Marshland restoration benefits Collembola recruitment: a long-term chronosequence study in Sanjiang mire marshland, China

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ABSTRACT

To examine the biodiversity restoration of marshlands after human-induced disturbances, a long-term chronosequence study of Collembola communities was completed that included cultivated treatment (marshes with 15 years of soybean cultivation; CU15), two restored treatments (with 6 and 12 years of agricultural abandonment; RE06 and RE12, respectively), and an intact marshland (IM) as a reference in the Sanjiang Plain, Northeastern China. Changes in the soil properties and Collembola communities under different treatments were analyzed. Soil parameters (i.e., soil organic carbon, available N, P and K, soil moisture) significantly increased from the cultivated treatment to the 6-year agricultural abandoned, and then 12-year agricultural abandoned treatment, indicating that the degraded soil began to recover after agricultural abandonment. The density, species richness and diversity of Collembola in RE12 were significantly higher than in RE06 and CU15, and even surpass the IM, indicating marshland restoration (after 12 years of agricultural abandonment) benefited recruitment and reconstruction of Collembola community. We found soil surface-dwelling Collembola recovered faster than eu-edaphic species, that is probably due to some common traits (i.e., parthenogenesis and fast dispersal) between epi- and hemi-edaphic species. The changes in the vegetation and soil properties during long-term soybean cultivation and agricultural abandonment were the key factors affecting the composition, density, and species richness of soil Collembola.

INTRODUCTION

Worldwide human exploitation and the conversion of ecosystems, including for agricultural practices and urbanization, have caused widespread biodiversity loss and
environmental quality decline, leading to the degradation of ecological functioning (Bullock et al., 2011; Butchart et al., 2010; Fischer & Lindenmayer, 2007). This is especially true in wetland ecosystems. Wetlands play a crucial role in ecosystem functioning and services such as the carbon cycle, carbon sequestration, conservation of biological diversity and flood protection (Verhoeven & Setter, 2010; Wang et al., 2012). With the increase in human population and economic growth, wetlands are ubiquitously being intensively used for agricultural purposes (Isunju & Kemp, 2016; Johnston, 2013; Song et al., 2012); more than half of the world’s wetlands disappeared during the 20th century (Davidson, 2014). As ecological restoration can potentially contribute to alleviating this biodiversity crisis, it is being increasingly implemented throughout the world (Benayas et al., 2009; Solis-Gabriel et al., 2017; Zedler & Kercher, 2005). Specially, the rate of abandonment of agricultural lands around the world began to increase exponentially since the 1950s because it was easier to restore natural wetlands lost compared with other human practices (Cramer, Hobbs & Standish, 2008; Mao et al., 2018). The shifts in the composition and structure of vegetation and soil chemical and physical properties caused by these extreme changes in wetlands are fairly well-known, but the knowledge associated with changes in soil biotic communities is still limited because belowground responses are slower than aboveground responses due to the different response rates of plants and soil organisms (Guan et al., 2015; Hedlund et al., 2010). Many studies have explored the response of soil environmental factors and biological diversity to serious agricultural disturbances (Hernández et al., 2017; Wang et al., 2012), but few studies have focused on the dynamics of biodiversity—especially soil biodiversity recovery—after agricultural abandonment, with fewer using a long-term chronosequence approach.

Within the soil, biotic communities play a fundamental role in key belowground processes such as nutrient capture and cycling, energy flow, and soil physical structure-building and control (Jouquet et al., 2006; Murray et al., 2009; De Ruiter, Neutel & Moore, 1998). In turn, interactions between plants and soil can considerably influence soil biota communities (Putten et al., 2013). Among the soil organisms, Collembola are abundant and diverse (Hopkin, 1997). Soil Collembola can be good indicators of soil health due to their close relationship with the soil environment and their sensitivity to habitat disturbance such as agricultural practices (Ponge et al., 2013; Rossetti et al., 2015; Sousa et al., 2006). However, the recovery process of soil Collembola communities in the same location over time after agricultural abandonment is poorly understood.

To recover after agricultural abandonment, organisms either have to survive the disturbance or recolonize disturbed patches from the surroundings (Lindberg & Bengtsson, 2005; Querner et al., 2018). Functional traits refer to the morphological and physiological characteristics that allow species to survive, perhaps differently, in dynamic landscapes. Most studies on how soil Collembola communities respond to succession only focus on their community composition, species richness and diversity, and few studies have used species life-history traits to predict responses to disturbances (Bokhorst, Berg & Wardle, 2017; Gagic et al., 2015; Messier, McGill & Lechowicz, 2010). Thus, in this study, we compared the differences in Collembolan taxonomic diversity and life-history traits in order to analyze and infer mechanisms involved in assembly processes in the wetland recovery.
process. In soil micro-arthropods, the body length, reproductive strategies, life form, and dispersal ability are probably the key factors regulating survival and colonization after disturbances (Driscoll & Weir, 2005; Lindberg & Bengtsson, 2005; Malmström, 2012).

The Sanjiang Plain in Northeastern China is one of the world’s largest freshwater marsh regions. However, the area of the total marsh region has decreased by 77% due to extensive agricultural exploitation since the 1950s (Wang et al., 2011). The conversion from native marshland to agricultural land caused significant changes in the vegetation and soil properties, leading to a sharp decrease in biodiversity (Liu, Lv & Zhang, 2004; Wang et al., 2012). Fortunately, a large number of marshland protection and restoration programs have been implemented since the 1990s due to the growing awareness of the important ecological function of marshlands. However, the effects of different restoration years on the wetland species composition and diversity have rarely been reported. Therefore, we used a chronosequence approach to study the effects of marshland restoration (after 0, 6, and 12 years of agricultural abandonment) on the taxonomic structure, diversity, and life-history traits of Collembola, along with soil physicochemical properties. The use of the chronosequence method enabled the observation of the dynamics of long-term changes in marshland succession after tillage.

