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Effects of Soil Fauna on Aggregate-Associated Soil Organic Carbon Allocation in Subtropical Forests with Different Management

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Abstract: Soil fauna contribute to soil aggregate formation and transformation through feeding, fragmentation, redistribution, and bioturbation, yet their effects on the distribution of aggregate-associated soil organic carbon (SOC) across forest types remain poorly understood. Within a long-term forest conversion experiment in subtropical China, we conducted a six-month *in situ* soil-column experiment across three forest types, including a natural broadleaved forest, a castanopsis (*Castanopsis carlesii*) plantation, and a fir (*Cunninghamia lanceolata*) plantation, each represented by three replicate plots. Soils were air-dried and passed through a 2 mm sieve to reduce resident soil fauna. Fauna access was manipulated using soil columns with 5 mm lateral openings and open bottoms to allow entry, or columns enclosed with 0.025 mm nylon mesh to restrict meso- and macrofauna entry. Aggregate mass proportions, SOC concentrations within different aggregate-size fractions, and their relative contributions to aggregate-associated SOC were quantified to characterize aggregate-associated SOC allocation. Soil fauna access altered SOC concentrations and relative SOC contributions in specific aggregate-size fractions, with responses varying among forest types. Under fauna access, the fir plantation showed lower mass proportions of the 0.25–1 mm and <0.053 mm fractions (by 4 and 6 percentage points, respectively) and a lower relative SOC contribution from the <0.053 mm fraction (by 17 percentage points) than the natural forest in the 0–10 cm soil layer. Compared with fauna exclusion, fauna access increased SOC concentrations in the 1–2 mm and 0.25–1 mm fractions of the fir plantation by 117–148%. Soil fauna abundance, biomass, and omnivore abundance showed depth- and fraction-specific associations with SOC concentration and relative SOC contribution, particularly in the 10–20 cm soil layer. Soil moisture, soil P, pH, litter N, and litter mass also showed potential associations with aggregate-associated SOC properties. Overall, these findings indicate that fauna-associated changes in aggregate-associated SOC allocation varied among forest types, while the natural forest showed a higher relative SOC contribution from the finest fraction than the fir plantation under fauna access, highlighting the potential importance of natural forest conservation for SOC allocation in subtropical forests.

Keywords: soil fauna; aggregate; soil organic carbon; subtropical forests

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1. Introduction

Soil organic carbon (SOC) constitutes the largest terrestrial organic carbon pool and plays a pivotal role in regulating the global carbon cycle and maintaining ecosystem functions [1,2]. The distribution of SOC is influenced not only by the amount of carbon stored in soil but also by its physical association with different soil structural components [3–5]. Soil aggregates, which are fundamental structural units formed by mineral particles, organic matter, and biologically derived binding agents, are important carriers of SOC and contribute to its physical protection [6,7]. By physically occluding organic matter within internal pores, aggregates limit direct contact between microorganisms, soil fauna, and labile substrates, thereby potentially reducing SOC decomposition [8,9]. The capacity of aggregates to protect SOC varies among size fractions [4]. While macroaggregates are generally associated with fresh organic matter inputs and physical protection [9,10], microaggregates and silt- and clay-sized fractions are more closely associated with physical protection and mineral interactions [11]. These patterns are further complicated by vertical heterogeneity [12]. Surface soils, characterized by greater organic matter inputs and rhizosphere activity, typically exhibit greater sensitivity to environmental changes than deeper soil layers [13,14]. However, the extent to which soil fauna access is associated with differences in aggregate-associated SOC allocation across forest types remains poorly understood.

Forest types differ markedly in litter quantity, litter quality, and soil nutrient availability [15–18], which may influence soil aggregate characteristics and SOC distribution [5]. Consequently, conversion from natural forests to plantations may alter soil aggregate dynamics and SOC allocation [19]. These changes can also reshape soil fauna communities through shifts in resource availability and habitat conditions. Although lower nutrient availability in plantations may contribute to reduced soil fauna richness [16], soil fauna responses to forest conversion may vary among forest types. Studies in coniferous forests have shown that thicker litter layers may provide additional habitat and resources for litter-dwelling fauna, with higher densities of mesofauna decomposers reported than in broadleaved forests [20,21]. Such variation in soil fauna communities may, in turn, influence aggregate-associated SOC through litter fragmentation, redistribution, fecal pellet production, and bioturbation, thereby promoting organic residue incorporation and soil particle rearrangement [22,23]. These effects may vary among functional groups because omnivores (OM), predators (PR), herbivores (PH), and saprophages (SA) differ in trophic position and resource use [23,24]. Conversely, soil fauna may facilitate organic matter decomposition by fragmenting litter and increasing its accessibility to microbial decomposers [25]. Thus, the effects of soil fauna on aggregate-associated SOC may depend on forest type and environmental conditions.

