrura</i> (HY.hy)	82	141	282	1363	1242	1567
	<i>Schoettella</i> (HY.sc)	110	145	184	110	411	709
Isotomidae	<i>Folsomia</i> (IS.fl)	4	0	8	0	0	0
	<i>Folsomides</i> (IS.fo)	16	82	298	35	251	82
	<i>Isotoma</i> (IS.is)	74	24	78	86	204	141
	<i>Proisotoma</i> (IS.pr)	8	16	35	0	0	0
	<i>Pseudanurophorus</i> (IS.pa)	345	196	1426	227	215	697
	<i>Pseudisotoma</i> (IS.pi)	55	16	43	4	20	90
	<i>Pseudofolsomia</i> (IS.po)	1680	6114	3388	1680	6768	3086
Odontellidae	<i>Odontella</i> (OD.od)	110	176	235	98	380	290
Onychiuridae	<i>Bionychiurus</i> (ON.bi)	881	411	975	396	290	654
	<i>Cribrochiurus</i> (ON.cr)	121	86	501	4	86	517
	<i>Onychiurus</i> (ON.on)	1618	1116	2272	1864	1520	2013
	<i>Probolaphorura</i> (ON.pb)	423	454	776	407	317	736
	<i>Protaphorura</i> (ON.pt)	1978	1351	2859	1524	1316	2154
	<i>Sensillonychiurus</i> (ON.se)	74	55	384	8	35	309
Tomoceroidea	<i>Plutomurus</i> (TO.pl)	47	168	486	337	956	2526
Total		7783	10744	14872	9401	15092	18116

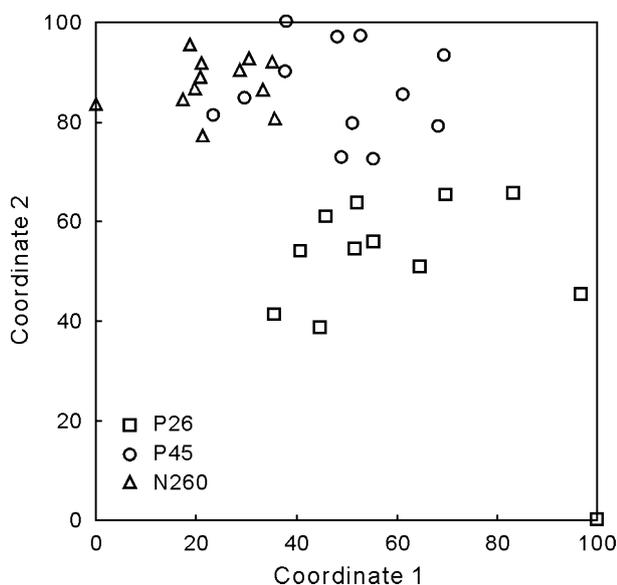


Fig. 2 Non-metric multidimensional scaling plot based on Bray-Curtis dissimilarity matrix derived from the $\log(n+1)$ transformed data of cumulative genus abundances of Collembola in the soil layers of the 26-year-old plantation (P26), 45-year-old plantation (P45), and 80–260-year-old natural forest (N260) in the Jundu Mountain of Beijing, China in 2008 and 2009.

the total variance. The litter depth, soil C/N, soil water content, and soil bulk density significantly affected the variation in the Collembola community composition and they explained 2.4%, 1.9%, 1.2%, and 3.8%, respectively, of the total variance. The NMDS ordination of the 36 soil samples at 12 sites (stress = 14.75) showed a clear transition from P26, on the under side of the graph, to N260 on the upside. Four samples (totally 12) of P45 reached the level of N260 in terms of Collembola community. Dispersion of cluster points was lower in N260 when compared to P26 and P45 (Fig. 2).

Collembola density

Different forest ages significantly impacted the density of Collembola in the litter ($P = 0.001$) and soil layers ($P < 0.001$) (Fig. 3). In the litter layer, the density of Collembola significantly decreased with the forest age, with mean densities over the 2 years being 15 606, 12 527, and 8 951 individuals m⁻² in N260, P45, and P26, respectively. The density of Collembola was significantly higher in N260 when compared to P26. The cu-

TABLE III

Densities of Collembolas in the soil layer of the 26-year-old plantation (P26), 45-year-old plantation (P45), and 80–260-year-old natural forest (N260) in the Jundu Mountain of Beijing, China in 2008 and 2009

