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Bamboo invasion alters Collembola community composition varying with life-forms

Headings: Bamboo invasion alters soil Collembola

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Abstract

BACKGROUND: Plant invasions are global concern. In eastern China, bamboo is rapidly expanding, negatively influencing neighbouring forest communities. However, the studies on how bamboo invasion affects belowground communities, especially for soil invertebrates, are still lacking. In the present study, we focused on a highly abundant and diverse fauna taxon – Collembola. Collembola communities have three typical life-forms (i.e., epedaphic, hemiedaphic and euedaphic) inhabiting different soil layers and playing distinct roles in ecological processes. Specifically, we studied their abundance, diversity, and community composition at the three stages of bamboo invasion: uninvaded secondary broadleaf forest, moderately invaded mixed bamboo forest, and completely invaded bamboo (*Phyllostachys edulis*) forest.

RESULTS: Our results showed that bamboo invasion negatively influenced Collembola communities by decreasing their abundance and diversity. Moreover, Collembola life-forms differed in their responses to bamboo invasion, with surface-dwelling Collembola being more vulnerable to bamboo invasion than soil-living Collembola.

CONCLUSION: Our findings indicate differential response patterns to bamboo invasion within Collembola communities. The negative effects of bamboo invasion on soil surface-dwelling Collembola may further influence ecosystem functioning.

Keywords: Community composition; High-throughput sequencing; Life-form; Molecular ecology; Plant invasion; Soil fauna

1. Introduction

Biological invasion is a universal driver of global change that threatens biodiversity globally with widespread economic consequences.[1-5] At a local scale, plant invasion threatens biodiversity of native communities which may degrade ecosystem functions and services.[1, 2, 6-8] Various studies have shown that invasive plants could decrease local plant species diversity[9-12] and negatively shift soil physicochemical properties through changing the quantity and quality of plant litter, further causing biodiversity loss in soils.[4, 5, 13, 14] This is of concern because the abundance, diversity, and community composition of soil organisms are important in regulating ecosystem functions, such as litter decomposition and nutrient cycling.[15-19]

In the process of plant invasion, studies on soil microorganisms, earthworms and microfauna have attracted widespread attention,[20-22] but less studies have focused on the community structure of soil mesofauna which can affect litter decomposition mainly by promoting microbial activity.[23] Collembola (springtails) are among the most widespread and abundant mesofauna in most terrestrial ecosystems.[24-26] Hence, they provide an excellent model for studying soil mesofauna responses in the context of environmental changes[27, 28]. Additionally, they are functionally diverse, serving as an important driving force in several key soil processes, such as litter decomposition and nutrient turnover.[29] Collembola can regulate the diversity and composition of the soil microbial community through disseminating microbiota propagules, and feeding on fungal mycelium and spores, as well as bacterial membranes.[25, 30, 31] Additionally, soil

Collembola can pose strong indirect effects on plant morphological characteristics and tissue chemistry by regulating the availability of soil nutrients.[32-35]

The structure and function of soil fauna communities varies with soil depth.[36, 37] Litter-dwelling fauna plays an important role in the earlier stage of decomposition, whereas soil-dwelling fauna plays a more important role in later stages of decomposition.[38] Further, surface-dwelling species are typically more sensitive to environment changes than soil-dwelling species.[39] According to the vertical stratification of soil Collembola, they are often divided into three life-forms: epedaphic (dwelling on the soil surface), euedaphic (dwelling in the soil), and hemiedaphic (showing intermediate characteristics between epedaphic and euedaphic).[25, 39, 40] Studying how these distinct Collembola life-forms respond to plant invasion is important to better understand and predict the consequences for ecosystem function.

In the past two decades, bamboo invasion has become a major concern, both in its native habits in China and Brazil, as well as and newly introduced habitats in Japan and North America.[41-44] As a native species in subtropical China, moso bamboo (*Phyllostachys edulis*) was widely planted for its ecological, economic and cultural values, and at its peak, this species accounted for about 70% of the nation's bamboo growing area.[45] However, a large number of bamboo plantation areas were abandoned in recent years and moso bamboo has spread from these former plantations, invading the adjacent broadleaf forests.[46, 47] This has negatively impacted the plant diversity and litter inputs of these forests,[41, 48-50] and thereby the soil physical and chemical properties, as well as the structure and function of soil communities.[46, 47, 49, 51] The bamboo invasion has been reported to cause biodiversity loss of soil mesofauna.[47] However, how different life-forms of soil Collembola will respond to bamboo invasion still remains unknown.

To test the impact of bamboo invasion on Collembola communities, we sampled secondary broadleaf forest, mixed bamboo forest and *Phyllostachys edulis* forest, representing three stages of invasion: uninvaded, moderately invaded, and completely invaded. We investigated the effects of bamboo invasion on Collembola taxonomic richness, diversity, abundance and community composition, with focus on the different life forms, and hypothesized that: (1) bamboo invasion decrease the diversity and abundance of Collembola; (2) bamboo invasion alter the community composition of Collembola from a more complex community to a less complex community; (3) Collembola life-forms differ in their response to bamboo invasion, with surface-dwelling species being more responsive than soil-living species.

