Soil meso- and micro-fauna community in response to bamboo-fungus agroforestry management

Jiancheng Zhao¹, Miao Liu², Jun Xu³, Zhenya Yang¹, Qin Li¹* & Chunju Cai²*

Bamboo-fungus agroforestry management is an ecological model of sustainable production of moso bamboo forest, and Stropharia rugosoannulata has been widely planted in moso bamboo forest. However, little attention has been paid to soil fauna community in bamboo-fungus agroforestry system. Thus, the aim of this study was to investigate the response of soil fauna communities to agroforestry management, and to explore the relationships between soil fauna communities and soil properties. An experiment with 0, 1, 2 and 3 years of planting was carried out in an existing moso bamboo forest. The community composition of soil meso- and micro-fauna was investigated, and the soil properties were determined. Results showed that a total of 2968 individuals of soil meso- and micro-fauna, belonging to 8 classes and 13 groups were detected. The group number and density of soil fauna was highest right and then decreased. Planting Stropharia rugosoannulata in moso bamboo forest increased the density of dominant groups, but did not change its composition. Shannon-Weiner diversity index (H), Margalef richness index (D) and Density-Group diversity index (DG) were the highest one year after planting the fungus, while Simpson dominance index (C) was the lowest in the meantime. Contents of soil moisture (SMC), organic matter (SOM), total nitrogen (TN), total phosphorus (TP) and total potassium (TK) increased first and then decreased with the increase of planting years, peaking at 1 year after planting, while the pH value continued to increase. Responses of soil fauna community were associated with soil physicochemical properties. Redundancy analysis (RDA) showed that SOM was the main environmental factor driving the variation of soil fauna community, followed by TP and TN. In conclusion, planting Stropharia rugosoannulata in moso bamboo increased the diversity and abundance of soil fauna communities due to its contribution to abundance of organic matter and supply of nutrients.

Moso bamboo (Phyllostachys edulis (Carrière) J. Houzeau) is one of the most important forest resources in Southern China, which is characterized by its fast growth during sprouting and rapid biomass accumulation¹–³. As a major non-wood resource, moso bamboo forest plays an important role in socioeconomic and international trade⁴–⁶. The yields of forest products (bamboo timber and bamboo shoots) have been stagnant at the current level of input⁷. Furthermore, the phenomenon of abandonment caused by the decrease of the bamboo shoot price and timber price and the increase of the labor costs has received an increasing attention in recent years, which reduced the enthusiasm of bamboo farmers for management⁸–¹⁰.

Agroforestry management determines the efficiency of forest land use, spatial utilization rate, diversity of forest products, farm benefit, and ecological functions⁹. Interplanting of edible fungus in moso bamboo forest is one of the systems of agroforestry, and bamboo-fungus agroforestry management is an ecological model of sustainable production of moso bamboo forest⁹. Stropharia rugosoannulata is one of such mushrooms that is recommended by United Nations Food and Agriculture Organization (FAO) for cultivation in developing countries¹⁰,¹¹. It has high nutritional value for human and certain pharmacological functions¹². Additionally,

¹Zhejiang Academy of Forestry, Zhejiang Provincial Key Laboratory of Bamboo Research, Northwest Zhejiang Bamboo Forest Ecological Station, Hangzhou 310023, Zhejiang, China. ²International Center for Bamboo and Rattan, Key Laboratory of Bamboo and Rattan, Beijing 100102, China. ³Natural Resources and Planning Bureau of Deqing County, Deqing 313200, Zhejiang, China. *email: liqin3860@163.com; caicj@icbr.ac.cn
it lives on decomposing grasses and the cultivation technique is simple. Therefore, this mushroom has a long history of cultivation in moso bamboo forest in China.

Soil fauna plays many important roles in soil ecosystem, such as litter decomposition, nutrient cycling, maintenance of soil structure and stability, and improvement of soil physicochemical properties\(^{11-17}\). As a result, soil fauna is an excellent indicator of soil quality\(^{18}\). Previous studies showed that soil fauna was sensitive to environmental changes\(^{18,19}\), and it was applied to indicate certain features of soil fertility. When soil environmental changes such as moisture exceeded limitation of the body adaption and regulation, the survival and reproduction of soil fauna could be affected\(^{20}\). Moreover, long-term fertilization in cropland affected soil properties by changing the species and quantity of plant residues and root exudates, which subsequently changed the diversity and composition of soil fauna communities by changing the ecosystem of the soil fauna\(^{21}\). Soil fauna first fracture the residues, thereby increasing the surface area available to microbes and through residues decomposition by microbes the availability of nutrients increases\(^{22}\). The quantities of groups and individuals of soil fauna communities in the fertilization regimes with crop residues returned were much greater than in the other sampling times, and a significant correlation between the main soil properties and the indices of soil fauna indicators was found\(^{23}\).