Family	Genus (abbreviation)	2008			2009		
		P26	P45	N260	P26	P45	N260
		individuals m ⁻²					
Arrhopalitidae	<i>Arrhopalites</i> (AR.ar)	0	0	4	12	8	33
Bourletiellidae	<i>Bourletiella</i> (BO.bo)	0	0	4	0	4	12
Brachystomellidae	<i>Setanodosa</i> (BR.se)	4	37	17	12	46	12
Entomobryidae	<i>Entomobrya</i> (EN.en)	21	8	8	50	71	112
	<i>Lepidocyrtus</i> (EN.le)	0	0	0	0	8	4
	<i>Marginobrya</i> (EN.ma)	4	0	12	12	8	37
Hypogastruridae	<i>Sinella</i> (EN.si)	0	0	21	0	8	29
	<i>Acherongia</i> (HY.ac)	8	100	171	4	42	46
	<i>Hypogastrura</i> (HY.hy)	42	254	808	204	687	350
Isotomidae	<i>Schoettella</i> (HY.sc)	12	137	187	25	75	167
	<i>Folsomia</i> (IS.fl)	0	0	0	0	0	4
	<i>Folsomides</i> (IS.fo)	37	175	71	21	142	221
	<i>Folsomina</i> (IS.fs)	0	0	4	0	0	0
	<i>Isotoma</i> (IS.is)	4	4	0	8	17	142
	<i>Proisotoma</i> (IS.pr)	0	0	4	0	0	0
	<i>Pseudanurophorus</i> (IS.pa)	17	62	87	0	29	4
	<i>Pseudisotoma</i> (IS.pi)	12	183	183	33	221	321
	<i>Pseudofolsomia</i> (IS.po)	262	1 812	1 341	550	2 075	2 541
Odontellidae	<i>Odontella</i> (OD.od)	54	187	146	67	129	175
Onychiuridae	<i>Bionychiurus</i> (ON.bi)	408	387	442	54	79	433
	<i>Cribrochiurus</i> (ON.cr)	29	42	292	46	87	317
	<i>Onychiurus</i> (ON.on)	712	492	637	1 233	887	1 300
	<i>Probolaphorura</i> (ON.pb)	437	350	379	321	229	562
	<i>Protaphorura</i> (ON.pt)	454	675	871	429	496	1 358
	<i>Sensillonychiurus</i> (ON.se)	12	17	196	0	21	162
Tomoceroidea	<i>Plutomurus</i> (TO.pl)	0	4	0	4	17	8
Total		2 533	4 928	5 887	3 087	5 387	8 353

TABLE IV

Canonical correspondence analysis with mean abundance of Collembola genus in the litter and soil layers of the plantations and natural forest with different ages in 2008 and 2009 in the Jundu Mountain of China

Variable	Litter layer			Soil layer		
	Variance explained	<i>F</i> value	<i>P</i> value ^{a)}	Variance explained	<i>F</i> value	<i>P</i> value
	%			%		
Forest age	11.0	9.53	0.001**	7.0	6.06	0.002**
Litter depth	7.3	4.71	0.003**	2.4	4.34	0.003**
Soil N	2.5	1.13	0.31	2.2	1.10	0.31
Soil C/N	3.2	2.77	0.02**	1.9	2.22	0.01**
Soil pH	4.3	1.07	0.38	2.0	0.71	0.78
Soil water content	2.6	0.73	0.75	1.2	1.95	0.03**
Soil bulk density	5.3	0.63	0.85	3.8	1.85	0.03**
Total variance explained (%)	36.2			20.5		

**Significant at $P < 0.01$.

^{a)} *P* values are based on a Monte Carlo permutation test.

mulative abundances of genera *Protaphorura* and *Plutomurus* were the highest ($P < 0.05$) in N260 (Fig. 4). The abundance of genus *Pseudofolsomia* was higher ($P < 0.05$) in P45 than N260 and P26 (Fig. 4).