2. Materials and Methods

2.1. Study site

Our study site was located at an altitude of about 500–650 m in the Tianmu Mountain National Nature Reserve (30°18’–30°25’N, 119°23’–119°29’E), in Zhejiang Province, eastern China. This area is dominated by a typical seasonal monsoon climate, with annual rainfall of 1829 mm and mean temperature of 15°C. After the abandonment of bamboo plantations in the 1970s, the research site has been severely affected by moso bamboo (*Phyllostachys edulis*) invasion.[52] We selected three types of forest stands at this site, representing three stages of invasion, i.e., secondary broadleaved forest (SBF, uninvaded native forest dominated by *Cunninghamia lanceolata*, *Quercus serrata* var. *brevipetiolata*, and *Pinus massoniana*), mixed bamboo forest (MBF, a transition zone moderately invaded by moso bamboo), and *Phyllostachys edulis* forest (PEF, completely invaded and occupied by moso bamboo).[47]

2.2. Experimental design and Collembola extraction

Four parallel transects (180 m in length and 50 m apart) were set up as four replicates along the invasion trajectory from broadleaved forest to moso bamboo forest, with three plots (each plot: 20 × 20 m) in each transect representing the three types of forest stands, resulting in 12 plots in total. In each of the 12 plots, we established four sub-plots (5 × 5 m, one for each season) (Fig. S1). For each sub-plot, we collected a cylindrical soil core (10 cm in diameter, 20 cm in depth) from five sampling points, including all surface litter (2–3 cm thickness). Materials collected from the five sampling points in each sub-plot were treated as one sample. Samples were collected in May 2018 (spring), August 2018 (summer), November 2018 (autumn) and February 2019 (winter), resulting 48 samples (3 forest types × 4 seasons × 4 replicates).

Modified Berlese-Tullgren funnels were used to extract Collembola.[53] The samples were placed on a sieve (2 mm-meshed diameter) above a funnel and exposed to white incandescent electric lamps for 48 h. Soil mesofauna were collected in conical flasks filled with anhydrous ethanol and all the collembolan were picked out for further study.

2.3. High throughput sequencing (HTS) and data processing

We used a highly efficient and reliable high-throughput sequencing (HTS) technique[54, 55] to obtain the DNA sequences of soil Collembola. The protocols of sequencing and data processing followed Wei *et al.*[47] Specifically, all 48 samples were ground and homogenized with liquid nitrogen for DNA extraction using DNeasy® Blood and Tissue kit (QIAGEN, Hilden, Germany). The primers Ill_B_F (5′. CCIGAYATRGCITTYCCICG. 3′[56] and Fol_degen_rev (5′. TANACYTCNGGRTGNCCRAARAAYCA. 3′[57] were used to amplify the 418 bp polymerase chain reaction (PCR) of the cytochrome oxidase subunit I (COI) gene (barcode fragment). Each sample was amplified for triplicates on an ABI GeneAmp ®9700 (Applied Biosystems, USA), following the PCR protocol of Arribas *et al.* [54]After adding dual-index barcodes (Illumina TruSeqTM DNA Sample Prep Kit), purified amplicons were pooled and were sequenced on an Illumina MiSeq platform (2 × 300 bp paired-end) after quality control. The raw sequences were quality-filtered by Trimmomatic [58] and amalgamated with FLASH.[59] Only contigs with the length of 418 bp were preserved.

Operational taxonomic units (OTUs) were clustered with 95% similarity cutoff using UPARSE version 7.1 with a novel 'greedy' algorithm that performs chimera filtering and OTU clustering simultaneously.[60] OTU is usually considered the biological equivalent of a species. The 5% value for OTU delimitation of Collembola is in line with levels defining intra- and interspecific differentiation for grouping barcode data.[26] In order to avoid sequencing error, low-abundant OTUs (total counts < 5) were eliminated. The trimmed mean of M values method (TMM) was used by the BioConductor package EdgeR to normalize the OTU counts of 48 samples.[61, 62] The result of TMM was used for subsequent analysis. We identified all the OTUs to the genus level based on the barcoding database of Collembola in eastern China with integration of morphological determination.[63, 64] We then classified observed Collembola into three life-forms, i.e., epedaphic, euedaphic and hemiedaphic (Table S1).

2.4. Data analyses

Collembola species richness (species number),[65] Shannon-Wiener diversity[66] and community composition (distribution of species in each sample) were calculated according to the sequence number of each OTU (= species) in each sample, while the relative abundance in the total sequence number of all 48 samples was used for abundance. Calculations were carried out using R v.4.0.3.[67] Species richness and Shannon-Wiener diversity of the total Collembola communities and separately for each of the three life-forms were computed using the R packages ‘vegan’ and ‘picante’.[68, 69] The effects of stand type, season, and their interaction on Collembola species richness, Shannon-Wiener diversity, abundance and community composition were estimated by permutational multivariate analysis of variance (PERMANOVA) with 999 permutations using the R package ‘vegan’.[61] In addition, we used the R packages ‘vegan’, ‘ape’ and ‘RColorBrewer’ to perform principal coordinate analysis (PCoA) based on Bray-Curtis distance to test the differences among the three types of forest stands, with the model constrained to the factor of interest while controlling for the other factors.[61, 70] These results were visualized using R packages ‘ggplot2’ and Origin (Origin Lab Corporation, Northampton, MA, USA). Based on Collembola abundance, a heatmap and Manhattan plots were used to demonstrate the variations in the community structure of the three life-forms of Collembola at the genus level in each sample. The heatmap was performed by R package ‘pheatmap’. The Manhattan plots were performed by R packages ‘edgeR’, ‘tidyverse’ and ‘ggplot2’ to further demonstrate the structural variation of Collembola communities among the three forest stands. Redundancy analysis (RDA) was performed using R packages ‘vegan’ and ‘ggplot2’ to evaluate the relationship between the Collembola life-forms and the environmental variables (i.e., the physical and chemical properties of litter and soil).

