

Relative Contributions of Spatial and Environmental Processes and Biotic Interactions in a Soil Collembolan Community

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Abstract: Understanding the underlying processes of how communities are structured remains a central question in community ecology. However, the mechanisms of the soil animal community are still unclear, especially for communities on a small scale. To evaluate the relative roles of biotic interactions and environmental and spatial processes in a soil collembolan community, a field experiment was carried out on a small scale (50 m) in the farmland ecosystem of the Sanjiang Plain, Northeast China. In August and October, 2011, we took 100 samples each month in a 50 m × 50 m plot using a spatially delimited sampling design. Variation partitioning was used to quantify the relative contributions of the spatial and environmental variables. A null model was selected to test for the non-randomness pattern of species co-occurrence and body size in assemblages of collembolans and to test whether the pattern observed was the result of environmental or biotic processes that structured the community on a small scale. The results showed that large variance was accounted for by spatial variables (18.99% in August and 21.83% in October, both were significant). There were relatively lower effects of environmental variation (3.56% in August and 1.45% in October, neither was significant), while the soil water content, soil pH and soybean height explained a significant portion of the variance that was observed in the spatial pattern of the collembolan community. Furthermore, the null model revealed more co-occurrence than expected by chance, suggesting that collembolan communities had a non-random co-occurrence pattern in both August and October. Additionally, environmental niche overlap and the body size ratio of co-occurrence showed that interspecific competition was not influential in collembolan community structuring. Considering all of the results together, the contributions of spatial and environmental processes were stronger than biotic interactions in the small-scale structuring of a soil collembolan community.

Keywords: spatial process; environmental filtering; biotic interactions; variation partitioning; small scale; collembolan community

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1 Introduction

One of the central goals in community ecology is understanding the processes that structure communities. Two

theories have been proposed for understanding community structuring in community ecology: the niche theory (Hutchinson, 1959; Diamond, 1975) and the neutral theory (Hubbell, 2001). Research on the niche theory

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suggested that many processes are important drivers in regulating communities, such as interspecific competition (Diamond, 1975), positive species facilitation (Bertness and Callaway, 1994; He *et al.*, 2013; Michalet *et al.*, 2015), and environmental filtering (Decaëns *et al.*, 2008; Jiménez *et al.*, 2012). The neutral theory emphasizes the importance of stochastic or random processes in community structuring (Hubbell, 2001). Based on both of the above-mentioned theories, local communities can be regulated by processes with dispersal limitation, environmental filtering and biotic interactions, such as interspecific competition (Leibold *et al.*, 2004). Many projects in community ecology aim to disentangle the relative contribution of each of the above processes (Bell, 2010; Dumbrell *et al.*, 2010; Ofiteru *et al.*, 2010; Caruso *et al.*, 2011; Caruso *et al.*, 2013). However, the relative contributions of those processes in structuring the community are still not clear, especially for below-ground communities.

Spatial patterns of soil organisms are spatially structured over distances of tens of centimeters to hundreds of meters, relying on the habits of organisms and dispersal abilities and interactions between organisms and environmental variables (Gutiérrez-López *et al.*, 2010; Hortal *et al.*, 2010; Jiménez *et al.*, 2012). Accordingly, the underlying mechanisms of co-existing species in soil organism communities can be recognized as scale-dependent (Bello *et al.*, 2013; Gao *et al.*, 2014). At scales from the landscape (1×10^4 – 2×10^5 m) to the local (1×10^3 – 1×10^4 m) (Hortal *et al.*, 2010), the underlying mechanisms of community assemblies have been partially evaluated and compared for soil organism communities, but the mechanism on a small scale (10 – 1×10^3 m) (Hortal *et al.*, 2010) is still unclear. Traditionally, environmental filtering (Jiménez *et al.*, 2012) and biotic interactions (especially for interspecific competition) (Nachman and Borregaard, 2010) based on the niche theory are assumed to be dominant drivers for community assembly on small scales. However, significant contributions of biotic interactions for structuring soil organism communities have not been detected on such small scales (Jiménez *et al.*, 2012). Because soil environmental heterogeneity has been proven to be an important driver for the soil animal community on a larger scale, the importance of relative environmental homogeneity on community structuring on a small scale should be more minor. Moreover, the dispersal behavior