In the soil layer, the density of Collembola significantly decreased with the forest age, with mean den-

sities over the 2 years being 7 120, 5 183, and 2 810 individuals m⁻² in N260, P45, and P26, respectively. The density of Collembola was the highest in N260 and the lowest in P26. The cumulative abundances of genera *Protaphorura* and *Bionychiurus* were higher in N260 when compared to P45 and P26. The cumulative

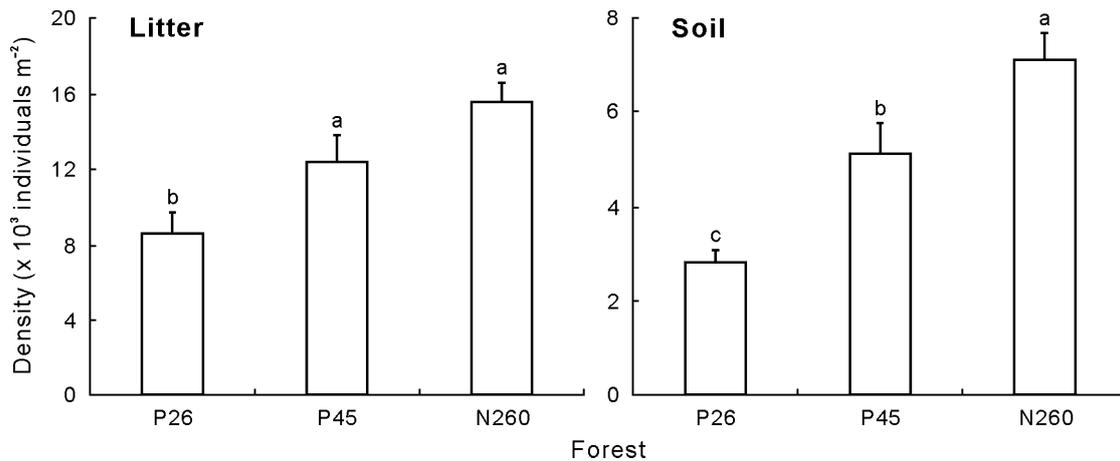


Fig. 3 Densities of Collembola in the litter and soil layers of the 26-year-old plantation (P26), 45-year-old plantation (P45), and 80–260-year-old natural forest (N260) in the Jundu Mountain of Beijing, China. Vertical bars indicate standard errors of the means ($n = 36$). Bars with the same letter are not significantly different by the least significant difference test ($P < 0.05$).

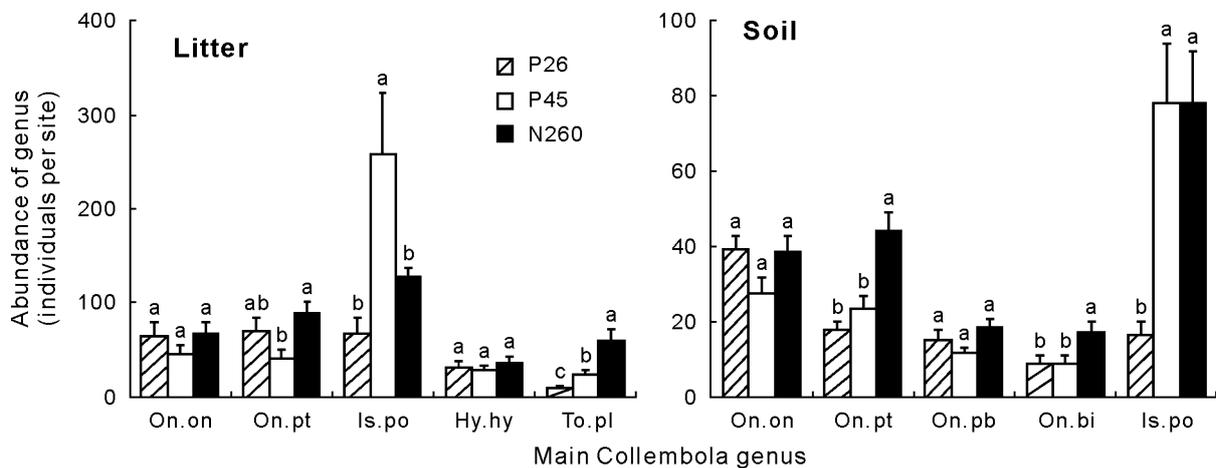


Fig. 4 Cumulative abundances of main Collembola genera in the litter and soil layers of the 26-year-old plantation (P26), 45-year-old plantation (P45), and 80–260-year-old natural forest (N260) in the Jundu Mountain of Beijing, China. Vertical bars indicate standard errors of the means ($n = 36$). Bars with the same letter for each Collembola genus are not significantly different by the least significant difference test ($P < 0.05$). See Table II for the detailed descriptions of the abbreviations of Collembola genera.

abundance of genus *Pseudofolsomia* was lower ($P < 0.05$) in P26 than in N260 and P45 (Fig. 4).