3. Results

3. 1. The responses of diversity indices to bamboo invasion

Bamboo invasion significantly reduced the species richness of total Collembola, as well as richness of epedaphic and hemiedaphic species but not euedaphic species ($P < 0.05$) (Table 1, Figure 1a). The species richness of Collembola communities was generally lower in winter than in other seasons (except for euedaphic species) (Table 1, Figure

1b). No interaction effects were detected between forest stand type and season on Collembola species richness (Table 1).

Except for hemiedaphic and euedaphic species, the Shannon-Wiener diversity of Collembola communities was significantly negatively affected by bamboo invasion ($P < 0.05$) (Table 1, Figure 2a). The Shannon-Wiener diversity was significantly affected by season only for epedaphic Collembola with the lowest diversity in winter ($P < 0.05$) (Table 1, Figure 2b). No interaction effects were detected between forest stand type and season on Shannon-Wiener diversity (Table 1).

3.2. The responses of abundance to bamboo invasion

The abundances of total and epedaphic Collembola were significantly lower in *Phyllostachys edulis* forest stands than in moderately invaded and uninvaded stands (i.e., secondary broadleaf forest and mixed bamboo forest) ($P < 0.05$) (Table 1, Figure 3a). However, the abundances of hemiedaphic and euedaphic did not respond to bamboo invasion (Table 1, Figure 3a). The abundances of total and epedaphic Collembola were generally higher in spring and lower in winter than in other seasons, while the abundances of hemiedaphic and euedaphic Collembola were not affected by season (Table 1, Figure 3b). No interaction effects were found between forest stand type and season on Collembola abundance (Table 1).

3.3. The responses of community composition to bamboo invasion

Bamboo invasion significantly affected Collembola community composition ($P < 0.05$) (Table 2). Principal coordinate analysis (PCoA) showed clear separation between uninvaded, moderately invaded, and completely invaded stands, for total Collembola and for the three Collembola life-forms ($P < 0.05$) (Figure 4). Specifically, PCo1 explained 59–85% of the variance while PCo2 accounted for 14–40% of the variance (Figure 4a). Except for hemiedaphic and euedaphic species, Collembola community composition also significantly varied among seasons ($P < 0.05$) (Table 2; Figure 4b). However, no any interaction effects between forest stand type and season were detected for Collembola community composition (Table 2).

In addition, we found that a total of 19 genera and 46 OTUs underwent significant changes in abundance in response to bamboo invasion ($P < 0.05$) (Figure S2). The first RDA axis accounted for 57% of the variation of Collembola community composition; epedaphic species explained most of the variation (Figure 5a). The abundance of epedaphic Collembola positively correlated to total carbon, carbon/nitrogen ratio, and cellulose in litter (Figure 5a), while their abundance positively correlated with soil temperature and negatively correlated with soil pH (Figure 5b).

4. Discussion

We examined the effects of bamboo invasion on the diversity, abundance, and community composition of soil Collembola across seasons using high-throughput sequencing. We found that bamboo invasion significantly reduced (1) Collembola species richness and (2) Collembola abundance, particularly for surface-dwelling species; (3) significantly shifted the taxonomic composition of Collembola communities.

4.1. How do Collembola diversity and abundance respond to bamboo invasion?

In support of our first hypothesis, bamboo invasion caused a significant reduction in diversity of total Collembola, including species richness and Shannon-Wiener diversity. This is in line with previous studies showing that plant invasion reduces the species richness of soil microarthropods.[5, 23] For example, changes in soil properties and vegetation composition as a result of *Robinia pseudoacacia* invasion has been shown to cause richness loss of soil mesofauna.[5] However, some other studies have shown that invasive plants do not always reduce the diversity of soil microarthropods, for example in case of *Solidago gigantea*.[71] This seems contradictory to our finding, but it could be indicate that that taller or woody plants (e.g., shrubs or trees) generally have a greater impact on soil biota.[72-74] Moso bamboo (*Phyllostachys edulis*) is a tall woody grass (Poaceae: Bambuseae). Bamboo invasion caused the species richness loss of the aboveground plant,[48] which might further reduce the soil Collembola diversity. Several previous studies have shown that low plant species richness may lead to a decline in the species richness of Collembola,[75-77] as plant-soil positive feedback interaction. Additionally, our finding is consistent with some other studies, showing reduced abundance of soil microarthropods after plant invasion.[5, 23] Indeed, bamboo invasion simplified the plant composition of subtropical forest and its litter types.[46, 78] This could explain the reason that lower numbers of surface-dwelling epedaphic Collembola in completely invaded forest stands could result in the abundance reductions of total Collembola in this study.