In subtropical forests, conversion from natural forests to plantations is often associated with simplified stand structure, reduced understory development, altered litter inputs, lower soil fertility, and decreased biodiversity, which can alter food resources and habitats and consequently reshape soil fauna communities [16,17,26]. However, how these changes in soil fauna communities are associated with aggregate-associated SOC allocation remains unclear. Here, aggregate-associated SOC allocation refers to the distribution of SOC among different aggregate-size fractions, as reflected by SOC concentration within each fraction and its relative contribution to aggregate-associated SOC. Accordingly, we selected three representative subtropical forest types: a natural broadleaved forest, a castanopsis (*Castanopsis carlesii*) plantation, and a fir (*Cunninghamia lanceolata*) plantation. We conducted an *in situ* soil-column experiment to manipulate soil fauna access and assess variation in aggregate mass distribution and aggregate-associated SOC allocation between fauna access and fauna exclusion treatments. We further evaluated their relationships with soil fauna community attributes, soil properties, and litter characteristics. We hypothesized that: (1) aggregate-associated SOC allocation would differ among forest types, with the natural forest showing relatively higher SOC concentrations and relative SOC contributions in finer aggregate fractions than the fir plantation, owing to differences in litter quantity and quality and soil nutrient conditions; and (2) the effects associated with soil fauna access would vary among forest types and aggregate-size fractions, with more pronounced effects expected in surface soil and in larger and intermediate aggregate fractions where litter inputs and fauna activity are concentrated.

2. Materials and Methods

2.1. Study Sites

The study was carried out at the National Field Observation and Research Station (Fujian Sanming) for Forest Ecosystem, Fujian Province, southeastern China (26.19° N, 117.36° E). The region is characterized by low mountains and hilly terrain, with a mean elevation of approximately 300 m and slopes generally ranging from 25° to 45°. The soils are mainly developed from granite parent material. The site experiences a subtropical monsoon climate, with mean annual temperature and precipitation of 19.3 °C and 1610 mm, respectively. Most rainfall occurs from March to August. Prior to 1958, the area was covered by natural broadleaved forests dominated by

Castanopsis carlesii. Subsequently, these forests were progressively harvested and converted into plantations or secondary forests through natural regeneration [27]. At present, *C. carlesii* remains the dominant species in both natural and secondary forests, together with other common broadleaved species such as *Castanopsis fissa*, *Schima superba*, and *Neolitsea aurata*. In contrast, the understory vegetation in fir plantations is dominated by *Dicranopteris linearis*.

The experimental site was located in a natural forest stand that had experienced minimal human disturbance since 1976. In 2011, a long-term forest conversion experiment was established within a natural forest patch of approximately 1.1 ha. For the present study, we selected three forest types from this experiment: natural forest, castanopsis plantation, and fir plantation. Three replicate plots (20 m × 20 m) were selected for each forest type, resulting in a total of nine plots (Figure 1a). The natural forest plots were maintained as intact natural broadleaved forest. For the two plantation forest types, the original natural forest was clear-cut in 2011, and the harvest residues were evenly distributed on the forest floor, air-dried under sunlight, and subsequently burned in March 2012. Castanopsis seedlings were planted at a density of 2400 trees ha^{-1}, whereas fir seedlings were established at a density of 2860 trees ha^{-1}. Neither plantation was fertilized or subjected to intensive management during the study period. More detailed information on plot establishment and subsequent management practices is available in Yang et al. [27].