Generic richness of Collembola

Different forest ages significantly affected generic richness of Collembola in the litter ($P < 0.001$) and soil layers ($P < 0.001$) (Fig. 5). Both in the litter and soil layers, the richness of Collembola genera significantly decreased with the forest age. The generic richness of Collembola was the highest in N260 and the lowest in P26.

DISCUSSION

Our study clearly revealed that both in the litter and soil layers, the density and generic richness

of Collembola were enriched during the forest maturation, which were the highest in N260 and the lowest in P26 after clear-cutting. Similarly, Addison *et al.* (2003a) found that the abundance and species richness of Collembola increased with increasing stand age in Douglas-fir dominated stands from 1993 to 1996. Chauvat *et al.* (2011) also found that the abundance and mean species richness of Collembola had higher values in 130-year-old than in 15-, 65- and 90-year-old beech forest stands. Several studies found that environmental conditions such as soil moisture (Chauvat *et al.*, 2003), SOM (Blair *et al.*, 1994), and soil pH (Ponge, 2000) had significant effects on Collembola community. The densities of soil microarthropods are positively related to SOM and soil moisture and inversely related to soil pH and bulk density (Blair *et al.*, 1994). Simi-

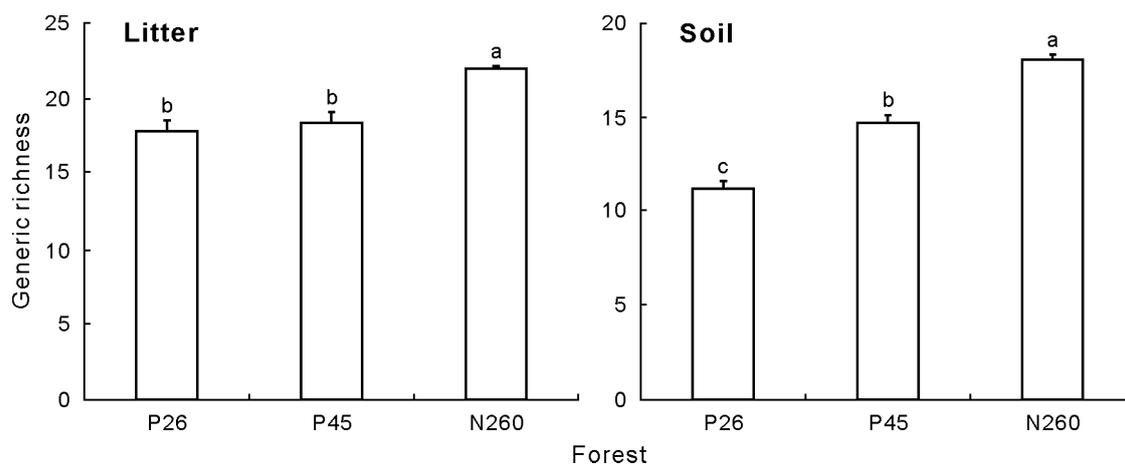


Fig. 5 Generic richness of Collembola in the litter and soil layers of the 26-year-old plantation (P26), 45-year-old plantation (P45), and 80–260-year-old natural forest (N260) in the Jundu Mountain of Beijing, China. Vertical bars indicate standard errors of the means ($n = 36$). Bars with the same letter are not significantly different by the least significant difference test ($P < 0.05$).

larly, we found that soil conditions in P26 and P45 were significantly deteriorated when compared with N260. There were lower values of SOM, soil N, litter depth, soil pH, and soil water content and a higher value of soil bulk density in P26 and P45 compared to N260. It was indicated that better soil conditions in N260 fostered more individuals and genera of Collembola. The CCA results also found that litter depth, soil C/N, soil water content and soil bulk density, but not soil pH, significantly affected the variation of Collembola community composition. The negative effect of acidifying litter on soil fertility is well known (Nihlgard, 1971). However, soil pH was not the primary factor correlated with the structure of collembolan community in the litter and soil layer. Ponge (2000) defined pH = 5 as a threshold value separating acid-tolerant from acid-intolerant collembolan species. All the values of soil pH measured in our study exceeded this threshold value and collembolans might not be harmed under such soil pH conditions.

Furthermore, from the NMDS ordination analysis, it can be seen that the samples in P26 could be obviously separated from those in N260 and only one third samples (4 of the total 12 samples) of P45 reached the level of N260 in terms of Collembola community. Dispersion of cluster points was lower in N260 when compared to P26 and P45. This result gave a hint that Collembola community did not recover to the level of natural forests after 26-year regeneration and that even after 45-year regeneration, Collembola community only showed a slight recovery to the level of natural forests.