Previous studies showed that intercropping in *Ginkgo biloba* forest increased the biodiversity of soil fauna\(^{24}\), and returning of organic matter in rice paddy increased the populations, groups and diversity of soil fauna\(^{25}\). These results indicated that the abundance and diversity of soil fauna community were significantly influenced by different tillage managements. During the cultivation of *Stropharia rugosoannulata*, organic matters (rice chaff and straw) were introduced into moso bamboo forest, which affected the soil microenvironment and soil properties\(^{26}\). Research on the mushroom yield, suitable bamboo forest density, soil physicochemical properties and microbial characteristics in the bamboo-fungus agroforestry system has received wide attention nowadays\(^{26}\). The extra economic return from the fungus was increased, and the diameter at breast height (DBH, 1.3 m) of new bamboo was also improved\(^{26}\). However, it is still unknown whether the system is beneficial to soil fauna and thereby contributes to improve soil quality.

Therefore, the purposes of this study were to investigate the diversity and abundance of soil meso- and micro-fauna following different years of mushroom growing in a bamboo-fungus agroforestry system, and to determine the relationship between major soil fauna groups and soil properties.

**Results**

**Soil fauna community composition.** In this study, 2968 individuals belonging to 8 classes and 13 groups were identified in the four sampling times. The mean density of soil fauna was 14,005.67 individuals m\(^{-2}\), ranging from 11,663.15 individuals m\(^{-2}\) in 3-year to 16,815.27 individuals m\(^{-2}\) in 1-year (Fig. 1). The communities were dominated by Acariformes, Parasitiformes and Collembola, which accounted for 48.86%, 19.50% and 11.32% of the total individual density, respectively (Table 1). The common groups accounted for 19.92% of total individuals, and the rare group (Julida) only represented 0.40% of the communities (Table 1).

The group number and density of soil fauna varied widely among different sampling times. With the increase of planting years, the group number and density of soil fauna increased first and then decreased. The highest group number and density of soil fauna were found in 1-year (Fig. 1), which was significantly higher than other sampling times (\(P<0.05\)). No significant difference was found between 0-year and 3-year (\(P>0.05\)). The density of dominant groups showed the same changes with the total density, while there was no significant difference between 1-year and 2-year (\(P>0.05\)).

**Diversity characteristics.** The diversity characteristics of soil fauna in different sampling times are listed in Table 2. The Shannon-Weiner diversity index (H), Margalef richness index (D) and Density-Group diversity
index (DG) increased first and then decreased with the increase of planting years, and the highest values were found in 1-year, with averages of 1.72, 2.43 and 8.05, respectively. The Pielou evenness index (J) decreased with the increase of planting years, and no significant difference was found among the four sampling times ($P > 0.05$). The Simpson dominance index (C) showed an opposite trend to H, and it was significantly lower in 1-year than that in other sampling times ($P < 0.05$).

0-year, 1-year, 2-year and 3-year represent before planting, planting for one year, two years and three years, respectively. H, Shannon-Weiner diversity index; J, Pielou evenness index; C, Simpson dominance index; D, Margalef richness index; DG, Density-Group diversity index. Different lowercase letters in the same column indicate significant differences among different sampling times ($P < 0.05$).

**Soil properties.** Different planting years showed significant impact on soil physicochemical properties (Table 3). With the increase of planting years, soil moisture content (SMC) increased first and then decreased, peaking at 1-year, while no significant difference was found among the four sampling times ($P > 0.05$). The pH

### Table 1. Composition of soil meso- and micro-fauna in different sampling times. *Rare groups, **Common groups, ***Dominant groups. 0-year, 1-year, 2-year and 3-year represent before planting, planting for 1 year, 2 years and 3 years, respectively.