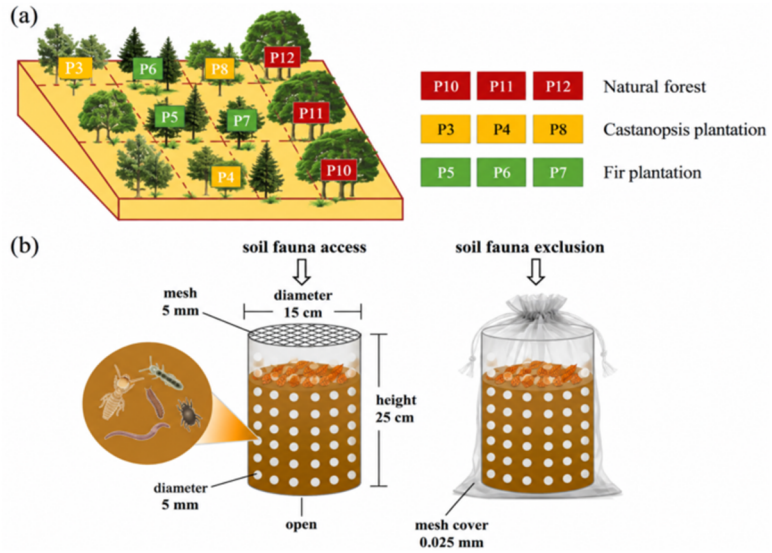

Figure 1. Experimental design and field layout. (**a**) Spatial arrangement of the three forest types and their replicate plots, including natural forest, Castanopsis plantation, and fir plantation. (**b**) Schematic illustration of the soil fauna access and soil fauna exclusion treatments.

2.2. Experimental Layout and Sampling

Following a preliminary survey of the study site (Table S1), the experiment was initiated in January 2025. To investigate differences in aggregate-associated soil organic carbon allocation among forest types, natural forest, castanopsis plantation, and fir plantation were selected as representative forest types. The plantations were approximately 13 years old, with nearly closed canopies and relatively stable community structures. Three replicate plots were established for each forest type. Within each forest type, soil samples were collected from the 0–10 cm and 10–20 cm layers. The collected soils were homogenized by forest type, air-dried for at least one week, and passed through a 2 mm sieve to remove most of the original soil fauna and standardize the initial soil conditions. The processed soils were then packed into soil columns and reburied in the corresponding plots for approximately six months under field conditions.

Because of the high mobility of soil fauna, a soil-column approach was used to manipulate soil fauna access under field conditions (Figure 1b). PVC tubes with an inner diameter of 15 cm and a height of 25 cm were used as soil columns, with a distance of 0.5 m between adjacent columns. Two treatments were established: a soil fauna-access treatment and a soil fauna-exclusion treatment. In the fauna-access treatment, 5 mm diameter openings were distributed along the lateral walls of the PVC tubes, the bottom of each column was left open to allow soil fauna access from the surrounding soil, and the top was covered with 5 mm mesh to allow soil fauna movement while preventing uncontrolled external litter input. In the fauna-exclusion treatment, the top, bottom, and lateral surfaces of the PVC tubes were enclosed with 0.025 mm nylon mesh to restrict the entry of soil meso- and

macrofauna. Based on the annual litterfall of each forest type, seasonally collected and air-dried litter was evenly added to the soil surface of both treatments every three months to standardize litter input. Thus, the two treatments received the same standardized litter input and differed primarily in soil fauna accessibility.

2.3. Soil Fauna and Aggregate

Soil sampling was conducted in late June 2025. In each plot, one soil column was collected from each of the two treatments. The soil samples were separated into the 0–10 and 10–20 cm layers, placed in labeled black breathable bags, stored at low temperature, and immediately transported to the laboratory for soil fauna extraction and subsequent physicochemical analyses. For each soil layer, the collected soil was divided into three subsamples, from which soil fauna were independently extracted using Tullgren funnels for 72 h [16,28]. All extracted soil fauna were preserved in vials containing 75% ethanol [28,29]. Individuals were subsequently sorted, counted, and morphologically identified to the lowest practical taxonomic level, generally to family level, under a stereomicroscope (Leica Microsystems, Wetzlar, Germany). Taxonomic identification was conducted primarily using Pictorial Keys to Soil Animals of China [30] and Insect Taxonomy [31], with additional taxonomic literature consulted when necessary. After identification, soil fauna were assigned to four functional groups according to their predominant feeding strategies: OM, PR, PH, and SA, following Zhang et al. [24].