4.2. How does Collembola community composition shift in response to bamboo invasion?

In line with our second hypothesis, bamboo invasion significantly altered the community composition of soil Collembola, from a complex community to a simplified community. Compositional shifts with less abundance and diversity are likely related to the changes in litter inputs with lower litter quality after bamboo invasion.[79] Specifically, bamboo invasion into neighboring evergreen broadleaved forests decreased litter production and quality,[80] and thereby soil detritivores.[81-84] Moreover, bamboo invasion into neighboring forests may significantly alter the community structure of microbial community, by increasing the abundance and activity of bacterial community; whereas by decreasing that of fungal community.[20, 50, 51, 85, 86] Further, such compositional changes in microbial communities may have lock-on effects on the community structure of microbivorous fauna, such as soil Collembola.[25, 47]

Additionally, changes in soil abiotic conditions and the composition structure of vegetation caused by plant invasion can have top-down effects on soil microarthropods,[5] which may further affect the community structure of Collembola. A better understanding of bamboo invasion effects on the community compositions of

Collembola may help to further predict how soil ecosystems will respond and adapt to plant invasion. As the functional role of Collembola depends on the vertical position of their specific life-forms, and bamboo invasion had stronger effects on the community composition of surface-dwelling Collembola,[38] and this may slow down the earlier stages of litter decomposition.

4.3 The sensitivity to bamboo invasion: surface-dwelling *vs.* soil-living Collembola

Our results support the third hypothesis that Collembola life-forms differ in response to bamboo invasion, i.e., the effects of bamboo invasion were more profound for surface-dwelling Collembola than for soil-living Collembola. Specifically, we found (stronger) negative effects of bamboo invasion on Shannon-Wiener diversity and abundance of epedaphic species than of euedaphic species. This could be explained by invasion-induced changes in soil condition (e.g. *via* litter inputs), that the epedaphic Collembola are more vulnerable to such environmental changes than euedaphic Collembola.[39, 87]

Therefore, the surface-dwelling epedaphic Collembola are better indicator for environmental changes. Previous studies showed that bamboo invasion decreased the litter quality by lowering the ratio of cellulose/lignin.[80, 85] As a consequence, this might be not conductive to epedaphic Collembola. As Collembola feed basically on fungi,[88-90] bamboo invasion into neighboring broadleaved forest may significantly decrease the abundance and activity of fungal community.[51] This supports our result that bamboo invasion had a negative effect on surface-dwelling Collembola. Besides, soil pH in bamboo invasion was confirmed to increase in previous studies;[20, 91, 92] we further found the increased pH value was significantly related to a decreased abundance of epedaphic Collembola. Such result to some extent can be supported by da Silva *et al.*,[36] who found pH was the main soil parameter that negatively influencing Collembola community. Taken together, bamboo invasion may cause negative shifts in Collembolan community through the regulation of physical and chemical properties of litter inputs and soil.[46, 51, 85, 91] Because the semi-field experiment is a simplified system, the results cannot be directly extrapolated to the field results. Such linkages therefore need to be confirmed by further comprehensive field investigation.

5. Conclusions

As bamboo invasion a case study, our results showed that plant invasion was able to influence soil invertebrate communities, i.e., reducing their diversity and abundance, and shifting their community composition, in a negative direction. Moreover, these detrimental effects were differential along the vertical distribution of soil invertebrate. For instance, Collembola provide as an excellent model taxon, which showed rather different responses among their life-forms (i.e., epedaphic, hemiedaphic, and euedaphic) to plant invasion. In general, surface-dwelling species were particularly more vulnerable, compared to soil-living species. These differential responses within soil communities along such a vertical stratification may have further cascading effects on ecosystem functions. For example, if such a detrimental effect on surface-dwelling

Collembola will slow down litter decomposition, particular for its earlier stages, which will potentially threaten the ecosystem function they provided. However, future empirical studies are encouraged to directly test how shifts in Collembola communities under plant invasion (other global changes) influence soil food web dynamics and associated soil carbon and nutrient cycling processes.

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Data Availability Statement

The sequencing data supporting the results of this study is deposited in the GenBank repository under the accession number SRR17653580.

Funding and/or Conflicts of interests/Competing interests

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Table 1. Results of PERMANOVA testing (*F*-values) the effects of stand, season, and their interaction on species richness, Shannon-Wiener diversity and abundance of total, epedaphic, hemiedaphic, and euedaphic communities of Collembola.

Indices	**Effects**	**df**	**Total**	**Epedaphic**	**Hemiedaphic**	**Euedaphic**
Species richness						
	Stand	2	0.31***	0.27***	0.33***	0.01
	Season	3	0.46***	0.50***	0.27***	0.11
	Stand × Season	6	0.05	0.06	0.09	0.14
Shannon-Wiener diversity						
	Stand	2	0.21**	0.24***	0.08	0.03
	Season	3	0.05	0.14*	0.05	0.06
	Stand × Season	6	0.12	0.19*	0.08	0.19
Abundance						
	Stand	2	0.14*	0.15*	0.09	0.04
	Season	3	0.26**	0.15*	0.09	0.05
	Stand × Season	6	0.07	0.10	0.06	0.19

Note: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; no asterisk, non-significant differences.

Table 2. Results of PERMANOVA testing (*R*-values) the effects of stand, season, and their interaction on community composition of total, epedaphic, hemiedaphic, and euedaphic Collembola.

Groups	df	Total	Epedaphic	Hemiedaphic	Euedaphic
Stand	2	0.15***	0.13***	0.17***	0.14***
Uninvaded vs moderately invaded	1	0.08**	0.09***	0.06	0.11***
Moderately vs completely invaded	1	0.12***	0.10***	0.13***	0.05
Uninvaded vs completely invaded	1	0.15***	0.10***	0.18***	0.16***
Season	3	0.15**	0.19***	0.08	0.05
Spring vs Summer	1	0.06*	0.11**	0.06	0.03
Spring vs Autumn	1	0.13**	0.17***	0.07	0.02
Spring vs Winter	1	0.14***	0.16***	0.07	0.03
Summer vs Autumn	1	0.09**	0.12***	0.04	0.04
Summer vs Winter	1	0.10**	0.13***	0.06	0.05
Autumn vs Winter	1	0.09*	0.12***	0.04	0.02
Stand × Season	6	0.09	0.10	0.09	0.12

Note: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; no asterisk, non-significant differences.