Within this context, we aimed to: (1) elucidate the changes in soil Collembola communities in marshes that have experienced different periods of agricultural abandonment and (2) investigate the recovery pattern of soil Collembola after agricultural abandonment. We hypothesized that: (1) the density, species richness, and diversity of Collembola increase after agricultural abandonment, and (2) surface-dwelling (epi- and hemi-edaphic) species recover faster than soil-dwelling (eu-edaphic) species in the soil profile.

**MATERIALS AND METHODS**

**Site description and experimental design**

The study was conducted at the Sanjiang Mire Marshland Experimental Station at the Chinese Academy of Sciences (47°35′N, 133°31′E) in the Sanjiang Plain, China (Fig. S1). The station is at an altitude representative of the natural freshwater marshland habitats of the Sanjiang Plain. The study site has a temperate continental monsoon climate with a mean annual air temperature of 2.52 °C, precipitation of 558 mm (more than 65% falls in July and August), and a frost-free period of 125 days (Zhang et al., 2014). The monthly mean temperature was −20 °C in January and 22 °C in July (Song et al., 2009).

Based on the marshland distribution and the present conditions of the farmland, four treatments, including one cultivation treatment, two restoration treatments and one reference, were established. The cultivation treatment (CU15) had been used for soybean planting since 1995 (CU15). The two restoration treatments (RE06 and RE12) were established on soybean fields that had been agriculturally abandoned since 2004 (RE06) and 1998 (RE12), respectively. Undisturbed natural marsh was chosen as intact marshland (IM). The dominant vegetation of the intact marshland and restored marshland both were *Calamagrostis angustifolia*.

Soil samples were taken on June 15, August 15, and October 15 yearly from 2010 to 2012. A total of 10 replicates were randomly selected from each sample site (50 × 50 m²),
and all soil samples (10 × 10 × 10 cm³) were carried in polythene bags to the laboratory. We recognize that these 10 samples per site are not true replicates for the sites, but consider that the pooled sample is sufficiently large to be representative of each treatment. Collembola were then extracted using a Tullgren apparatus (Van Straalen & Rijninks, 1982). The extracted Collembola were preserved in 95% ethanol and identified to species or assigned a morphospecies according to the keys developed by Bellinger, Christiansen & Janssens (1996–2012) and Yin (1992, 1998) using a light microscope.

Analysis of soil physicochemical properties
The soil physicochemical properties were analyzed based on the methods described in Lu (2000). Soil moisture (SM) content was measured by oven drying (105 °C, 48 h). Soil pH was measured in a soil water suspension (1:2.5 w/v) with a pH meter. Soil organic carbon (SOC) was determined by dry combustion using a C/N analyzer (LECO Corporation, St. Joseph, MI, USA). The available nitrogen (AN), available phosphorus (AP), and available potassium (AK) were quantified using the alkaline hydrolysis diffusion method, Bray-1 method, and ammonium acetate extraction method, respectively.

Statistical analysis
We calculated the number of individuals for all identified species and morphospecies for each soil sample. We then used the number of individuals to account for the total amount of captured individuals to classify the quantitative degree of each taxon: the number of individuals that accounted for more than 10% of the total number of captured individuals was dominant species, the number of individuals that accounted for 1.0–10.0% were common species, and the number of individuals that accounted for less than 1% were rare species (Gao et al., 2016). We also explored several parameters to monitor the composition and biodiversity changes in the different wetlands. First, we determined the collembolan density (number of individuals per unit area) and the species richness (number of taxa) for each soil sample. Then we used Shannon-Wiener diversity (H') (Shannon & Warren, 1949) to evaluate soil collembolan diversity in each habitat.

In order to determine whether marsh cultivation and restoration induced changes in the life-history traits of Collembola, we selected four traits that have previously explained shifts in Collembola species composition (Bokhorst et al., 2012; Makkonen et al., 2011; Vanhee et al., 2017; Widenfalk et al., 2015). The selected traits were body length of adults, life form, reproductive mode, and dispersal traits. Table S1 provides definitions and ecological significance (Berg et al., 1998; Ponge et al., 2006; Rusek, 2007). Trait values (Table S2) were obtained from various literature sources (Chen & Christiansen, 1996; Li, Hua & Chen, 2008; Palaciosvargas & Martinez, 2014; Vanhee et al., 2017; Yun & Gao, 2015). We calculated the community weighted mean (CWM) trait values for each of four traits according to Garnier et al. (2004), weighing species traits in each sample by the relative abundance. For each sample, the CWM trait values were calculated as follows:

\[ CWM = \sum_{i=1}^{n} p_i \times T_i \]
where $p_i$ is the relative abundance of collembolan species $i$, $T^{pi}$ is trait score of species $i$, and $n$ is the number of species included in the calculation.

Means and standard errors were calculated for soil parameters and the Collembolan indices of samples from each treatment. One-way analysis of variance (one-way ANOVA) was used to test the difference significance of the soil properties among treatments. In addition, repeated measures ANOVA was used to test for significant differences in density, species richness, Shannon-Wiener diversity, and CWM trait values among different treatments. The significance of post hoc pairwise comparisons were determined using Fisher’s least significant difference (LSD) tests under significance levels of 0.05. In addition, a Spearman correlation analysis was conducted to identify correlations between the soil properties and the response variables of the Collembola, including the abundance of taxa, species richness, and diversity. All statistical analyses were performed using the software package IBM SPSS statistics 22.0 for Windows (IBM SPSS Inc., Armonk, NY, USA).