of soil organisms may be not limited to being grounded on short distances on a small scale (Fuentes, 2002). Therefore, the limitation of dispersal based on the neutral theory might not be an important driver of community structuring on a small scale ((Gao *et al.*, 2014) for a description of the fine scale). Thus, the relative importance of biotic interactions, environmental filtering and dispersal limitations on soil community assembly need to be examined carefully on such a small scale.

Arthropods in general provide a powerful opportunity to study how species spatial patterns are shaped by different underlying processes across different spatial scales (Hortal *et al.*, 2010). Among soil arthropod communities, springtails (*Hexapoda*, *Collembola*) have been chosen to study because these wingless hexapods good agents to evaluate general biological principles (Straalen *et al.*, 2008). In fine-scale (5 m) structuring of a collembolan community in a temperate deciduous forest, both spatial processes and environmental heterogeneity were suggested to be important drivers, but the significant contributions of biotic interactions were not obviously detected for the collembolan assembly. In addition, the contributions of those processes for soil collembolan assemblages on a small scale are not well known. Recognizing the contributions of these processes for soil community structuring on different scales will accelerate the understanding of community assembly. Therefore, in the present study, we attempted to recognize the relative roles of biotic interactions, environmental filtering and dispersal limitation in shaping a soil collembolan community on a small scale (50 m \times 50 m) in farmland of the Sanjiang Plain, Northeast China.

2 Materials and Methods

2.1 Study area

The study area is located in the Sanjiang Plain, Northeast China, which is one of the largest marshy regions in the Heilong River Basin. The three main river systems include the Heilong River, the Wusuli River and the Songhua River. The study area is in the temperate zone, with a continental monsoon climate that has clear seasonal periods: long and cold in winter and warm and humid in summer. Annual rainfall, which occurs primarily in July and August, accounts for more than 65% of the annual precipitation which averages 550–600 mm. The average altitude range is between 55.0 m and

57.9 m. The mean annual temperature is approximately 1.9°C, and the frost-free period is approximately 125 d. Sampling was performed on the farmland of the integrated experimental wetland field of the Chinese Academy of Sciences (47°35'N, 133°31'E). The soil type is albic soil. The crop in the farmland at the time of the experiment was soybean, planted in 2011.

2.2 Collembolan assemblages and soil sampling

The dimensions of the experimental plot were 50 m × 50 m. It was divided into 100 squares of 5 m × 5 m. Samples were collected from the bottom left-hand region of each square in August and October, 2011, respectively. Four soil sample replicates (a cylinder with a 7-cm inner diameter that was 10 cm deep) were taken from each site for the extraction of the collembolan communities in the laboratory. The collembolans were extracted by means of a Berlese-Tullgren apparatus (Nef, 1960). Pitfall traps filled with vinegar and sugar (attractant) and alcohol (preservative) were selected to collect the epigeic collembolans. At each square, three pitfall traps (33-mm diameter, 54 mm depth) were set and left for three days and three nights. The captured collembolans were preserved in a 95% alcohol solution, identified and counted for each sample. Because we wanted to identify the underlying processes of the soil collembolan community, the species data from the pitfall traps and soil samples within each sample were combined before analysis.

The soil pH, soil water content and plant biomass are considered to be important factors for the soil animal community (Arbea and Blasco-Zumeta, 2001; Kaneda and Kaneko, 2002), and these parameters were analyzed as follows. In each of the 100 squares, a soil core (diameter 7 cm, depth 10 cm) was taken just to the right of the point where the collembolan soil samples were taken. Then, the soil pH and soil water content were analyzed in the laboratory. The average soybean height was also measured: in each square, 10 soybeans were randomly selected and the plant heights were measured (in cm) from the ground to the terminal node of each plant. The average soybean height was just measured in August, as the soybean has been harvested in October.