Air-dried undisturbed soil samples passed through a 2 mm sieve were weighed, and the particle-size distribution of water-stable aggregates was determined using the wet-sieving method [32,33]. The sieve mesh sizes were arranged from top to bottom as 1 mm, 0.25 mm, and 0.053 mm. Four size fractions were obtained: 1–2 mm, 0.25–1 mm, 0.053–0.25 mm, and <0.053 mm.

2.4. Soil and Litter Properties

Physicochemical properties of soil and litter were determined. Soil samples were air-dried and passed through a 2 mm sieve prior to analysis. Soil pH was measured potentiometrically in a soil–water suspension at a ratio of 1:2.5 (w/v) after equilibration [16]. For elemental stoichiometric analysis, soil and litter samples were finely ground and passed through a 100-mesh sieve. SOC and N concentrations in soil, as well as C and N concentrations in litter, were determined using a CHNS-O elemental analyzer (vario EL cube, Elementar Analysensysteme GmbH, Langenselbold, Germany) following standard procedures [34]. Soil total phosphorus (TP) was determined using a continuous flow analyzer (Skalar San++, Skalar, the Netherlands) after $HClO_4$–H_2SO_4 digestion [35]. Litter C/N ratio was calculated from the measured C and N concentrations, and litter lignin and cellulose concentrations were determined using the Van Soest detergent method [36].

Litter collected from each sampling unit was air-dried and weighed, and litter quantity was expressed as litter mass per unit area (g m^{-2}). Specific litter area was measured using an intelligent leaf area measurement system. Soil fauna abundance was expressed as the number of individuals per unit soil area (ind m^{-2}), and soil fauna biomass (g m^{-2}) was estimated using allometric models [37]. In addition, soil temperature and moisture (TH-GTS3, Shandong Tianhe Environmental Technology Co., Ltd., Weifang, China) were recorded in each plot using automatic monitoring instruments at the field station. Litter properties, soil physicochemical properties (Table S2), and soil fauna community characteristics (Tables S2 and S3) are presented as mean ± standard error (SE) to describe the environmental and biological characteristics of the different forest types.

2.5. Statistical Analysis

Prior to statistical analysis, the normality and homogeneity of variance of the data were tested. Aggregate mass proportions and aggregate-associated SOC concentrations that did not meet the assumption of normality were logarithmically transformed before further analysis. One-way analysis of variance (ANOVA) was used to evaluate differences among forest types in aggregate mass proportion, SOC concentration, and relative SOC contribution for each aggregate-size fraction. When significant differences were detected, mean comparisons were performed using the least significant difference (LSD) post hoc test at $p < 0.05$. Independent-sample *t*-tests were used to compare fauna-access and fauna-exclusion treatments within each forest type. The relative change in SOC concentration between the two treatments was calculated according to Equation (3). Two-way ANOVA was conducted to examine the effects of forest type, soil fauna treatment, and their interaction on aggregate mass proportion, aggregate-associated SOC concentration, and relative SOC contribution (Table S4).

$$\text{SOC contribution}_i = \text{Mass proportion}_i \times \text{SOC concentration}_i \quad (1)$$

$$\text{SOC contribution percent}_i = \frac{\text{SOC contribution}_i}{\sum \text{SOC contribution}_i} \times 100 \quad (2)$$

$$\text{Change rate (\%)} = \frac{\text{Fauna-No fauna}}{\text{No fauna}} \times 100 \quad (3)$$

where (i) represents a specific aggregate-size fraction; (SOC contribution$_i$) represents the weighted SOC contribution of aggregate fraction (i); (Mass proportion$_i$) is the mass proportion of aggregate fraction (i); (SOC concentration$_i$) is the SOC concentration of aggregate fraction (i); and (SOC contribution percent$_i$) represents the relative contribution percentage of aggregate fraction (i) to the total aggregate-associated SOC within the same sample and soil layer.

Spearman's rank correlation analysis was used to examine the relationships between soil fauna attributes and soil aggregate-related variables, including aggregate mass proportion, aggregate-associated SOC concentration, and relative SOC contribution. The analyses were conducted separately for the 0–10 and 10–20 cm soil layers using samples from the fauna-access treatment only, because no soil fauna were recovered from the fauna-exclusion treatment. Total fauna abundance, biomass, and functional-group abundances were included as fauna variables. PR and PH abundances were excluded from the 10–20 cm analysis because of insufficient non-zero observations.