However, our study showed that nearly all the genera could be found in each forest, with the exception of genus *Folsomia*, which was not distributed in P45. The abundances of some main Collembola genera

(*Protaphorura* and *Plutomurus* in litter layer and *Protaphorura*, *Bionychiurus*, and *Pseudofolsomia* in soil layer) increased with the forest age. It seemed that the Collembola communities were similar in the generic composition but different in the structure in different forests. For example, chronosequence studies in Douglas-fir forests conducted by Addison *et al.* (2003a) showed that the species diversity of Collembola was not significantly affected by the different forest ages analyzed. In a study of deciduous forests, Hasegawa *et al.* (2006) observed that the total species richness of collembolans recovered within 4 years after clear-cutting. This result suggested that the structure of collembolan communities in younger plantations would have the potential to recover to the level of the natural mature forests.

Collembolans were thought to be bioindicators for the alterations of soil conditions caused by forest management (Cassagne *et al.*, 2006). We found that certain groups of collembolans were favored by forest types with particular ages. The epedaphic collembolans with large body size such as genus *Plutomurus* (TO.pl) were more abundant in N260 than in P45 and P26. Similarly, Salamon *et al.* (2008) found that the abundance of collembolans with large body size (family Entomobryidae) in 120-year-old stands significantly exceeded that in 30-year-old stands. Our study found that N260 had the lowest soil bulk density among the three forests surveyed. That is to say, the soil porosity was the highest in N260. The soil in this forest could furnish a greater amount of space to allow the collembolans with large body size to survive in the winter. Moreover, the Tomoceroidae (*e.g.*, *Tomocerus*) are classified as hygrophilous collembolans (Ponge, 1993). The soils with higher water content in

N260 might furnish favorable environmental conditions for the Tomoceroidean collembolan *Plutomurus*. The genus *Pseudofolsomia* was more abundant in P45 than in the other two forests. Pine trees are self-thinning after approximately 34 years of growth and can thus foster the development of the herb layer (Liu, 2003). They might provide additional food resources to the collembolans of genus *Pseudofolsomia*. Similarly, Salamon *et al.* (2008) found a well-developed herb layer in 120-year-old stands with relatively open canopies.

It was indicated that the effects of forest types and ages on Collembola was species-specific. The forest N260 was associated with relatively high abundance of *Plutomurus* collembolans, and P45 was associated with relatively high population densities of *Pseudofolsomia* collembolans.

CONCLUSIONS

Soil properties and Collembola were significantly affected by different forest ages, *i.e.*, 26-year-old plantation (P26), 45-year-old plantation (P45), and 80–260-year-old natural pine forest (N260). Soil properties were worse in P26 and P45 when compared to N260. There were lower values of SOM, soil N, litter depth, soil pH, and soil water content and a higher value of soil bulk density in P26 and P45. Both in the litter and soil layers, density and generic richness of Collembola were the highest in N260 and the lowest in P26. Collembolan community structure did not recover to the level of natural forests in 26-year regeneration after clear-cutting. Even after 45-year regeneration following clear-cutting, the collembolan community only showed a slight recovery toward the level of natural forests. The same genera of Collembola tended to occur in all the studied forests. Some collembolan groups were sensitive to the soil conditions in particular forest ages. N260 was associated with relatively high abundance of *Plutomurus* collembolans and P45 with relatively high abundance of *Pseudofolsomia* collembolans. These results suggest that the collembolan community may undergo successional changes along with forest succession. Although the collembolan communities were similar in genus composition, they differed in community structure, depending on forest age. Collembola community did not recover to the level of natural forest after 26- and 45-year regeneration following clear-cutting, but it might have the potential to recover in the future.