2.3 Statistical analysis

To determine the effects of the local environmental and spatial processes on the soil collembolan community

assembly, we separated the analyses of the environmental and spatial variables. To identify the importance of the spatial variables on the soil collembolan community, the powerful method of distance-based Moran's eigenvector maps (MEM) were used (Borcard and Legendre, 2002; Dray *et al.*, 2006). The MEM was recommended by Dray Legendre and Peres Neto (Dray *et al.*, 2006) and then was used to analyze the sample spatial distance matrix. The analysis produced a number of eigenvectors that accounted for the spatial patterns that could be solved by the sampling design (Borcard and Legendre, 2002; Borcard *et al.*, 2004; Dray *et al.*, 2006; Caruso *et al.*, 2013). The adjusted *R*-square was used to select the linear combination of vectors that described the largest amount of variation in the species matrix with the minimum number of vectors (Dray *et al.*, 2006). Those selected significant spatial vectors with positive eigenvalues were introduced into the statistical processes of variance partitioning and partial redundancy analysis (pRDA) (described below). Then, the relative contribution of environmental heterogeneity was evaluated in terms of the following parameters: soil pH, soil water content and average plant height.

We used variance partitioning to quantify the amount of variation attributed to environmental heterogeneity and the spatial variables (Smith and Lundholm, 2010). The significance of each source of variation was tested by a permutation test performed on the relevant pRDA (Oksanen *et al.*, 2015). All of the multivariate statistical analyses were performed with functions of 'PCNM', 'RsquareAdj', 'forward.sel' and 'varpart' in R software version 3.0.1 (<http://www.R-project.org>) using the 'vegan' (Oksanen *et al.*, 2015) and 'PCNM' (Legendre *et al.*, 2012) packages.

Collembolan species composition was further analyzed to recognize the importance of species interactions. To provide an initial description of patterns of species covariation, we calculated all of the pair-wise Pearson correlation coefficients and corresponding *P* values with a Bonferroni correction. Then, we performed a formal null model analysis (Gotelli, 2000; Gotelli and Ulrich, 2012) evaluating whether patterns of species co-occurrence in the overall matrix showed the deterministic signals of non-random processes. To quantify the patterns of species co-occurrence, the indices of the *C*-score and *V*-ratio were selected for their powerful ability. The *V*-ratio is not valid for the fixed-fixed (FF)

algorithm, as it is judged by the row and column sums of the matrix (Gotelli, 2000). Therefore, the values of the C -score with three algorithms (fixed row-fixed column, fixed row-equiprobable column, and fixed row-probability column) and V -ratio with two algorithms (fixed row-equiprobable column, and fixed row-probability column) were calculated (Gotelli, 2000; Gotelli and Ulrich, 2010; Gotelli and Ulrich, 2012). Important information about species interactions can be obtained by testing for non-random patterns in species association on a species-pair basis. However, this provides the opportunity to increase the risk of Type-I error (Gotelli and Ulrich, 2010). Thus, we followed the method introduced by Gotelli and Ulrich (2010), which is based on building confidence limits using the empirical Bayes approach. Then, the standardized effect size (SES) was measured to compare the results of the study. A 95% confidence interval of the SES values was expected to be distributed between -2.0 and 2.0 when assuming a normal distribution of the SES. The SES was calculated as ((observed value – mean of simulated value) / standard deviation of simulated value). For the C -score, an SES higher than 2 represents significant species segregation and an SES lower than 2 indicates significant species aggregation. For the V -ratio, an SES higher than 2 represents significant species aggregation, and an SES lower than 2 indicates significant species segregation. The analyses of the C -score and V -ratio indices were performed by using the software Ecosim 7.0 (Gotelli and Entsminger, 2009), and pairwise co-occurrences were calculated by using the software PAIRS (Ulrich, 2008).