Redundancy analysis (RDA) was used to assess the multivariate relationships between environmental factors and aggregate-associated SOC properties separately for the two soil layers. Prior to RDA, variance inflation factors (VIFs) were calculated to assess multicollinearity among environmental variables [38]. Based on multicollinearity screening and ecological relevance, soil moisture, pH, soil phosphorus (P), litter mass, and litter N were included as explanatory variables. Soil fauna treatment was included as a conditional variable in partial RDA to account for differences between fauna-access and fauna-exclusion treatments. Permutation tests were used to evaluate the significance of the overall RDA models. To avoid perfect linear dependence among compositional variables, one aggregate mass-proportion fraction and one relative SOC contribution fraction were omitted from the RDA response matrix. All statistical analyses were performed using SPSS 27.0 (SPSS Inc., Chicago, IL, USA) and R version 4.4.2. Spearman correlation heatmaps and RDA ordinations were generated in R, primarily using the vegan and ggplot2 packages, whereas other figures were prepared using Origin (OriginLab Corporation, Northampton, MA, USA).

3. Results

3.1. Soil Aggregate Distribution across Forest Types and Soil Fauna Treatments

Soil aggregate mass distribution varied with forest type and soil fauna treatment, with differences depending on aggregate size (Figure 2). Across both soil depths, the 0.25–1 mm and <0.053 mm fractions dominated, accounting for 30–44% and 23–40% of the total aggregate mass, respectively. In the 0–10 cm layer, forest type effects were most pronounced in the 1–2 mm, 0.25–1 mm, and <0.053 mm fractions ($p < 0.05$). Under the fauna-access treatment, the fir plantation had a significantly higher mass proportion of the 1–2 mm fraction than the natural forest, whereas the mass proportions of the 0.25–1 mm and <0.053 mm fractions were significantly lower, by 4 and 6 percentage points, respectively ($p < 0.05$). These differences largely disappeared under fauna exclusion. Notably, the 0.25–1 mm fraction showed the most pronounced treatment-related difference in the castanopsis plantation, with the aggregate mass proportion being 5 percentage points lower under fauna access than under fauna exclusion. In contrast, aggregate mass distribution in the 10–20 cm layer showed fewer significant differences among forest types and between fauna treatments.

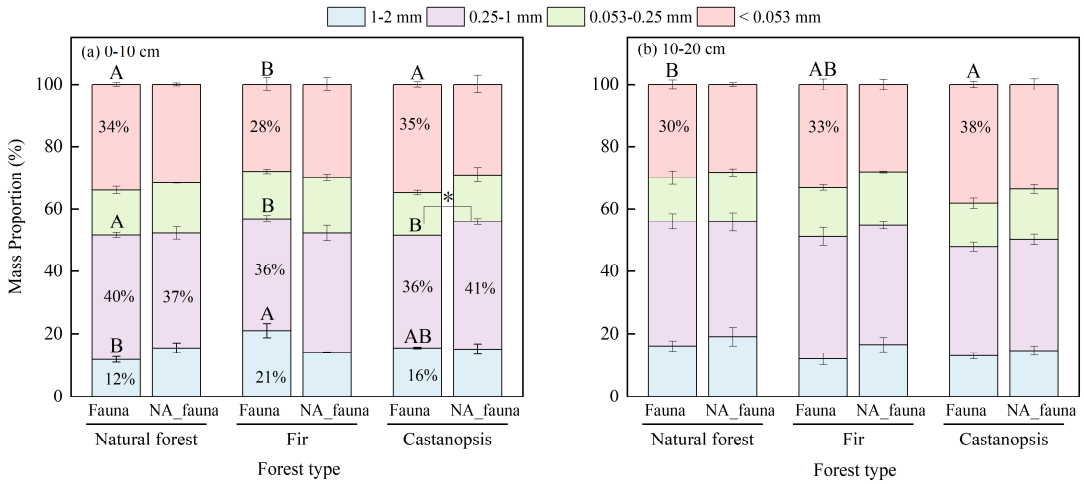

Figure 2. Effects of forest type and soil fauna treatment on soil aggregate-size distribution. Values are means ± standard error (n = 3). Different uppercase letters indicate significant differences among forest types under the fauna-access treatment; Asterisks indicate significant differences between the fauna-access and fauna-exclusion treatments within the same forest type ($p < 0.05$).