| Groups             | 0-year | 1-year | 2-year | 3-year | Mean       |
|--------------------|--------|--------|--------|--------|------------|
|                    | Density (Ind m$^{-2}$) | Relative abundance (%) | Density (Ind m$^{-2}$) | Relative abundance (%) | Density (Ind m$^{-2}$) | Relative abundance (%) | Density (Ind m$^{-2}$) | Relative abundance (%) |
| Acariiformes       | 6058.03 | 48.20*** | 7784.85 | 46.30*** | 7416.84 | 49.53*** | 6114.65 | 52.43*** | 6843.60 | 48.86*** |
| Parasitiformes     | 2689.31 | 21.39*** | 3283.79 | 19.53*** | 2887.47 | 19.28*** | 2866.53 | 17.72*** | 2731.78 | 19.50*** |
| Collembola         | 1472.05 | 11.71*** | 1896.67 | 11.28*** | 1698.51 | 11.34*** | 1273.89 | 10.92*** | 1585.28 | 11.32*** |
| Diptera            | 481.25  | 3.83**  | 962.49  | 5.73**  | 764.33  | 5.19**  | 566.17  | 4.85**  | 693.56  | 4.95**  |
| Symphyla           | 481.25  | 3.83**  | 537.86  | 3.20**  | 368.01  | 2.46**  | 452.94  | 3.88**  | 460.01  | 3.29**  |
| Diplura larvae     | 169.85  | 1.35**  | 424.63  | 2.53**  | 396.32  | 2.65**  | 283.09  | 2.43**  | 318.47  | 2.27**  |
| Coleoptera larvae  | 283.09  | 2.25**  | 339.70  | 2.02**  | 311.39  | 2.08**  | 283.09  | 2.43**  | 304.32  | 2.17**  |
| Coleoptera adult   | 254.78  | 2.03**  | 283.09  | 1.68**  | 368.01  | 2.46**  | 198.16  | 1.70**  | 276.01  | 1.97**  |
| Pseudoscorpiones   | 254.78  | 2.03**  | 283.09  | 1.68**  | 254.78  | 1.70**  | 84.93   | 0.73*   | 219.39  | 1.57**  |
| Scolopendromorpha  | 113.23  | 0.90*   | 311.39  | 1.85**  | 198.16  | 1.32**  | 113.23  | 0.97*   | 184.01  | 1.31**  |
| Protura            | 0       | 0*      | 481.25  | 2.86**  | 0       | 0*      | 84.93   | 0.73*   | 141.54  | 1.01**  |
| Pauropoda          | 311.39  | 2.48**  | 113.23  | 0.67*   | 226.47  | 1.51**  | 113.23  | 0.97*   | 191.08  | 1.37**  |
| Julida             | 0       | 0*      | 113.23  | 0.67*   | 84.93   | 0.57*   | 28.31   | 0.24*   | 56.62   | 0.40*   |

### Table 2. Diversity characteristics of soil meso- and micro-fauna in different sampling times.

| Sampling time | H      | J    | C     | D     | DG    |
|---------------|--------|------|-------|-------|-------|
| 0-year        | 1.58 ± 0.08b | 0.70 ± 0.01a | 0.30 ± 0.01b | 2.02 ± 0.33c | 5.54 ± 1.07b |
| 1-year        | 1.72 ± 0.08a | 0.69 ± 0.02a | 0.27 ± 0.02c | 2.43 ± 0.15a | 8.05 ± 1.25a |
| 2-year        | 1.61 ± 0.07b | 0.68 ± 0.01a | 0.30 ± 0.01b | 2.19 ± 0.23b | 6.92 ± 1.59a |
| 3-year        | 1.53 ± 0.09b | 0.68 ± 0.04a | 0.33 ± 0.04a | 2.05 ± 0.14c | 4.67 ± 0.32b |

### Table 3. Main soil physicochemical properties in different sampling times.

| Soil properties | 0-year | 1-year | 2-year | 3-year |
|-----------------|--------|--------|--------|--------|
| SMC (%)         | 33.57 ± 5.07a | 38.05 ± 5.73a | 36.14 ± 4.34a | 33.85 ± 3.32a |
| pH              | 4.77 ± 0.14c | 4.89 ± 0.14b | 5.01 ± 0.12a | 5.05 ± 0.09a |
| SOM (g kg$^{-1}$) | 44.88 ± 4.22c | 66.57 ± 8.24a | 62.45 ± 4.17a | 53.29 ± 6.83b |
| TN (g kg$^{-1}$) | 2.23 ± 0.28c | 3.14 ± 0.53a | 2.83 ± 0.74b | 2.41 ± 0.27c |
| C/N             | 11.74 ± 0.88a | 12.73 ± 3.47a | 13.69 ± 4.25a | 12.83 ± 6.65a |
| TP (g kg$^{-1}$) | 0.26 ± 0.04c | 0.35 ± 0.07a | 0.29 ± 0.02b | 0.27 ± 0.05c |
| TK (g kg$^{-1}$) | 23.97 ± 1.88b | 26.97 ± 4.09a | 25.58 ± 2.43a | 23.05 ± 2.14b |
value increased with the increase of planting years, and 2-year and 3-year were significantly higher than 0-year and 1-year (P < 0.05). Contents of SOM, TN, TP and TK increased first and then decreased with the increase of planting years. Contents of TN and TP were significant higher in 1-year than those in other sampling times (P < 0.05). Contents of SOM and TK in 1-year and 2-year showed no significant difference (P > 0.05), while they were significantly higher than those in 0-year and 3-year (P < 0.05). There was no significant difference in C/N among all sampling times (P > 0.05).