To identify whether the pattern that was observed was the result of environmental heterogeneity or biotic interactions that drive the collembolan community, community-level Pianka's O_{jk} niche overlap index (Pianka, 1973) was calculated by using the mean niche overlap of all of the collembolan species pairs. If the community is competitively structured, the mean niche overlap index should be lower than that expected by chance (EBC). If the collembolan community is regulated by environmental heterogeneity, the observed niche overlap index would be higher than that EBC (Albrecht and Gotelli, 2001). Then, the soil collembolan assemblage in August was randomly selected to compute the mean niche overlap index. Niche partitioning for environmental variables and body size (length, mm) were calculated according to the method of Jiménez *et al.* (2012). Calculation and tests were performed with the 'niche overlap' and 'size overlap' modules of the software Ecosim 7.0 (Gotelli and Entsminger, 2009).

3 Results

3.1 Collembolan community composition

We collected more collembolan species in August than in October, but more collembolan individuals in October than in August. The most abundant and frequent species was *Allonychiurus* sp. n. 1 in August (11 280 individuals, present in all 100 samples) and October (46 297 individuals, also present in all 100 samples) (Table 1). Overall, the rarefaction curves showed that the sampling efforts were sufficient to describe the overall richness of this system at such a scale (Fig. 1).

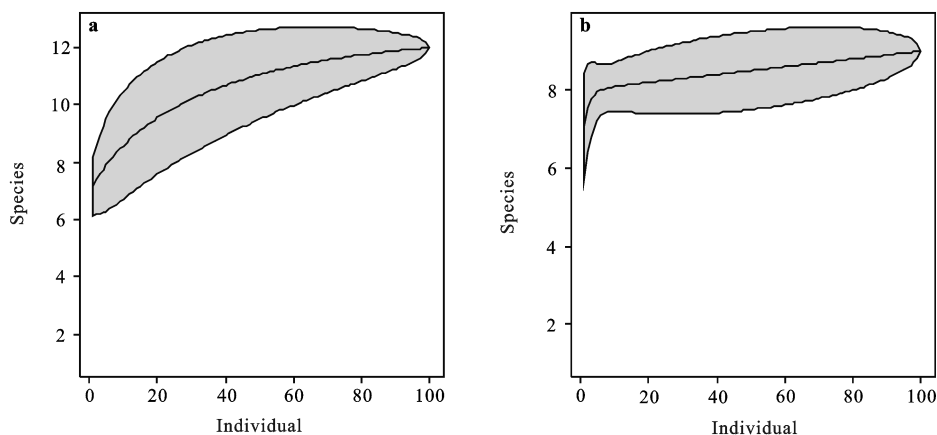


Fig. 1 Individual-based rarefaction curves for collembolan communities in experimental plot in August (a) and October (b), 2011. The solid curves represent the means of repeated re-sampling of all of the pooled samples. The grey areas represent the 95% confidence limits of the curves

Table 1 Species richness (number of collembolan species) and abundance (total individuals) of soil collembolan communities in experimental plot in August and October, 2011

Species	August		October	
	Individual	Frequency in all of 100 samples	Individual	Frequency in all of 100 samples
<i>Protaphorura</i> sp. 1	465±7	74	942±18	65
<i>Oligaphorura ursi</i> Fjellberg	1172±15	82	2233±31	93
<i>Allonychiurus</i> sp. n. 1	11280±103	100	46297±427	100
<i>Sminthurinus</i> sp. 1	859±5	98	55±2	17
<i>Arrhopalites</i> sp. 1	48±1	29	132±2	47
<i>Sminthurinus</i> sp. 2	108±2	47	3±1	3
<i>Sphyrotheca</i> sp. 1	22±1	13	NF	NF
<i>Tullbergia</i> sp. 1	2656±24	97	6007±61	99
<i>Folsomia</i> sp.2	67±2	23	NF	NF
<i>Folsomia</i> sp. 1	257±7	53	383±5	72
<i>Desoria</i> sp. 1	597±11	55	1788±34	65
<i>Entomobrya</i> sp. 2	502	90	213±3	65
<i>Entomobrya</i> sp. 1	109±1	58	10±1	8
<i>Entomobrya</i> sp. 3	34±1	25	352±5	81
<i>Entomobrya koreana</i> Yosii	1±1	1	NF	NF
<i>Hypogastrura</i> sp. 1	31±1	17	862±25	65
<i>Lepidocyrtus felipei</i> Wang, Chen & Christiansen	660±4	100	756±8	93
Species richness		17		14
Total number of mite		18868		60033