The Collembola community was further analyzed using the software package CANOCO Version 5.0 for Windows. To test the relationships between Collembola community and recovery years, we performed analyses using redundancy analysis (RDA) based on the species abundance. The soil properties and species abundance were standardized via log transformation before analysis. The significance of the RDA results was determined using a permutation test (499 permutations). We also used an interactive forward-selection RDA (using the “manual selection of environmental variables” option in CANOCO 5.0) to test which variable among the soil properties significantly influenced the Collembola composition. The selection procedure was stopped when the next factor to be added was no longer significant (Xu et al., 2017).

**RESULTS**

**Soil physicochemical properties**

All soil properties were significantly different among treatments (Table 1). Generally, SOC, available N, P and K, and SM significantly increased from the cultivated treatment to the 6-year agricultural abandoned, and then 12-year agricultural abandoned treatment (Table 1). By contrast, soil pH value in the intact marshland was significantly lower than the cultivated and agricultural-abandoned treatments (Table 1).

| Table 1 Mean values (mean ± SE) and significance tests of soil properties across all sites. |
|--------------------------------------------|-----------------|-----------------|-----------------|-----------------|-----------------|-----------------|
| pH | SOC (%) | AN (mg/kg) | AP (mg/kg) | AK (mg/kg) | SM (%) |
| IM | 5.01 ± 0.11b | 8.13 ± 0.70a | 562.80 ± 96.55a | 53.73 ± 2.20a | 404.13 ± 60.40a | 32.87 ± 0.28b |
| CU15 | 5.28 ± 0.03a | 2.32 ± 0.13c | 211.68 ± 30.22b | 21.20 ± 1.83b | 69.12 ± 7.75c | 24.64 ± 0.65c |
| RE06 | 5.40 ± 0.02a | 4.90 ± 0.20b | 351.12 ± 17.90b | 23.39 ± 3.34b | 167.39 ± 8.15b | 32.69 ± 0.64b |
| RE12 | 5.36 ± 0.04a | 5.74 ± 0.80b | 403.20 ± 49.70a | 44.47 ± 1.97a | 298.43 ± 31.72a | 44.59 ± 2.82a |
| ANOVA | 0.002 | <0.001 | <0.001 | <0.001 | <0.001 |<0.001 |

Notes: IM, intact marshland; CU15, soybean soils cultivated for fifteen years; RE06, agricultural abandoned for six years; RE12, agricultural abandoned for twelve years; SOC, soil organic carbon; AN, available soil N; AP, available soil P; AK, available soil K; SM, soil moisture. Different superscript lowercase letters within the same row indicate significant differences between treatments based on the least significant different (LSD) test (one-way ANOVA; $p < 0.05$).
Community composition of collembola
In total, 8,171 individuals and 28 species, with 4,669/25, 5,132/28, 8,539/28 of Collembola (Table S3) in the IM, CU15, RE06 and RE12 fields, respectively, were identified. Five Collembola species—Bourletiella sp. 2, Entomobrya sp. 2, Tomocerus nigrus, Desoria sp. 3, and Folsomia sp. 3—disappeared in the cultivated fields, and all of these species recovered in the restored wetlands (Table S3). Allonychiurus songi was the dominant species at all sites (Table S3). Desoria sp. 1, Desoria sp. 2, Desoria sp. 4, Hypogastrura sp. 1, and Hypogastrura sp. 2 were rare species in the cultivated fields but were common species in the marshlands (Table S3). Entomobrya sp. 1 and Folsomides sp. 1, which were absent in the IM soils, occurred in the cultivated and restored fields. Entomobrya sp. 3, Isotomodes sp. 1, and Tullbergia sp. 1 were absent in the restored fields whereas Hypogastrura sp. 3 only appeared in these fields (Table S3).

The first two RDA axes together explained 29.60% of the variation in the Collembola community ($p = 0.032$) (Fig. 1). The first axis explained 19.39% of the total variance in species composition and represented mainly SOC, AN, AK, and SM gradient. The second axis which accounted for 10.21% of the total variance was mainly represented by SM and soil pH. The interactive forward selection showed that SOC ($p = 0.006$) significantly affected soil Collembola structures, explaining 15.7% of the total variation.

Density, richness, and diversity of Collembola
The density and species richness showed a significantly increasing trend in the order of CU15, RE06, IM, and RE12 (Figs. 2A and 2B). The density of the hemi-edaphic Collembola species increased significantly with the length of agricultural abandonment (Table S4). The Shannon-Wiener diversity value was significantly higher in the RE12 than in the IM, RE06, and CU15 soils, whereas no significant variations were found between the IM and RE06 sites (Fig. 2C). The Spearman correlation analysis showed that the total abundance was positively correlated with soil SOC, AN, and AP (Table 2). The epi-edaphic species abundance was positively correlated with soil pH and SM (Table 2). Hemi- and eu-edaphic species abundance were positively correlated with soil SOC, AN, and SM (Table 2).

Species richness was positively correlated with soil SOC and AN.

Markedly significant effects on all CWM trait values were affected by different periods of agricultural abandonment. The $\text{CWM}_{\text{BL}}$ ($F = 14.94, p < 0.001$) of the cultivated treatment (CU15) was higher than that of the IM and restored treatment (Fig. 3A). The $\text{CWM}_{\text{RM}}$ was highest for the CU15 field and lowest for the RE06 field ($F = 7.53, p < 0.001$) (Fig. 3B). The $\text{CWM}_{\text{DI}}$ was significantly higher for RE06 than for the IM and CU15 fields ($F = 6.05, p = 0.002$) (Fig. 3C). The $\text{CWM}_{\text{LF}}$ for RE06 was significantly higher than that for RE12, and for RE12, this index was higher than for the cultivated treatments and the IM ($F = 27.54, p < 0.001$) (Fig. 3D).