0-year, 1-year, 2-year and 3-year represent before planting, planting for one year, two years and three years, respectively. SMC, soil moisture content; SOM, soil organic matter; TN, total nitrogen; TP, total phosphorus; TK, total potassium; C/N, ratio of carbon to nitrogen. Different lowercase letters in the same row indicate significant differences among different sampling times (P < 0.05).

Effects of soil properties on soil fauna community. Redundancy analysis (RDA) showed that the soil fauna explained 68.30% of the total variation in the measured soil properties (Fig. 2). The first canonical axis was mainly determined by SOM, TP, TN and SMC, and explained 65.24% of total variation. The second canonical axis included pH and C/N, and explained 1.81% of total variation. SOM explained the largest variation of soil fauna community variation (43.2%), indicating that SOM was the main environmental factor driving the variation of soil fauna community (Table 4). The explanatory degrees of TP and TN were more than 30%, which could be considered to have a certain impact on the variation of soil fauna community (Table 4). The number of individuals of Acariformes, Parasiformes, Collembola, Scolopendromorpha, Protura; Pau., Pauropoda; Jul., Julida; TG, total groups of soil fauna community; TI, total individuals of soil fauna community; H, Shannon–Weiner diversity index; J, Pielou evenness index; C, Simpson dominance index; D, Margalef richness index; DG, Density-Group diversity index.

![Figure 2. Results of redundancy analysis of soil fauna groups and diversity characteristics in association with soil properties. Hollow arrow points represent soil properties labeled as: soil moisture content (SMC), pH, soil organic matter (SOM), total nitrogen (TN), total phosphorus (TP), total potassium (TK) and ratio of carbon to nitrogen (C/N). Solid arrow points represent groups and diversity characteristics of soil fauna labeled as: Aca., Acariformes; Para., Parasiformes; Col., Collembola; Dip., Diptera; Sym., Symphyla; Dip.L., Diplura larvae; Cole.L., Coleoptera larvae; Cole.A., Coleoptera adult; Pse., Pseudoscorpiones; Sco., Scolopendromorpha; Pro., Protura; Pau., Pauropoda; Jul., Julida; TG, total groups of soil fauna community; TI, total individuals of soil fauna community; H, Shannon–Weiner diversity index; J, Pielou evenness index; C, Simpson dominance index; D, Margalef richness index; DG, Density-Group diversity index.](image-url)
Discussion

Effects of agroforestry management on soil properties. Previous study showed that bamboo-fungus agroforestry management could change the soil micro-environment\(^6\). Interplanting edible fungi in moso bamboo forest improved soil quality and soil fertility due to the decomposition of the residue\(^27\). In our study, contents of SOM and nutrients (TN, TP and TK) reached the maximum in 1 year and subsequently decreased. The increase of SOM and nutrients contents may be explained by different mechanisms as reported earlier. Firstly, the decomposition of mulches (rice chaff and straw) may improve the contents of SOM and nutrients\(^27\). Secondly, the growth of hypha promoted the formation of soil aggregate structure and increased the porosity of soil\(^28\). Additionally, the increase of SOM and nutrients contents increased the microbial biomass and soil enzyme activities, and then promoted the decomposition of residues\(^27\). Finally, microbial residues produced by the iterative cycle of microbial growth, death and turnover were important part of SOM\(^29\). With the extension of planting years and the decomposition of mulches, the contents of SOM and nutrients gradually decreased and restored to that before planting.

In our study, we also found that the pH value increased with the increase of planting years, indicating that planting *Stropharia rugosoannulata* in moso bamboo forest could effectively reduce soil acidification. Our results disagree with the result of Zhao et al. in moso bamboo forest, who found a decline trend with the increase of mulching years\(^2\). Researches showed that SOM accumulation could mitigate soil acidification, and the acidity might be neutralized by net mineralization of SOM\(^30,31\). The introduction of mulches was beneficial to the increase of species and quantity of soil microorganisms, and the increase of biological activity promoted the mineralization of organic nitrogen and the consumption of protons, which increased the pH value\(^9\). In addition, the decomposition of organic matter increased the organic anions, which was conducive to neutralize acidity\(^30,32\).