Note: NF indicates not found

3.2 Relative contributions of spatial and environmental processes

The results of variation partitioning showed that the two sets of variables (spatial and environmental variables) that were used to predict multivariate species distributions accounted for 23.31% and 23.61% of the overall variance in the species matrices in August and October, respectively. The variation explained by the soil collembolan communities, which was uniquely attributed to the spatial variables, was higher than the amount explained by the environmental variables only. Little explained variation was shared between both the spatial and environmental variables (Table 2). By not accounting for the conditional effect of the spatial variables (Table 3), the soil pH and soybean height were important for the soil collembolan community in August and the soil water content and soil pH were important for the community in October in the redundancy analysis.

Null model analysis results performed on the entire species matrix showed that regarding the *C*-score with the FF algorithm, species co-occurred significantly lower than EBC in both August and October, indicating

that the collembolan communities represented significant non-random species segregation. Otherwise, according to the *C*-score and *V*-ratio with the FE and FP algorithms, species co-occurred significantly more often

Table 2 Variance partitioning based on partial redundancy analysis (pRDA) that used species tables as a response matrix and environmental and spatial variables as predictors

	August		October	
	Variance (%)	<i>P</i> value	Variance (%)	<i>P</i> value
Environmental variable	3.56	0.19	1.45	0.65
Spatial variable	18.99***	< 0.001	21.83***	< 0.001
Environmental variable + spatial variable	0.76	NT	0.33	NT

Notes: NT not testable. ***, *P* < 0.001

Table 3 Effects of environmental factors on community structure analyzed by redundancy analysis and a Monte Carlo permutation test (999)

Factor	August	October
Soil water content	<i>P</i> = 0.099	<i>P</i> = 0.015
Soil pH	<i>P</i> < 0.001	<i>P</i> = 0.019
Soybean height	<i>P</i> < 0.001	NT

Note: NT is not tested

than EBC (Mean of simulated index) in both August and October, indicating that the collembolan communities showed non-random species aggregation (Table 4).

The matrices of species pairwise correlations showed that no species pairs were significant in both August and October (after Bonferroni correction). Pair-based co-occurrence analysis showed that, in August, one out of four species pairs co-occurred less often than EBC, while three out of four co-occurred more often than EBC. In October, only one species pair co-occurred more often than EBC. Nevertheless, based on the conservative empirical Bayes mean based criterion, two species pairs co-occurred more often than EBC, while

one species pair co-occurred less often than EBC in August. In October, no significant species pair was detected based on the empirical Bayes mean criterion (Table 5).

With regard to environmental niche dimensions, the community O_{jk} niche overlap index was higher than the simulated values both in August and October. The average community O_{jk} index for environmental variables was 0.97 and 0.96 in August and October, respectively, indicating that the soil collembolan communities were not competitively structured (Table 6).

The difference in the body size ratio of co-occurring *Collembola* in August was not different from mean of simulated index (a random distribution) (Table 7).

Table 4 Observed and expected by chance (EBC) values of null-model indices for presence-absence matrices of collembolan communities

Month	Index	Null model	Observed index	Mean of simulated index	Standardized effect size	<i>P</i> value
August	C-score	FE	157.80	180.00***	-3.72	< 0.001
		FF	157.80	155.18*	2.11	0.02
		FP	157.80	171.56*	-2.03	0.02
	V-ratio	FE	1.59	1.00***	4.33	< 0.001
		FP	1.59	1.20**	2.44	0.01
		FF	142.38	179.60***	-5.29	< 0.001
October	C-score	FF	142.38	137.35**	3.02	< 0.01
		FP	142.38	166.30**	-2.89	< 0.01
		FE	1.91	1.00***	6.75	< 0.001
	V-ratio	FP	1.91	1.29***	3.72	< 0.001