**DISCUSSION**

Recovery of soil properties
In our study, the soil nutrient levels, such as SOC, AN, and AP, decreased after marshland conversion to cultivation and increased after agricultural abandonment. These results were
consistent with the findings of Xu et al. (2017). We speculated that two factors potentially contributed to the loss of nutrients after reclamation. One is that the grain and straw were harvested and removed off-site, greatly reducing the input of the organic matter which then decreased. Another reason is that wetland soil was water-saturated over long periods of time, and the organic matter decomposed more slowly and even gradually accumulated because of the anaerobic conditions (Compton & Boone, 2000). Once converted to agriculture, the removal of vegetation for cultivation and the exposure of the soil to the wind and sun increased the aeration and soil temperature, leading to increased soil organic matter decomposition. Besides, tillage generally decreased soil organic matter due to erosion and disruption of the physical, biochemical, and chemical mechanisms of SOM stabilization, and increase soil available C, K, and P leaching (Wei et al., 2014). In contrast, the increase of nutrients found in the restoration treatments could be ascribed to the increased litter input after agricultural abandonment, as the straw and grains were no
Figure 2 Effects of marshland management on density (A), species richness (B), and Shannon-Wiener diversity index (C) (mean ± SE) of Collembola across all sites. Different letters indicate a significant effect among habitats based on LSD test (repeated measurement ANOVA; \( p < 0.05 \)).

Table 2 Spearman correlation coefficients of Collembola community variables with soil pH, SOC, AN, AP, AK, and SM.

|                      | pH   | SOC  | AN   | AP   | AK   | SM   |
|----------------------|------|------|------|------|------|------|
| Total abundance      | −0.011 | 0.508* | 0.506* | 0.447* | 0.274 | 0.226 |
| Epi-edaphic species  | 0.621** | 0.066 | 0.084 | −0.079 | −0.050 | 0.462* |
| Hemi-edaphic species | 0.331 | 0.481* | 0.465* | 0.397 | 0.395 | 0.598** |
| Eu-edaphic species   | 0.313 | 0.564** | 0.537* | 0.380 | 0.396 | 0.582** |
| Species richness     | 0.109 | 0.481* | 0.449* | 0.432 | 0.349 | 0.412 |
| Shannon-Wiener       | 0.178 | 0.395 | 0.377 | 0.346 | 0.299 | 0.362 |

Note: Values in bold indicate significant correlations (\(* p < 0.05\), ** \( p < 0.01 \)).
longer removed from the marshland system. In addition, SOM and available nutrients can generally accumulate after the cessation of cultivation. In short, our findings strongly indicate that the cultivation of marshland led to soil degradation and that agricultural abandonment could improve soil quality.

**Recovery of the Collembola community**

In line with our first hypothesis, we found the density, species richness, and Shannon-Wiener diversity of Collembola sharply decreased in CU15 fields and increased in the restoration sites. Furthermore, the RDA result showed that the first axis separated the cultivated treatments from the IM and restored treatments, and the IM and restored treatment were separated by the second axis. They all indicated that marshland management significantly

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**Figure 3** Effects of marshland management on community weighted mean (CWM) body length (A), reproduction (B), dispersal (C), and life form (D) (mean ± SE) of Collembola across all sites. Different letters indicate significant differences among treatments based on the least significant difference (LSD) test (repeated measurement ANOVA; $p < 0.05$).

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affect the community structure of Collembola. For instance, five species of Collembola which disappeared in the cultivated fields all recovered in the restored wetlands; however, the community structure of Collembola in restored marshland were also different from intact marshland. *Folsomia bidendata* and *Tullbergia* sp. 1 were more frequent identified in intact marshland soils while *Entomobrya* sp. 4, *Folsomides* sp. 2 and *Folsomia* sp. 2 were more frequent in restored marshland soils. *Entomobrya* sp. 3, *Isotomodes* sp. 1 and *Tullbergia* sp. 1 existed in the intact marshland soils while disappeared in the restored fields. *Hypogastrura* sp. 3 which was the new introduced species only existed in the restored marshland. We may infer that marshland restoration (after 12 years of agricultural abandonment) can significantly promote the recovery of the species diversity of Collembola; however, it might be difficult to restore to its original state once the composition of the marshland Collembola community has been altered by tillage. That is to say, natural restoration can recruit and reconstruct Collembola community composition.

In the present study, we found that the Collembola community was significantly affected by the SOC. This supports Pipan & Culver (2013) assumption that the SOC content is an important factor limiting the occurrence of organisms in shallow subterranean habitats, as the SOC could provide soil fauna with abundant food resources. In addition, the correlation analysis of the Collembola variables with environmental variables exhibited the significant positive correlation of AN and AP with total abundance and species richness of the Collembola. The reason for this relationship may be the fact that N and P can indirectly influence the habitat and diet of Collembola (Setälä, Marshall & Trofymow, 1995). Compared with RE06, the soil parameters of the RE12 were more similar to those of IM, demonstrating that 12 years was enough time for the species composition or diversity of Collembola to fully recover from a strong disturbance such as long-term soybean cultivation. Thus, in present study, we concluded that the soil Collembola communities were influenced by multiple soil parameters and were most affected by the SOC and nutrients that provide food and habitat for organisms (Birkhofer et al., 2012; Yin et al., 2018).