Link between soil fauna and soil properties. Previous studies revealed that the numbers of groups and individuals of soil fauna were mainly affected by soil environmental factors\(^33\). Bamboo-fungus agroforestry management significantly increased the numbers of groups and individuals of soil fauna. In this study, the quantity of soil fauna groups and individuals in planting *Stropharia rugosoannulata* in pure moso bamboo forest were still high, indicating that planting *Stropharia rugosoannulata* in moso bamboo forest could effectively reduce soil acidification. Our results disagree with the result of Zhao et al. in moso bamboo forest, who found a decline trend with the increase of mulching years\(^2\). Researches showed that SOM accumulation could mitigate soil acidification, and the acidity might be neutralized by net mineralization of SOM\(^30,31\). The introduction of mulches was beneficial to the increase of species and quantity of soil microorganisms, and the increase of biological activity promoted the mineralization of organic nitrogen and the consumption of protons, which increased the pH value\(^9\). In addition, the decomposition of organic matter increased the organic anions, which was conducive to neutralize acidity\(^30,32\).

Table 5. Person correlation coefficients between soil fauna and soil properties. *\(P<0.05\); **\(P<0.01\).

| Variables          | SMC | pH  | SOM  | TN   | TP   | TK   | C/N  |
|--------------------|-----|-----|------|------|------|------|------|
| Acariformes        | 0.503* | 0.160 | 0.646** | 0.585** | 0.522** | 0.188 | 0.020 |
| Parasitiformes     | 0.391 | −0.224 | 0.563** | 0.351 | 0.594** | 0.411* | 0.159 |
| Colembola          | 0.285 | −0.117 | 0.517** | 0.319 | 0.602** | 0.337 | 0.134 |
| Diptera            | 0.343 | 0.067 | 0.565** | 0.219 | 0.400 | 0.342 | 0.355 |
| Symphyyla          | 0.113 | −0.315 | −0.100 | 0.032 | −0.145 | 0.007 | −0.078 |
| Diploura larvae    | 0.326 | 0.217 | 0.498** | 0.601** | 0.301 | 0.409* | −0.101 |
| Coleoptera larvae  | −0.320 | 0.165 | −0.172 | 0.203 | −0.175 | 0.401 | −0.344 |
| Coleoptera adult   | −0.036 | 0.097 | 0.135 | 0.403 | 0.096 | −0.104 | −0.271 |
| Psseudoscorpiones  | 0.151 | 0.030 | 0.062 | 0.161 | 0.197 | 0.292 | −0.122 |
| Scolopendromorpha  | 0.365 | 0.199 | 0.528** | 0.268 | 0.471* | 0.187 | 0.156 |
| Protura            | 0.429* | −0.164 | 0.554** | 0.563** | 0.652** | 0.119 | −0.117 |
| Pauropoda          | 0.043 | −0.079 | −0.344 | −0.267 | 0.037 | 0.025 | −0.100 |
| Julida             | −0.071 | 0.188 | 0.268 | 0.623** | 0.029 | 0.327 | −0.311 |
| TG                 | 0.188 | 0.288 | 0.554** | 0.532** | 0.391 | 0.393 | −0.041 |
| TI                 | 0.489* | 0.014 | 0.680** | 0.602** | 0.639** | 0.395 | 0.025 |
| H                  | 0.133 | 0.040 | 0.313 | 0.482** | 0.363 | 0.497* | −0.210 |
| J                  | −0.011 | −0.443* | −0.345 | −0.029 | 0.056 | 0.299 | −0.280 |
| C                  | −0.102 | 0.214 | −0.221 | −0.293 | −0.391 | −0.540* | 0.097 |
| D                  | 0.067 | 0.341 | 0.453* | 0.452* | 0.270 | 0.335 | −0.062 |
| DG                 | 0.279 | 0.124 | 0.464* | 0.586** | 0.401 | 0.453* | −0.161 |
respectively3,4. The moso bamboo forest was characterized by a stand density of 1576 individuals ha−1, a mean bamboo of 1 (I) “du” corresponds to 1–2 years, and consequently, 2 (II) and 3 (III) “du” indicate 3–4 and 5–6 years, all plants within a plot were measured. Additionally, the age of all plants were estimated expressed by “du”. Bamboo (20 m × 20 m) were established as three replications. The diameter at breast height (DBH, 1.3 m) and height of 13.8 m, an average DBH of 10.9 cm, and a canopy cover of 70%. The age structure was 4:3:3 (I:II:III).