Notes: FE is the fixed row and equiprobable column null model. FF is the fixed row and fixed column null model. FP is the fixed row and proportional column null model. *, $P < 0.05$, **, $P < 0.01$, ***, $P < 0.001$

Table 5 Significant association species pairs in collembolan community

Month	Species A	Species B	Observed C-score	Simulated C-score	Simulated SD	CL	BM
August	<i>Entomobrya</i> sp. 1	<i>Hypogastrura</i> sp. 1	0.645	0.300	0.100	3.46	3.46
	<i>Desoria</i> sp. 1	<i>Folsomia</i> sp. 2	0.083	0.302	0.079	-2.78	-2.78
	<i>Arrhopalites</i> sp. 1	<i>Sphyrotheca</i> sp. 1	0.279	0.577	0.138	-2.16	-2.16
	<i>Folsomia</i> sp. 1	<i>Folsomia</i> sp. 2	0.112	0.319	0.086	-2.42	0.00
October	<i>Lepidocyrtus felipei</i>	<i>Folsomia</i> sp. 1	0.003	0.016	0.005	-2.37	0.00

Notes: Species A and B are significant non-random species pairs. SD, standard deviation. Collembolan community that were identified by simple confidence limits criterion (CL) and empirical Bayes mean based criterion (BM) (Gotelli and Ulrich, 2010) with fixed row and fixed column sums null model

Table 6 Community niche analysis for selected environmental variable

	Environmental variable	Observed index	Mean of simulated index	Average SES	<i>P</i> value
August	Soil water content	0.99***	0.45	16.02	< 0.001
	Soil pH	0.97***	0.63	15.48	< 0.001
	Soybean height	0.94***	0.55	14.59	< 0.001
October	Soil water content	0.99***	0.40	13.74	< 0.001
	Soil pH	0.94***	0.56	11.81	< 0.001

Notes: ***, $P < 0.001$. The standardized effect size (SES) was measured to compare the results of this study and it was calculated as ((observed value, mean of simulated value) / standard deviation of simulated value)

Table 7 Size ratio analysis of collembolan community in August

Observed index	Mean of simulated index	Standardized effect size	<i>P</i> value
0.00094	0.00181	-0.58517	NS

Note: NS, not significant

4 Discussion

The difference between the collected species numbers in August and October was not significant, while the difference between the observed abundances of the communities in those seasons was obvious (Gao *et al.*, 2014). The collembolan community and specific species showed significantly spatial autocorrelations and spatially structured patterns in this multi-scale experiment in August and October, respectively (Gao *et al.*, 2014). Accordingly, the collembolan community exhibited temporal dynamics in abundance and spatial patterns at such a small scale. The difference and dynamics for the above mentioned factors thus help us to reveal the assembly rules of soil collembolan communities on a small scale.

A relatively low proportion (~24%) of the variation was determined by both environmental and spatial variables. This fraction can be further divided into purely environmental effects, purely spatial effects and spatially structured environmental effects (a combination of purely environmental effects and spatial effects). Our results demonstrated that the collembolan community of the farmland in the Sanjiang Plain depended on spatial effects in both August and October, indicating that the soil collembolan community assembly can be partially explained by dispersal limitation. A much lower and non-significant proportion of the variation was accounted for by spatially structured environmental factors. Additionally, a relatively lower amount of variation (3.56% in August and 1.45% in October, respectively) was accounted for by the environmental variables. Moreover, the environmental variables alone could not explain the significant amount of variation in August or October according to the results of the pRDA. However, we could not ignore the relative contribution of environmental filtering on the soil collembolan assemblage. This result was supported by the results of the redundancy analysis. Obviously, when omitting the conditional effect of spatial variables, the soil water content, soil pH and soybean height were important for soil collembolan community assemblages. It is important to note that approximately 76% of the variation was unde-

termined. This finding can be explained by a high proportion of unaccounted variation, e.g., other non-spatially structured biological or environmental factors that were not measured in the field (Legendre *et al.*, 2009). It is likely that the variation decomposition (shown in Table 2 and Table 3) will be altered if other environmental (e.g., soil organic matter content) or biological (e.g., species functional traits) variables are recorded and included in the analysis (John *et al.*, 2007). However, we suspect that this would not change the finding that the spatial effect (based on pure spatial effects) is a significant component of the collembolan community.