Figure legends

Fig. 1 Effects of stand type (a) and season (b) on species richness of total, edaphic, hemiedaphic and euedaphic Collembola. Boxplots show median (horizontal line), the mean (black dot), first and third quartile (rectangle), 1.5 × interquartile range (whiskers), and data distribution (scattered dots). Lowercase letters represent significant differences between stand types and seasons at $P < 0.05$. SBF, uninvaded secondary broadleaved forest; MBF, moderately-invaded mixed bamboo forest; PEF, completely invaded *Phyllostachys edulis* forest; ***, $P < 0.001$.

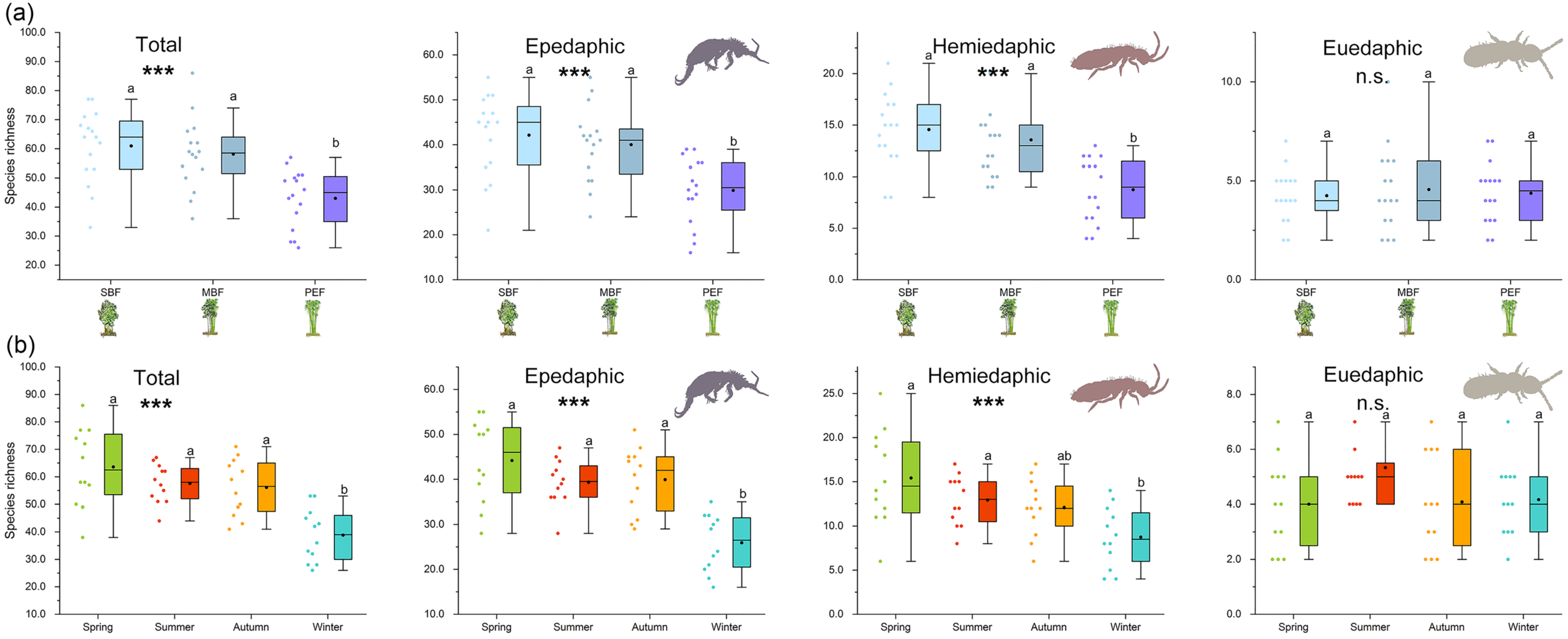
Fig. 2 Effects of stand type (a) and season (b) on Shannon-Wiener diversity of total, edaphic, hemiedaphic and euedaphic Collembola. Boxplots show the median (horizontal line), mean (black dot), first and third quartile (rectangle), 1.5 × interquartile range (whiskers), and data distribution (scattered dots). Lowercase letters represent significant differences between stand types and seasons at $P < 0.05$. SBF, uninvaded secondary broadleaved forest; MBF, moderately-invaded mixed bamboo forest; PEF, completely invaded *Phyllostachys edulis* forest; n.s., $P > 0.05$, **, $P < 0.01$; ***, $P < 0.001$.

Fig. 3 Effects of stand type (a) and season (b) on relative abundance of total, edaphic, hemiedaphic, and euedaphic Collembola. Boxplots show the median (horizontal line), the mean (black dot), first and third quartile (rectangle), 1.5 × interquartile range (whiskers), and data distribution (scattered dots). Lowercase letters represent significant differences between stand types and seasons at $P < 0.05$. SBF, uninvaded secondary broadleaved forest; MBF, moderately-invaded mixed bamboo forest; PEF, completely invaded *Phyllostachys edulis* forest; n.s., $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$.