Experimental design. This study was conducted in a pure moso bamboo forest. Three experimental plots (20 m × 20 m) were established as three replications. The diameter at breast height (DBH, 1.3 m) and height of all plants within a plot were measured. Additionally, the age of all plants were estimated expressed by “du”. Bamboo of 1 (I) “du” corresponds to 1–2 years, and consequently, 2 (II) and 3 (III) “du” indicate 3–4 and 5–6 years, respectively44. The moso bamboo forest was characterized by a stand density of 1576 individuals ha−1, a mean height of 13.8 m, an average DBH of 10.9 cm, and a canopy cover of 70%. The age structure was 4:3:3 (I:II:III).

In October 2017, weeds and shrubs in moso bamboo forest were removed, and furrows (0.3 m in width and 0.2 m in depth) along the contour were established. The distance between two adjacent furrows was about 1 m. Stropharia rugosaannulata was planted in moso bamboo forests in November 2017 after the application of 7.5 kg m−2 of rice chaff in the furrows. The furrows were than covered by straw at 7.5 kg m−2 and 5 cm soil. After the edible fungi were harvested, no continuous cultivation was done. In order to maintain a stable bamboo density, bamboo timber cutting was carried out every year.

Soil sampling and measurement. Soils were sampled annually from 2017 to 2020. Four sampling times were set up, namely (1) before planting as control (October 2017, 0-year); (2) planting for one year (October 2018, 1-year); (3) planting for two years (October 2019, 2-year); and (4) planting for three years (October 2020, 3-year).

Before soil sampling, litters and mulches (rice chaff and straw) were removed from the plot to prevent the contamination of the organic matters to surface soil. Soil samples (0–10 cm) were collected randomly using a soil sampler (5 cm in diameter) at the furrows. Soils from three sample points (planting furrows) in the same plot were mixed as one soil sample. For each plot, three replicated soil samples were sealed separately in three bags, placed in a cooler and transported to laboratory immediately. Soil meso- and micro-fauca community was determined by modified Tullgren techniques10,33. The soil meso- and micro-fauna were divided into dominant groups (the number of individuals represented over 10% of the total sample), common groups (the number of individuals represented between 1 and 10% of the total sample) and rare groups (the number of individuals represented less than 1% of the total sample).

Similarly, another three soil samples (0–10 cm) were collected near the previous sample points in each plot. Samples were divided into two parts: one part was placed in an aluminum box for the determination of soil moisture content (SMC); the other part was air-dried at room temperature, ground and sieved through 2-mm and 0.15-mm meshes before chemical analysis. The identifiable plant residues, stones and root fragments were removed during sieving.

In the laboratory, the aluminum boxes were oven-dried at 105 °C for the determination of SMC. Soil pH was measured in a 1:2.5 (m/v) soil/water suspension. Soil organic matter (SOM) content was determined by the H2SO4-K2Cr2O7 wet oxidation method38. Total nitrogen (TN) content was measured by the Kjeldahl’s method39. Total phosphorus (TP) content was determined using H2SO4/H2O2 digestion followed by colorimetric analysis40.
Total potassium (TK) content was measured using atomic absorption spectrophotometry after H₂SO₄/H₂O₂ digestion.23

**Calculation methods.** The following formulas were used to analyze the diversity of soil meso- and micro-fauna community23,33,40:

\[ H = - \sum_{i=1}^{S} P_i \ln P_i \]

\[ J = H / \ln S \]

\[ C = \sum (P_i)^2 \]

\[ D = (S - 1) / \ln N \]

\[ DG = \left( \frac{S}{G} \right) \sum_{i=1}^{g} \left( \frac{D_i C_i}{D_{i_{\text{max}}} C} \right) \]

where \( H \) is the Shannon–Wiener diversity index; \( J \) is the Pielou evenness index; \( C \) is the Simpson diversity index; \( D \) is the Margalef richness index; \( DG \) is the Density-Group diversity index; \( P_i \) is the relative percentage of the soil meso- and micro-fauna of type “i” in each plot; \( S \) is the number of groups; \( N \) is the total number of individuals in the soil meso- and micro-fauna; \( g \) is the number of groups in each repetition; \( G \) is the total number of groups in each sampling time; \( C_i / C \) is the ratio of the “i” group in each sampling time; and \( D_i \) is the density of the “i” group; and \( D_{i_{\text{max}}} \) is the maximum density.

**Statistical analysis.** One-way analysis of variance (ANOVA) and Duncan's multiple comparisons were used to analyze the significant differences between sampling times. The differences were considered significant at \( P < 0.05 \). Figures were prepared using the Origin 8.6 software program. Redundancy analysis (RDA) was used to analyze the relative contributions of soil properties to the communities composition of the soil meso- and micro-fauna.