In support of our second hypothesis, we found higher CWM life forms of Collembola in the restoration sites, which is indicative of a community that has a greater contribution of surface-dwelling species. This is consistent with the observed increasing trend in the density of hemi-edaphic species after agricultural abandonment. This response of Collembola to marshland recovery is likely due to changes in the vegetation and soil properties after agricultural abandonment. Sabais, Scheu & Eisenhauer (2011) found that Collembola density and diversity increased with an increase in plant species and plant functional richness. Vegetation offers ecological links between the aboveground and belowground biota, affecting the diversity and quality of the litter that serves as a habitat and food resource for Collembola (Hopkin, 1997; Wardle, 2013). Particularly, the density of hemi-edaphic species living in upper soil and litter continue to increase and are likely influenced by the increased plant diversity and litter input after agricultural abandonment, as the straw and grains are no longer removed from the ecosystem. In the present study, we found the lowest CWM life form for Collembola in the intact marshland, which indicated the greater contribution of eu-edaphic species. This observation could
be explained by the fact that the intact marshland habitat has thicker litter layers, allowing the maintenance of a higher resource quality and more stable conditions in terms of moisture and temperature, which is a preferable environment for soil-dwelling species (Berg & Bengtsson, 2007; Heiniger et al., 2015). Thus, the CWM trait of the life forms at the sites showed a response to the site gradient and soil properties, with a higher proportion of epi-edaphic and hemi-edaphic Collembola species at the recovery sites compared with the intact marshland and soybean fields. Similar results were reported by Da Silva et al. (2016).

In this study, the mean traits of the Collembola community differed remarkably between the cultivated and restoration treatments. We found $CWM_{RL}$ increased at the farmland sites, which is indicative of a community that the decline in smaller size individuals of collembolan and the community turns to a $K$-strategy. However, the $CWM_{RL}$ at the restoration sites declined to similar level as the control sites, it means the body length of collembolan go back to the original levels after marshland restoration. In general, parthenogenetic species were more ready to occupy new territory and became an invasive one, because parthenogenesis is an advantageous trait for colonization (Norton, 1994) which may facilitate the establishment of populations from very few individuals (Lindberg & Bengtsson, 2005). In our study, the peak $CWM_{RM}$ was found in the CU15 fields and the minimum $CWM_{RM}$ occurred in the RE06 fields. It may be caused by two reasons. First, the natural disturbance caused by flooding and dry-wet alternate action in marshland was greater than the human-caused disturbance in farmland due to the consistent state of dry field. Second, abundant food resources were conducive to the rapid reproduction of parthenogenetic groups. Compared with farmland, the food resources in marshland were relatively abundant because the litter always exit. So we considered the parthenogenetic taxa recovered faster than sexual individuals. Lindberg & Bengtsson (2006) found a tendency for the more mobile species of arthropods to recover faster than slow moving species. This was also found to be true in our study, where communities in areas undergoing restoration treatments were faster-moving species. Species with a high dispersal ability have an advantage in the colonization of habitats after disturbances (Burrows & Sutton, 2008) and the traits associated with dispersal were selected by land-use change in this prior study. In the present study, we use life history traits to reveal the recovery patterns in Collembola community after different periods of agricultural abandonment. Compared with taxonomic indices, the use of species traits is genetic and reduces environmental dependency, allowing for widely application of monitoring studies (Da Silva et al., 2016; Pey et al., 2014).

CONCLUSIONS

Our study showed that the density, species richness and Shannon-Wiener diversity of Collembola increased in the restoration sites. The results indicated that marshland restoration (after 12 years of agricultural abandonment) benefited recruitment and reconstruction of the community composition of Collembola. It also significantly promoted the recovery the species diversity of Collembola which mainly due to the improvement of soil properties. We also observed that surface-dwelling species recover faster than soil-dwelling species, maybe due to some common traits.
(i.e., parthenogenesis and fast dispersal) between epi- and hemi-edaphic species. Both taxonomic indices and functional indices based on life history traits revealed different aspects of community assembly. Therefore, we believed that the combination of both taxonomic indices and life history traits of Collembola is a promising tool for monitoring and understanding the mechanisms underlying community patterns after human-induced disturbances.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests
The authors declare that they have no competing interests.

Author Contributions
• Yongjing Dou conceived and designed the experiments, performed the experiments, analyzed the data, contributed reagents/materials/analysis tools, prepared figures and/or tables, authored or reviewed drafts of the paper, approved the final draft.
• Bing Zhang conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, approved the final draft.
• Xin Sun performed the experiments, contributed reagents/materials/analysis tools, approved the final draft.
• Liang Chang performed the experiments, contributed reagents/materials/analysis tools, approved the final draft.
Donghui Wu conceived and designed the experiments, contributed reagents/materials/analysis tools, approved the final draft.

Data Availability
The following information was supplied regarding data availability:

The functional trait modalities of the collembolan species collected during the study are available in Table S1.

Supplemental Information
Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.7198#supplemental-information.

REFERENCES

Bellinger PF, Christiansen KA, Janssens F. 1996–2012. Checklist of the Collembola of the world. Available at http://www.collembola.org.

Benayas JMR, Newton AC, Diaz A, Bullock JM. 2009. Enhancement of biodiversity and ecosystem services by ecological restoration: a meta-analysis. Science 325(5944):1121–1124 DOI 10.1126/science.1172460.

Berg MP, Bengtsson J. 2007. Temporal and spatial variability in soil food web structure. Oikos 116(11):1789–1804 DOI 10.1111/j.0030-1299.2007.15748.x.