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REFERENCES

- Addison J A, Trofymow J A, Marshall V G. 2003a. Abundance, species diversity, and community structure of Collembola in successional coastal temperate forests on Vancouver Island Canada. *Appl Soil Ecol.* **24**: 233–246.
- Addison J A, Trofymow J A, Marshall V G. 2003b. Functional role of Collembola in successional coastal temperate forests on Vancouver Island Canada. *Appl Soil Ecol.* **24**: 247–261.
- Behan-Pelletier V, Newton G. 1999. Linking soil biodiversity and ecosystem function—The taxonomic dilemma. *BioScience.* **49**: 149–153.
- Blair J M, Parmelee R W, Wyman R L. 1994. A comparison of the forest floor invertebrate communities of four forest types in the northeastern U.S. *Pedobiologia.* **38**: 146–160.
- Butterfield J. 1999. Changes in decomposition rates and Collembola densities during the forestry cycle in conifer plantations. *J Appl Eco.* **36**: 92–100.
- Cassagne N, Gauquelin T, Bal-Serin M C, Gers C. 2006. Endemic Collembola, privileged bioindicators of forest management. *Pedobiologia.* **50**: 127–134.
- Cassagne N, Gers C, Gauquelin T. 2003. Relationships between Collembola, soil chemistry and humus types in forest stands (France). *Biol Fert Soils.* **37**: 355–361.
- Chauvat M, Trap J, Perez G, Delporte P, Aubert M. 2011. Assemblages of Collembola across a 130-year chronosequence of beech forest. *Soil Organ.* **83**: 405–418.
- Chauvat M, Zaitsev A S, Wolters V. 2003. Successional changes of Collembola and soil microbiota during forest rotation. *Oecologia.* **137**: 269–276.
- Christiansen K, Bellinger P. 1980. The Collembola of North America, North of the Rio Grand. Grinnell College, Grinnell, Iowa.
- Hågvar S. 1982. Collembola in Norwegian coniferous forest soils. I. Relations to plant communities and soil fertility. *Pedobiologia.* **24**: 255–296.
- Hasegawa M, Fukuyama K, Makino S, Okochi I, Goto H, Mizoguchi T, Sakata T, Tanaka H. 2006. Collembolan community dynamics during deciduous forests regeneration in Japan. *Pedobiologia.* **50**: 117–126.
- Johnston J M, Crossley D A Jr. 2002. Forest ecosystem recovery in the southeast US: soil ecology as an essential component of ecosystem management. *Forest Eco Manag.* **155**: 187–203.
- Kazda M, Pichler M. 1998. Priority assessment for conversion of Norway spruce forests through introduction of broadleaf species. *Forest Ecol Manag.* **102**: 245–258.
- Liu Z H. 2003. A preliminary study on community characteristics of *Pinus tabulaeformis* f. *shekannensis* on Loess Plateau. *Acta Bot Borea Occident Sin* (in Chinese). **23**: 1486–1490.
- Macfadyen A. 1961. Improved funnel-type extractors for soil arthropods. *J Anim Ecol.* **30**: 171–184.
- Nihlgard B. 1971. Pedological influence of spruce planted on former beech forest soils in Scania, South Sweden. *Oikos.* **22**: 302–314.

- Osler G H R, Sommerkorn M. 2007. Toward a complete soil C and N cycle: Incorporating the soil fauna. *Ecology*. **88**: 1611–1621.
- Pollierer M M, Langel R, Körner C, Maraun M, Scheu S. 2007. The underestimated importance of belowground carbon input for forest soil animal food webs. *Ecol Lett*. **10**: 729–736.
- Ponge J F. 1993. Biocenoses of Collembola in Atlantic temperate grass-woodland ecosystems. *Pedobiologia*. **37**: 223–244.
- Ponge J F. 2000. Acidophilic Collembola: living fossils? *Contr Biol Lab Kyoto Univ*. **29**: 65–74.
- Salamon J A, Scheu S, Schaefer M. 2008. The Collembola community of pure and mixed stands of beech (*Fagus sylvatica*) and spruce (*Picea abies*) of different age. *Pedobiologia*. **51**: 385–396.
- Scheu S, Falca M. 2000. The soil food web of two beech forests (*Fagus sylvatica*) of contrasting humus type: stable isotope analysis of a macro- and a mesofaunadominated community. *Oecologia*. **123**: 285–296.
- Verhoef H A. 1981. Water balance in Collembola and its relation to habitat selection: Water content, haemolymph osmotic pressure and transpiration during an instar. *J Insect Physiol*. **27**: 755–760.
- Wall D. 1999. Biodiversity and ecosystem functioning: A special issue devoted to belowground biodiversity in soils and freshwater and marine sediments. *BioScience*. **49**: 107–108.
- Yin W Y. 1998. Pictorial Keys to Soil Animals of China. Science Press, Beijing.
- Zhang Y X. 2006. Change analysis on Chinese forest construction from year 1950 to 2003. *J Beijing Forest Univ* (in Chinese). **28**: 80–87.