**Statement.** The collection of soil samples was permitted by local famers orally. The study complied with local (Zhejiang Province) and national (China) regulations. All the methods in this manuscript were carried out in accordance with relevant guidelines and regulations.

**Data availability** The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Received: 7 March 2022; Accepted: 19 September 2022

**References**

1. Jiang, Z. H. Bamboo and Rattan in the World (China Forest Publishing House, 2007).
2. Zhao, J., Wang, B., Li, Q., Yang, H. & Xu, K. Analysis of soil degradation causes in Phyllostachys edulis forests with different mulching years. *For. Ecol. Manag.* 9(3), 149 (2018).
3. Su, W., Fan, S., Zhao, J. & Cai, C. Effects of various fertilization placements on the fate of urea-¹⁵N in moso bamboo forests. *For. Ecol. Manag.* 453, 117632 (2019).
4. Zhao, J. et al. Ammonia volatilization and nitrogen runoff losses from moso bamboo forests under different fertilization practices. *Can. J. For. Res.* 49(3), 213–220 (2019).
5. Yin, J. et al. Abandonment lead to structural degradation and changes in carbon allocation patterns in Moso bamboo forests. *For. Ecol. Manag.* 449, 117449 (2019).
6. Xu, Q. F. et al. Rapid bamboo invasion (expansion) and its effects on biodiversity and soil processes. *Glob. Ecol. Conserv.* 21, e00787 (2020).
7. Prayogo, C., Sholehuddin, N., Putra, E. Z. H. S. & Rachmawati, R. Soil macrofauna diversity and structure under different management of pine-coffee agroforestry system. *J. Deprade. Min. Land Manake.* 6(3), 1727–1736 (2019).
8. Coleman, B. R., Martin, A. R., Thevathasan, N. V., Gordon, A. M. & Isaac, M. E. Leaf trait variation and decomposition in short-rotation woody biomass crops under agroforestry management. *Agric. Ecosyst. Environ.* 298, 106971 (2020).
9. Cai, C. J., Fan, S. H., Liu, G. L., Wang, S. M. & Feng, Y. Research and development advance of compound management of bamboo forests. *World Bamboo Rattan* 16(5), 47–52 (2018) (in Chinese).
10. Song, Z. et al. Characteristics of Se-enriched mycelia by *Stropharia rugoso-annulata* and its antioxidant activities in vivo. *Biol. Trace Elem. Res.* 113(1), 81–89 (2009).
11. Wang, Q. et al. Effects of drying on the structural characteristics and antioxidant activities of polysaccharides from *Stropharia rugoso-annulata*. *J. Food Sci. Technol.* 58, 3622–3631 (2021).
12. Yan, P., Jiang, J. & Cui, W. Characterization of protoplasts prepared from the edible fungus, *Stropharia rugoso-annulata*. *World J. Microbiol. Biotechnol.* 20(2), 173–177 (2004).
13. Frouz, J. Effects of soil macro- and mesofauna on litter decomposition and soil organic matter stabilization. *Geoderma* 332, 161–172 (2018).
14. Lin, D. et al. Soil fauna promote litter decomposition but do not alter the relationship between leaf economics spectrum and litter decomposability. Soil Biol. Biochem. 136, 107519 (2019).
15. Meehan, M. L. et al. Response of soil fauna to simulated global change factors depends on ambient climate conditions. Pedobiologia 83, 150672 (2020).
16. Tan, B. et al. Soil fauna show different degradation patterns of lignin and cellulose along an elevational gradient. Appl. Soil Ecol. 155, 103673 (2020).
17. John, K., Zaitsev, A. S. & Wolters, V. Soil fauna groups respond differentially to changes in crop rotation cycles in rice production systems. Pedobiologia 84, 150703 (2021).
18. Qin, Z. et al. Changes in the soil meso- and micro-fauna community under the impacts of exotic Ambrosia artemisiifolia. Ecol. Res. 34(2), 265–276 (2019).
19. Chauvat, M., Titsch, D., Zaytesev, A. S. & Wolters, V. Changes in soil faunal assemblages during conversion from pure to mixed forest stands. For. Ecol. Manag. 262(3), 317–324 (2011).
20. Yan, S. et al. A soil fauna index for assessing soil quality. Soil Biol. Biochem. 47(2), 158–165 (2012).
21. Reeve, J. R. et al. Effects of soil type and farm management on soil ecological functional genes and microbial activities. ISME J. 4, 1099–1107 (2010).
22. Lavelle, P., Bignell, D. & Lepage, M. Soil function in a changing world: The role of invertebrate engineers. Eur. J. Soil Biol. 33, 159–193 (1997).
23. Zha, X. & Zhu, B. Diversity and abundance of soil fauna as influenced by long-term fertilization in cropland of purple soil, China. Soil Till. Res. 146, 39–46 (2015).