Berg MP, Kniese JP, Bedaux J JM, Verhoeof HA. 1998. Dynamics and stratification of functional groups of micro- and mesoarthropods in the organic layer of a Scots pine forest. Biology and Fertility of Soils 26(4):268–284 DOI 10.1007/s003740050378.

Birkhofer K, Schoning I, Alt F, Herold N, Klarner B, Maran M, Marhan S, Oelmann Y, Wubet T, Yurkov A, Begerow D, Berner D, Buscot F, Daniel R, Diekotter T, Ehnes RB, Erdmann G, Fischer C, Foesel B, Groh J, Gutknecht J, Kandeler E, Lang C, Lohaus G, Meyer A, Nacke H, Nather A, Overmann J, Polle A, Pollierer MM, Scheu S, Schloter M, Schulze ED, Schulze W, Weinert J, Weisser WW, Wolters V, Schrumpf M. 2012. General relationships between abiotic soil properties and soil biota across spatial scales and different land-use types. PLOS ONE 7(8):e43292 DOI 10.1371/journal.pone.0043292.

Bokhorst S, Berg MP, Wardle DA. 2017. Micro-arthropod community responses to ecosystem retrogression in boreal forest. Soil Biology and Biochemistry 110:79–86 DOI 10.1016/j.soilbio.2017.03.009.

Bokhorst S, Phoenix GK, Bjerke JW, Callaghan TV, Huyer-Brugman F, Berg MP. 2012. Extreme winter warming events more negatively impact small rather than large soil fauna: shift in community composition explained by traits not taxa. Global Change Biology 18(3):1152–1162 DOI 10.1111/j.1365-2486.2011.02565.x.

Bullock JM, Aronson J, Newton AC, Pywell RF, Rey-Benayas JM. 2011. Restoration of ecosystem services and biodiversity: conflicts and opportunities. Trends in Ecology & Evolution 26(10):541–549 DOI 10.1016/j.tree.2011.06.011.

Burrows M, Sutton GP. 2008. The effect of leg length on jumping performance of short- and long-legged leafhopper insects. Journal of Experimental Biology 211(8):1317–1325 DOI 10.1242/jeb.015354.

Butchart SH, Walpole M, Collen B, Van Strien A, Scharlemann JP, Almond RE, Baillie JE, Bomhard B, Brown C, Bruno J, Carpenter KE, Carr GM, Chanson J, Chenery AM, Cslirke J, Davidson NC, Dentener F, Foster M, Galli A, Galloway JN, Genovesi P, Gregory RD,
Hockings M, Kapos V, Lamarque JF, Leverington F, Loh J, McGeoch MA, McRae L, Minasyan A, Hernández Morcillo M, Oldfield TE, Pauly D, Quader S, Revenca C, Sauer JR, Skolnik B, Spear D, Stanwell-Smith D, Stuart SN, Symes A, Tierney M, Tyrrell TD, Vié JC, Watson R. 2010. Global biodiversity: indicators of recent declines. Science 328(5982):1164–1168 DOI 10.1126/science.1187512.

Chen J-X, Christiansen K. 1996. A new species of Ptenothrix from China (Collembola: Dicyrtomidae). Florida Entomologist 79(4):586–591 DOI 10.2307/3496072.

Compton JE, Boone RD. 2000. Long-term impacts of agriculture on soil carbon and nitrogen in New England forests. Ecology 81(8):2314–2330 DOI 10.2307/177117.

Cramer VA, Hobbs RJ, Standish RJ. 2008. What’s new about old fields? Land abandonment and ecosystem assembly. Trends in Ecology & Evolution 23(2):104–112 DOI 10.1016/j.tree.2007.10.005.

Da Silva PM, Carvalho F, Dirilgen T, Stone D, Creamer R, Bolger T, Sousa JP. 2016. Traits of collembolan life-form indicate land use types and soil properties across an European transect. Applied Soil Ecology 97:69–77 DOI 10.1016/j.apsoil.2015.07.018.

Davidson NC. 2014. How much wetland has the world lost? Long-term and recent trends in global wetland area. Marine and Freshwater Research 65(10):936–941 DOI 10.1071/mf14173.

De Ruiter PC, Neutel A-M, Moore JC. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16(3):265–280 DOI 10.1111/j.1466-8238.2007.00287.x.

Dou et al. (2019), PeerJ, DOI 10.7717/peerj.7198
Hernández M, Conrad R, Klose M, Ma K, Lu Y. 2017. Structure and function of methanogenic microbial communities in soils from flooded rice and upland soybean fields from Sanjiang plain, NE China. *Soil Biology and Biochemistry* 105:81–91 DOI 10.1016/j.soilbio.2016.11.010.

Hopkin SP. 1997. *Biology of the springtails: (Insecta: Collembola)*. New York: Oxford University Press.

Isunju JB, Kemp J. 2016. Spatiotemporal analysis of encroachment on wetlands: a case of Nakivubo wetland in Kampala, Uganda. *Environmental Monitoring and Assessment* 188(4):203 DOI 10.1007/s10661-016-5207-5.

Johnston CA. 2013. Wetland losses due to row crop expansion in the Dakota prairie pothole region. *Wetlands* 33(1):175–182 DOI 10.1007/s13157-012-0365-x.

Jouquet P, Dauber J, Lagerlöf J, Lavelle P, Lepage M. 2006. Soil invertebrates as ecosystem engineers: Intended and accidental effects on soil and feedback loops. *Applied Soil Ecology* 32(2):153–164 DOI 10.1016/j.apsoil.2005.07.004.

Li Z, Hua C, Chen J. 2008. Bourletiella, a genus new to china, with redescription to bourletiella arvalis (fitch) (Collembola, symphypleona). *Acta Zootaxonomica Sinica* 33:807–809.