Fig. 4 Constrained effects of stand type (a) and season (b) on Collembola community composition. Principal coordinate analysis (PCoA) using the Bray-Curtis distances for total, epedaphic, hemiedaphic, and euedaphic Collembola. Ellipses indicate 95% confidence intervals. SBF, uninvaded secondary broadleaved forest; MBF, moderately-invaded mixed bamboo forest; PEF, completely invaded *Phyllostachys edulis* forest; n.s.; $P > 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Fig. 5 Redundancy analysis (RDA) showing the relationship between Collembola life-forms and the physical and chemical properties of litter (a) and soil (b). Each colored dot indicates one sample. Green arrows indicate Collembola life forms, while black arrows indicate environmental factors. SBF, uninvaded secondary broadleaved forest; MBF, moderately-invaded mixed bamboo forest; PEF, completely invaded *Phyllostachys edulis* forest.

Fig. 1


(a)
Total
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Species richness
100.0
90.0
80.0
70.0
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20.0
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a
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SBF
MBF
PEF
Epedaphic
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Hemiedaphic
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Euedaphic
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SBF
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(b)
Total
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Species richness
100.0
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80.0
70.0
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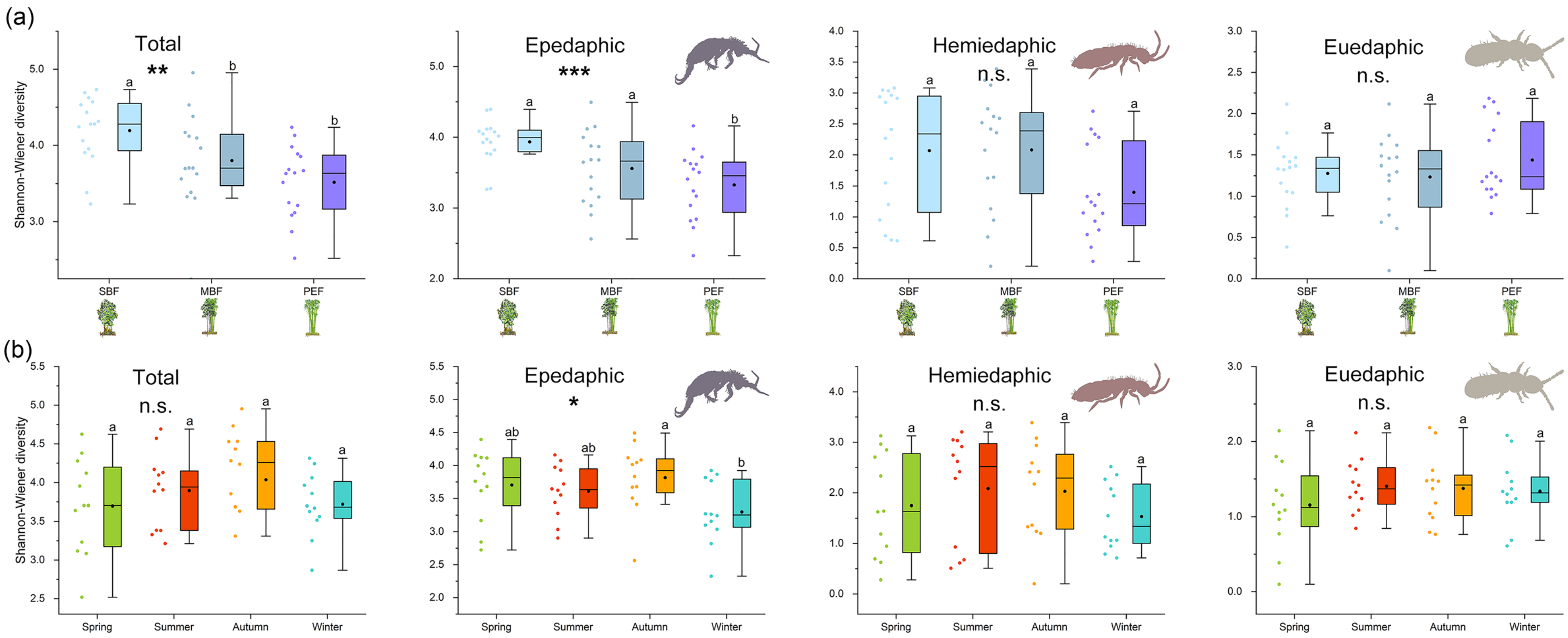
Fig. 2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Shannon-Wiener diversity
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Shannon-Wiener diversity
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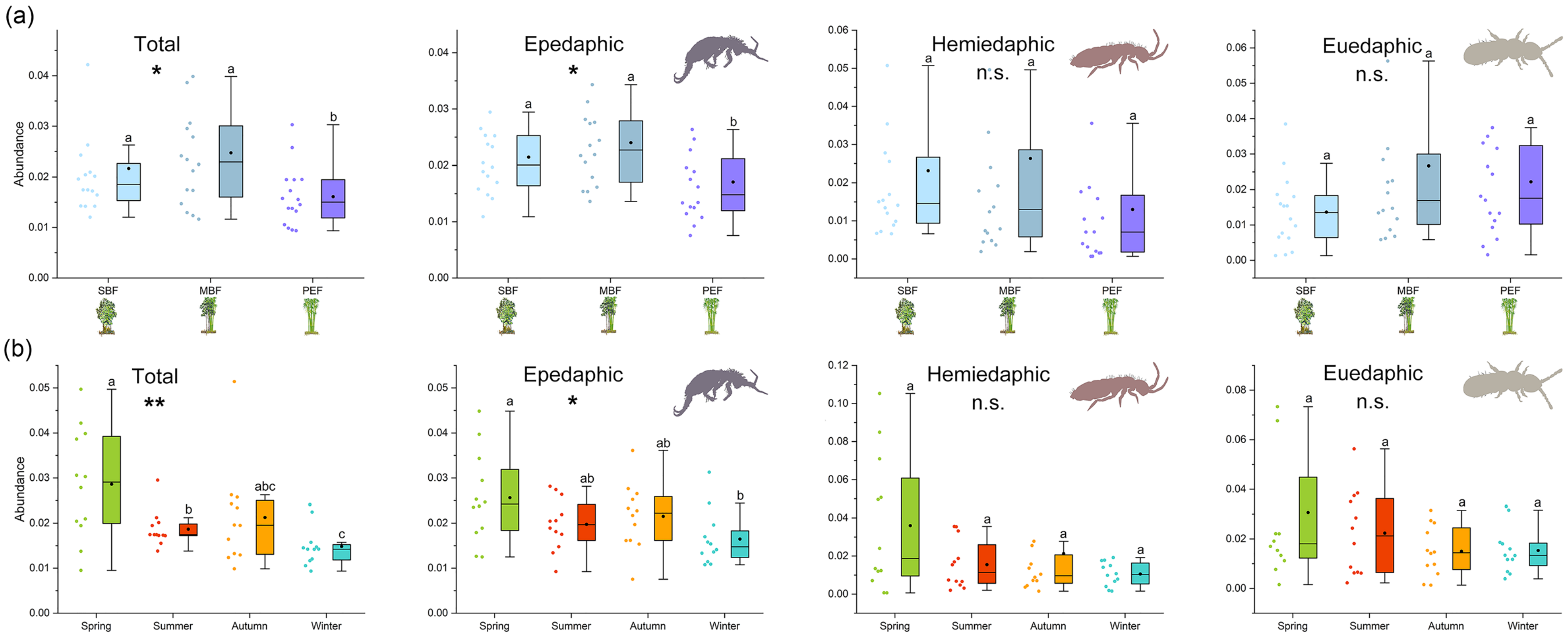
Fig. 3