24. Zhang, L., Wang, G. & Cao, F. The effect of ginkgo agroforestry patterns on soil fauna diversity. J. Nanjing For. Univ. 39(2), 27–32 (2015) (in Chinese).
25. Liu, P. et al. Impact of straw returning on cropland soil mesofauna community in the western part of black soil area. Chin. J. Ecol. 37(1), 139–146 (2018) (in Chinese).
26. Liu, M. Study on the model of interplanting edible fungi under bamboo (Phyllostachys edulis) forest and comprehensive benefit comparative. Master's Thesis, Chinese Academy of Forestry (2021) (in Chinese).
27. Wang, B., Shen, Q., Zhu, W., Shen, X. & Li, Q. Effects of interplanting Dictyophora echinovolvata on physicochemical properties, phospholipid fatty acids characters and enzyme activities in soil of Phyllostachy heterocycla cv. pubescens. For. Environ. Sci. 32(4), 28–32 (2016) (in Chinese).
28. Ying, G. H. et al. Effect of cultivation of Dictyophora echinovolvata on shoot yield and soil under Phyllostachy heterocycla cv. pubescens stand. J. Zhejiang For. Sci. Technol. 34(6), 63–67 (2014) (in Chinese).
29. Sokol, N. W. et al. Life and death in the soil microbiome: How ecological processes influence biogeochemistry. Nat. Rev. Microbiol. 20, 415–430 (2022).
30. Fuji, K., Hayakawa, C., Inagaki, Y. & Kosaki, T. Effects of land use change on turnover and storage of soil organic matter in a tropical forest. Plant Soil 446(1), 425–439 (2020).
31. Fuji, K. & Toma, T. Comparison of soil acidification rates under different land uses in Indonesia. Plant Soil 465(1–2), 1–17 (2021).
32. Poss, R., Smith, C. J., Dunin, F. X. & Angus, J. F. Rate of soil acidification under wheat in a semi-arid environment. Plant Soil 177, 85–100 (1995).
33. Yin, X. et al. Distribution and diversity patterns of soil fauna in different salinization habitats of Songnen Grasslands, China. Appl. Soil Ecol. 123, 375–383 (2018).
34. Luo, M. L. et al. Effects of different rice straw returning quantities on soil fauna community structure. J. Zhejiang A&F Univ. 37(1), 85–92 (2020) (in Chinese).
35. Peng, C. Y. et al. Community structure characteristics of medium- and small-sized soil faunas in typical artificial plantation in the upper reaches of Yangtze River. J. Zhejiang Univ. 45(5), 585–595 (2019) (in Chinese).
36. Carmen, M. U., Edmond, R. Z. & Michelle, M. W. Nematode indicators as integrative measures of soil condition in organic cropping systems. Soil Biol. Biochem. 64, 103–113 (2013).
37. Kamau, S., Karanja, N. K., Ayuke, F. O. & Lehmann, J. Short-term influence of biochar and fertilizer–biochar blends on soil nutrients, fauna and maize growth. Biol. Fertil. Soils 55(7), 661–673 (2019).
38. Fu, X., Shao, M., Wei, X. & Horton, R. Soil organic carbon and total nitrogen as affected by vegetation types in Northern Loess Plateau of China. Geoderma 155(1–2), 31–35 (2010).
39. Guan, F., Tang, X., Fan, S., Zhao, J. & Peng, C. Changes in soil carbon and nitrogen stocks followed the conversion from secondary forest to Chinese fir and Moso bamboo plantations. Catena 133, 445–460 (2015).
40. Liu, Y. et al. Higher soil fauna abundance accelerates litter carbon release across an alpine forest–tundra ecotone. Sci. Rep. 9, 10561 (2019).

Acknowledgements
This work was supported by the Special Project of Zhejiang Provincial Scientific Research Institutes (2021F1065-3) and the Key Technologies Research and Development Program of China (2018YFD060010502). We are sincerely grateful to Deying Li from North Dakota State University for helping to review the earlier draft of the manuscript and Weibin Fang for field investigation and soil sampling. We also thank the anonymous reviewers and editors for their valuable suggestions to improve the article.

Author contributions
J.Z., Q.L. and C.C. contributed to the study conception and design. Material preparation, soil samples collection and analysis were performed by J.Z., M.L., J.X. and Z.Y. The first draft of the manuscript was written by J.Z. and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Competing interests
The authors declare no competing interests.

Additional information
Correspondence and requests for materials should be addressed to Q.L. or C.C.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher’s note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.