Lindberg N, Bengtsson J. 2005. Population responses of oribatid mites and collembolans after drought. *Applied Soil Ecology* 28(2):163–174 DOI 10.1016/j.apsoil.2004.07.003.

Lindberg N, Bengtsson J. 2006. Recovery of forest soil fauna diversity and composition after repeated summer droughts. *Oikos* 114(3):494–506 DOI 10.1111/j.2006.0030-1299.14396.x.

Liu HY, Lv X, Zhang SK. 2004. Landscape biodiversity of wetlands and their changes in 50 years in watersheds of the Sanjiang Plain. *Acta Ecologica Sinica* 24(7):1472–1479.

Lu R. 2000. *Analytical methods of soil agrochemistry*. Beijing: Chinese Agriculture Science and Technology Press.

Makkonen M, Berg MP, Van Hal JR, Callaghan TV, Press MC, Aerts R. 2011. Traits explain the responses of a sub-arctic Collembola community to climate manipulation. *Soil Biology and Biochemistry* 43(2):377–384 DOI 10.1016/j.soilbio.2010.11.004.

Malmström A. 2012. Life-history traits predict recovery patterns in Collembola species after fire: a 10 year study. *Applied Soil Ecology* 56:35–42 DOI 10.1016/j.apsoil.2012.02.007.

Mao D, Luo L, Wang Z, Wilson MC, Zeng Y, Wu B, Wu J. 2018. Conversions between natural wetlands and farmland in China: a multiscale geospatial analysis. *Science of the Total Environment* 634:550–560 DOI 10.1016/j.scitotenv.2018.04.009.

Messier J, McGill BJ, Lechowicz MJ. 2010. How do traits vary across ecological scales? A case for trait-based ecology. *Ecology Letters* 13(7):838–848 DOI 10.1111/j.1461-0248.2010.01476.x.

Murray PJ, Clegg CD, Crotty FV, De La Fuente Martinez N, Williams JK, Blackshaw RP. 2009. Dissipation of bacterially derived C and N through the meso- and macrofauna of a grassland soil. *Soil Biology and Biochemistry* 41(6):1146–1150 DOI 10.1016/j.soilbio.2009.02.021.

Norton RA. 1994. *Evolutionary aspects of oribatid life histories and consequences for the origin of the astigmata*. New York: Springer US.

Palaciosvargas JG, Martinez AES. 2014. A new species of Tullbergia (Collembola, Tullbergiidae) from Buenos Aires, Argentina. *Zookeys* 416:23–30 DOI 10.3897/zookeys.416.6923.

Pey B, Nahmani J, Auclerc A, Capowiez Y, Cluzeau D, Cortet J, Decaëns T, Deharveng L, Dubs F, Joimel S, Briard C, Grumiaux F, Laporte M-A, Pasquet A, Pelosi C, Pernin C, Ponge J-F, Salmon S, Santorufo L, Hedde M. 2014. Current use of and future needs for soil invertebrate functional traits in community ecology. *Basic and Applied Ecology* 15(3):194–206 DOI 10.1016/j.baae.2014.03.007.
Pipan T, Culver DC. 2013. Organic carbon in shallow subterranean habitats. *Acta Carsologica* 42(2–3):291–300 DOI 10.3986/ac.v42i2.603.

Ponge J-F, Dubs F, Gillet S, Sousa J, Lavelle P. 2006. Decreased biodiversity in soil springtail communities: the importance of dispersal and landuse history in heterogeneous landscapes. *Soil Biology and Biochemistry* 38(5):1158–1161 DOI 10.1016/j.soilbio.2005.09.004.

Ponge J-F, Péres G, Guernion M, Ruiz-Camacho N, Cortet J, Pernin C, Villenave C, Chaussod R, Martin-Laurent F, Bispo A, Cluzeau D. 2013. The impact of agricultural practices on soil biota: a regional study. *Soil Biology and Biochemistry* 67:271–284 DOI 10.1016/j.soilbio.2013.08.026.

Putten WHVD, Bardgett RD, Bever JD, Bezemer TM, Casper BB, Fukami T, Kardol P, Klironomos JN, Kulmatiski A, Schweitzer JA. 2013. Plant–soil feedbacks: the past, the present and future challenges. *Journal of Ecology* 101:265–276.

Querner P, Milasowszy N, Zulka KP, Abensperg-Traun M, Willner W, Sauberer N, Jakomini C, Wrbka T, Schmitzberger I, Zechmeister HG. 2018. Habitat structure, quality and landscape predict species richness and communities of Collembola in dry grasslands in Austria. *Insects* 9(3):81 DOI 10.3390/insects9030081.

Rossetti I, Bagella S, Cappai C, Caria MC, Lai R, Roggero PP, Da Silva PM, Sousa JP, Querner P, Seddaia G. 2015. Isolated cork oak trees affect soil properties and biodiversity in a Mediterranean wooded grassland. *Agriculture, Ecosystems & Environment* 202:203–216 DOI 10.1016/j.agee.2015.01.008.

Rusek J. 2007. A new classification of Collembola and Protura life forms. In: Tajovsky K, Schlaghamersky J, Pizl V, eds. *Contributions to Soil Zoology in Central Europe II. Proceedings of the 8th Central European Workshop on Soil Zoology*. České Budějovice: Biological Centre AS CR - Institute of Soil Biology, 109–115.

Sabais ACW, Scheu S, Eisenhauer N. 2011. Plant species richness drives the density and diversity of Collembola in temperate grassland. *Acta Oecologica* 37(3):195–202 DOI 10.1016/j.actao.2011.02.002.