(a)
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Abundance
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Fig. 4

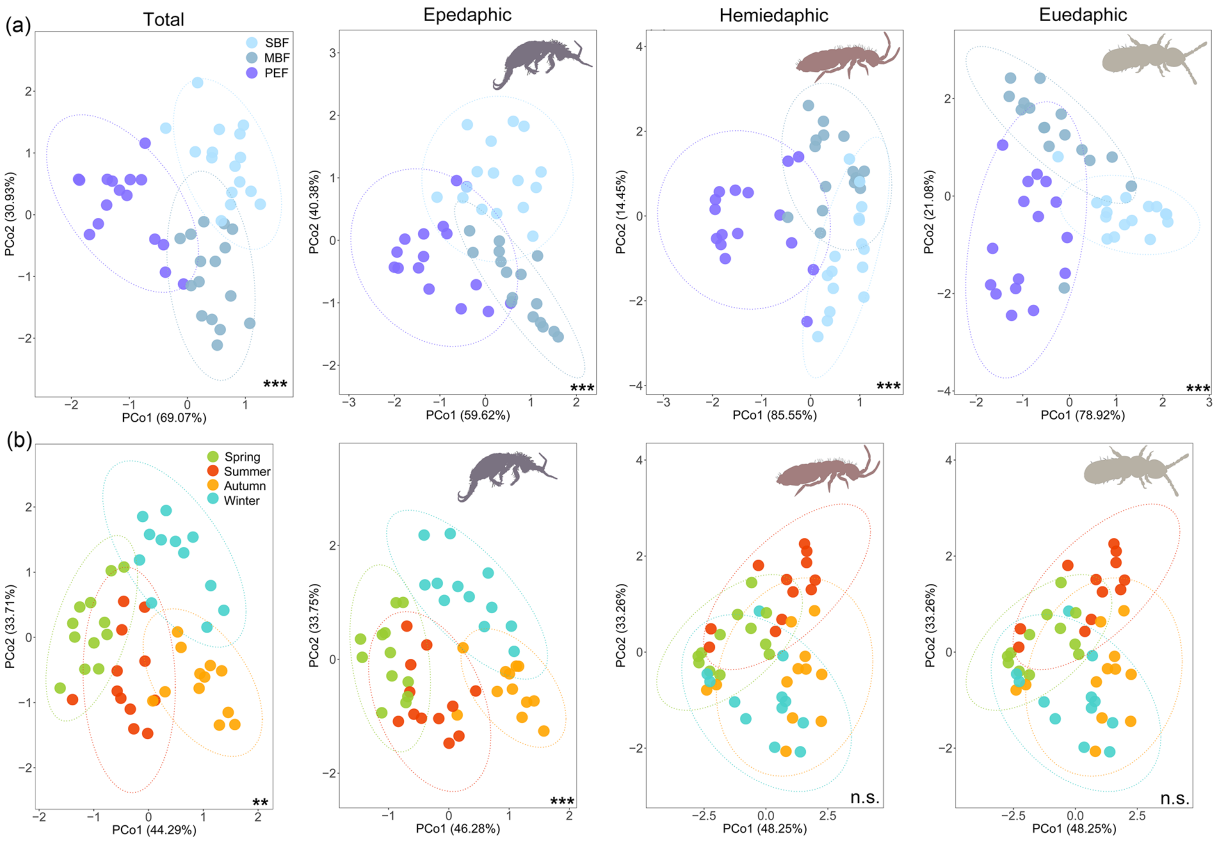
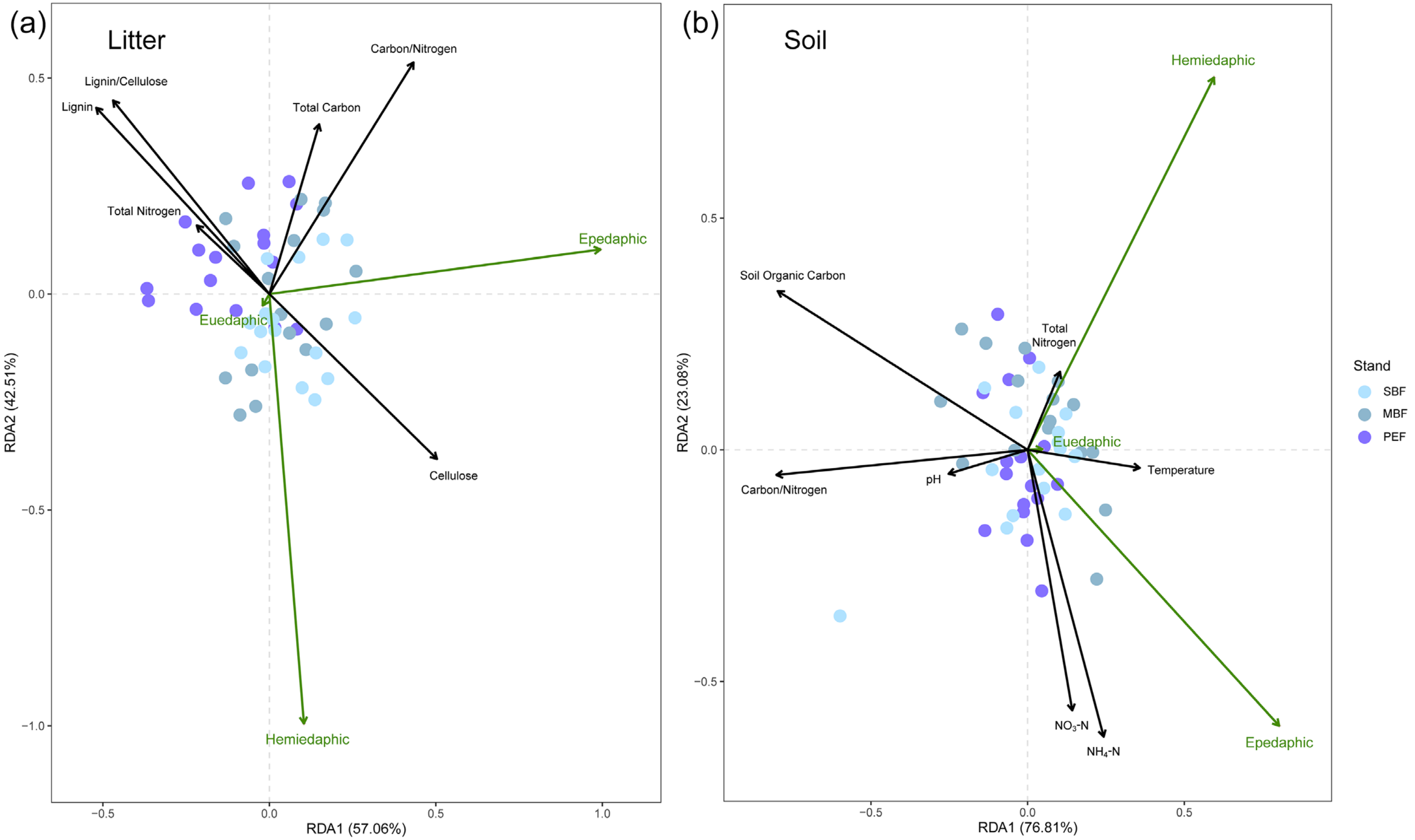

(a)
Total
SBF
MBF
PEF
PCo1 (69.07%)
PCo2 (30.93%)
***
Epedaphic
PCo1 (59.62%)
PCo2 (40.38%)
***
Hemiedaphic
PCo1 (85.55%)
PCo2 (14.45%)
***
Euedaphic
PCo1 (78.92%)
PCo2 (21.08%)
***
(b)
Spring
Summer
Autumn
Winter
PCo1 (44.29%)
PCo2 (33.71%)
**
PCo1 (46.28%)
PCo2 (33.75%)
***
PCo1 (48.25%)
PCo2 (33.26%)
n.s.
PCo1 (48.25%)
PCo2 (33.26%)
n.s.

Fig. 5


(a)
Litter
Carbon/Nitrogen
Lignin/Cellulose
Lignin
Total Carbon
Total Nitrogen
Epedaphic
Euedaphic
Cellulose
Hemiedaphic
0.5
0.0
−0.5
−1.0
−0.5
0.0
0.5
1.0
RDA2 (42.51%)
RDA1 (57.06%)
(b)
Soil
Hemiedaphic
Soil Organic Carbon
Total Nitrogen
Euedaphic
Temperature
pH
Carbon/Nitrogen
NO_3-N
NH_4-N
Epedaphic
0.5
0.0
−0.5
−0.5
0.0
0.5
RDA2 (23.08%)
RDA1 (76.81%)
Stand
SBF
MBF
PEF