The species distribution of the collembolan community was significantly different from the random distributions in August and October. In terms of the results of the *C*-score with the FF algorithm on the overall species matrices, the collembolan communities represented significant non-random species segregations both in August and October. According to the results of the *C*-score and *V*-ratio with the FE and FP algorithms, the collembolan community showed non-random species aggregation in August and October, respectively. Thus, it is difficult to conclude that biotic interactions due to interspecific competition can be a fundamental structuring force in collembolan communities. Based on the pairwise null model analysis using the conservative empirical Bayes approach (Gotelli and Ulrich, 2010), we detected more positive associations than negative associations in August and detected no significant associations in October. Those negative species pairs may not significantly contribute the community structure based on the dilution effects (Gotelli and Ulrich, 2010). Furthermore, the results of environmental niche partitioning and body size overlap indicated that the soil collembolan community was not shaped by interspecific competition and that other factors influenced the co-occurrence of species on a small scale, such as environmental filtering (Jiménez *et al.*, 2012). Moreover, the differences of the species co-occurrence pattern and species pairs between August and October were detected. The differences showed that the seasonal dynamics of the species co-occurrence pattern and species pairs might exist in small-scale collembolan communities. However, it is difficult to deny the importance of interspecific competition according to the pattern detected. We suggest that other methods, such as a stable-isotope and molecular tools, should be introduced to identify the contribution of biotic interac-

tions in the future (Emerson and Gillespie, 2008; Ma-raun, Erdmann *et al.*, 2011).

According to the classical niche theory, the small experimental farmland plot is relatively environmentally homogeneous; therefore, we should have found a minor role for environmental filtering. Because the spatial effects (e.g., dispersal limitation) are related to the logarithm of the geographical distance (Hubbell, 2001) per unit distance, its effects should be weaker at small spatial distances. However, these expectations were not confirmed based on this field investigation. Environmental filtering and interspecific competition are expected to have an opposing influence on community structuring (Mayfield and Levine, 2010). Either a non-random aggregated community or significantly environmental niche partitioning higher than EBC suggested a stronger contribution of environmental filtering than interspecific competition (Mayfield *et al.*, 2005). In this field experiment, non-random aggregation, less significantly negative species pairs and significant environmental niche partitioning higher than EBC were detected in communities both in August and October, emphasizing the greater importance of the environmental process than biotic interactions. The dispersal abilities of collembolan species depend on the dispersal mode and habitat preference (such as more efficient dispersal for epigeic species than for edaphic ones) (Ojala and Huhta, 2001), and the probabilities of reaching adaptive habitats strongly rely on the distance and configuration of the connections between different plots (Fahrig and Merriam, 1994). As a type of lower active disperser, soil mite species might not track environmental heterogeneity efficiently on a fine scale (5 m); thus, the limitation of dispersal was suggested to be an important driver of community assembly (Gao *et al.*, 2014). Indeed, most soil collembolan species exhibit lower dispersal rates than soil mite species, and many collembolan species are not able to traverse a distance of 30 m (especially for those edaphic species) (Ojala and Huhta, 2001). Therefore, it is still difficult for collembolan species to track environmental variability due to their limited dispersal capabilities, inferring the important contribution of dispersal limitation for collembolan community structuring.

5 Conclusions

This study identified the relative contributions of spatial

and environmental processes and biotic interactions in a soil collembolan community in the Sanjiang Plain, Northeast China. Both spatial and environmental processes were found to be important for controlling a soil collembolan community in growing and non-growing seasons on a small scale (50 m) in the farmland, while the biotic interactions were less influential. This study just performed on a small scale, and the relative roles of those processes in other spatial scales should be further studied.

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