Setälä H, Marshall VG, Trofymow JA. 1995. Influence of micro- and macro-habitat factors on collembolan communities in Douglas-fir stumps during forest succession. *Applied Soil Ecology* 2(4):227–242 DOI 10.1016/0929-1393(95)00053-9.

Shannon CE, Warren W. 1949. *The mathematical theory of communication*. Urbanna: University of Illinois Press.

Solis-Gabriel L, Mendoza-Arroyo W, Boege K, Del-Val E. 2017. Restoring lepidopteran diversity in a tropical dry forest: relative importance of restoration treatment, tree identity and predator pressure. *PeerJ* 5:e3344 DOI 10.7717/peerj.3344.

Song K, Wang Z, Li L, Tedesco L, Li F, Jin C, Du J. 2012. Wetlands shrinkage, fragmentation and their links to agriculture in the Muleng-Xingkai Plain, China. *Journal of Environmental Management* 111:120–132 DOI 10.1016/j.jenvman.2012.06.038.

Song C, Xu X, Tian H, Wang Y. 2009. Ecosystem-atmosphere exchange of CH4and N2O and ecosystem respiration in wetlands in the Sanjiang Plain, Northeastern China. *Global Change Biology* 15(3):692–705 DOI 10.1111/j.1365-2486.2008.01821.x.

Sousa JP, Bolger T, Da Gama MM, Lukkari T, Ponge J-F, Simón C, Traser G, Vanbergen AJ, Brennan A, Dubs F, Ivitis E, Keating A, Stofer S, Watt AD. 2006. Changes in Collembola richness and diversity along a gradient of land-use intensity: a pan European study. *Pedobiologia* 50(2):147–156 DOI 10.1016/j.pedobi.2005.10.005.

Van Straalen N, Rijninks P. 1982. Efficiency of Tullgren apparatus with respect to interpreting seasonal changes in age structure of soil arthropod populations. *Pedobiologia* 244:197–209.
Vanhee B, Salmon S, Devigne C, Leprêtre A, Deharveng L, Ponge J-F. 2017. The ‘terrill’ effect: coal mine spoil tips select for collembolan functional traits in post-mining landscapes of northern France. *Applied Soil Ecology* **121**:90–101 DOI 10.1016/j.apsoil.2017.09.027.

Verhoeven JTA, Setter TL. 2010. Agricultural use of wetlands: opportunities and limitations. *Annals of Botany* **105**(1):155–163 DOI 10.1093/aob/mcp172.

Wang Y, Liu J-S, Wang J-D, Sun C-Y. 2012. Effects of wetland reclamation on soil nutrient losses and reserves in Sanjiang Plain, Northeast China. *Journal of Integrative Agriculture* **11**(3):512–520 DOI 10.1016/s2095-3119(12)60037-9.

Wang Z, Song K, Ma W, Ren C, Zhang B, Liu D, Chen JM, Song C. 2011. Loss and Fragmentation of Marshes in the Sanjiang Plain, Northeast China, 1954–2005. *Wetlands* **31**(5):945–954 DOI 10.1007/s13157-011-0209-0.

Wardle DA. 2013. *Communities and ecosystems: Linking the aboveground and belowground components* (MPB-34). Princeton: Princeton University Press.

Wei G, Zhou Z, Guo Y, Dong Y, Dang H, Wang Y, Ma J. 2014. Long-term effects of tillage on soil aggregates and the distribution of soil organic carbon, total nitrogen, and other nutrients in aggregates on the semi-arid Loess Plateau, China. *Arid Land Research and Management* **28**(3):291–310 DOI 10.1080/15324982.2013.845803.

Widenfalk LA, Bengtsson J, Berggren A, Zwiggelaar K, Spijkman E, Huyer-Brugman F, Berg MP. 2015. Spatially structured environmental filtering of collembolan traits in late successional salt marsh vegetation. *Oecologia* **179**(2):537–549 DOI 10.1007/s00442-015-3345-z.

Xu S, Zhang B, Ma L, Hou A, Tian L, Li X, Tian C. 2017. Effects of marsh cultivation and restoration on soil microbial communities in the Sanjiang Plain, Northeastern China. *European Journal of Soil Biology* **82**:81–87 DOI 10.1016/j.ejsobi.2017.08.010.

Yin W. 1992. *Subtropical Soil Animals of China*. Beijing: Science Press.

Yin W. 1998. *Pictorial Keys to Soil Animals of China*. Beijing: Science Press.

Yin X, Ma C, He H, Wang Z, Li X, Fu G, Liu J, Zheng Y. 2018. Distribution and diversity patterns of soil fauna in different salinization habitats of Songnen Grasslands, China. *Applied Soil Ecology* **123**:375–383 DOI 10.1016/j.apsoil.2017.09.034.

Yun B, Gao Y. 2015. Paratullbergia Womersley in China: the description of a new species and a key to the genus (Collembola, Tullbergiidae). *Zookeys* **534**:55–60 DOI 10.3897/zookeys.534.6036.

Zedler JB, Kercher S. 2005. WETLAND RESOURCES: status, trends, ecosystem services, and restorability. *Annual Review of Environment and Resources* **30**(1):39–74 DOI 10.1146/annurev.energy.30.050504.144248.

Zhang X, Song C, Mao R, Yang G, Tao B, Shi F, Zhu X, Hou A. 2014. Litter mass loss and nutrient dynamics of four emergent macrophytes during aerial decomposition in freshwater marshes of the Sanjiang plain, Northeast China. *Plant and Soil* **385**(1–2):139–147 DOI 10.1007/s11104-014-2217-3.