3.2. Distribution and Contribution of Aggregate-Associated SOC in Different Forest Types

Aggregate-associated SOC concentration varied markedly among aggregate-size fractions, forest types, and soil fauna treatments (Figure 3). Across both soil layers, the <0.053 mm fraction consistently exhibited the highest SOC concentration, peaking at 32.08 g kg^{-1}. In the 0–10 cm layer, forest type effects were most pronounced in the fine fractions (0.053–0.25 mm and <0.053 mm). Specifically, SOC concentration in the <0.053 mm fraction under the natural forest was 1.5–1.7 times as high as that under the castanopsis and fir plantations ($p < 0.05$). Fauna-access effects varied among forest types and aggregate-size fractions. In the fir plantation, fauna access was associated with 117–148% higher SOC concentrations in the 1–2 mm and 0.25–1 mm fractions than fauna exclusion. Conversely, in the castanopsis plantation, SOC concentration in the 1–2 mm fraction was 32% lower under fauna access than under fauna exclusion. The 0.053–0.25 mm fraction also showed marked increases under fauna access, particularly in the natural forest and fir plantation ($p < 0.05$). These treatment-related differences were less pronounced in the 10–20 cm soil layer.

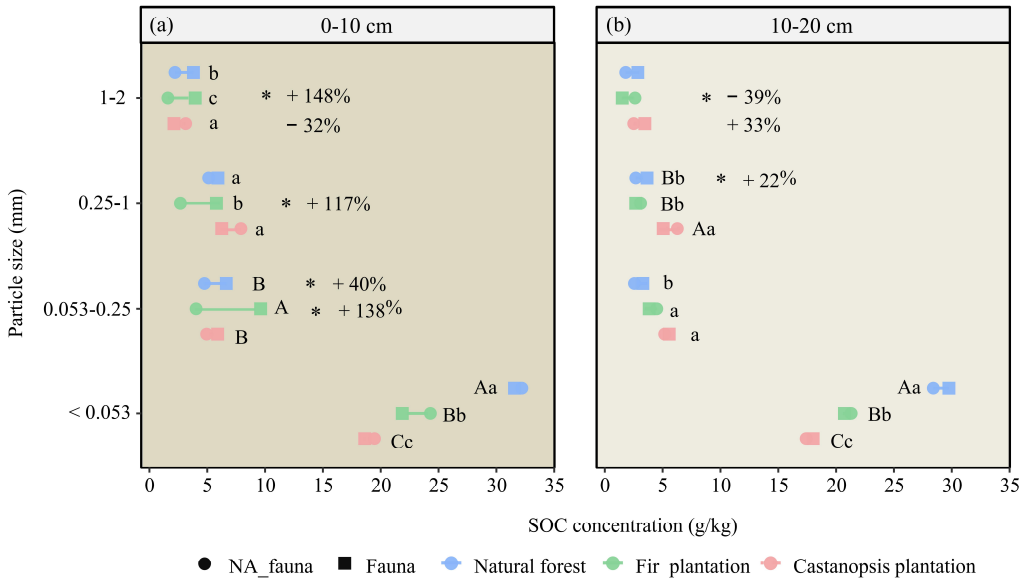

Figure 3. Effects of forest type and soil fauna treatment on aggregate-associated SOC concentration. Values are means ± standard error (n = 3). Different uppercase letters indicate significant differences among forest types under the fauna-access treatment, whereas different lowercase letters indicate significant differences among forest types under the fauna-exclusion treatment. Asterisks indicate significant differences between the fauna-access and fauna-exclusion treatments within the same forest type ($p < 0.05$). Percentages indicate the relative change in SOC concentration in the fauna-access treatment compared with the fauna-exclusion treatment.

Regarding relative SOC contribution, the <0.053 mm fraction dominated, accounting for approximately 55–82% of aggregate-associated SOC across both depths (Figure 4). In the 0–10 cm layer, forest type differences in relative SOC contribution were most evident in the 0.25–1 mm, 0.053–0.25 mm, and <0.053 mm fractions. Notably, under fauna access, the relative SOC contribution of the <0.053 mm fraction was 17 percentage points higher in the natural forest than in the fir plantation. Similar trends were observed in the 10–20 cm layer; however, forest type and fauna treatment differences were less pronounced than in the surface soil (Table S4).

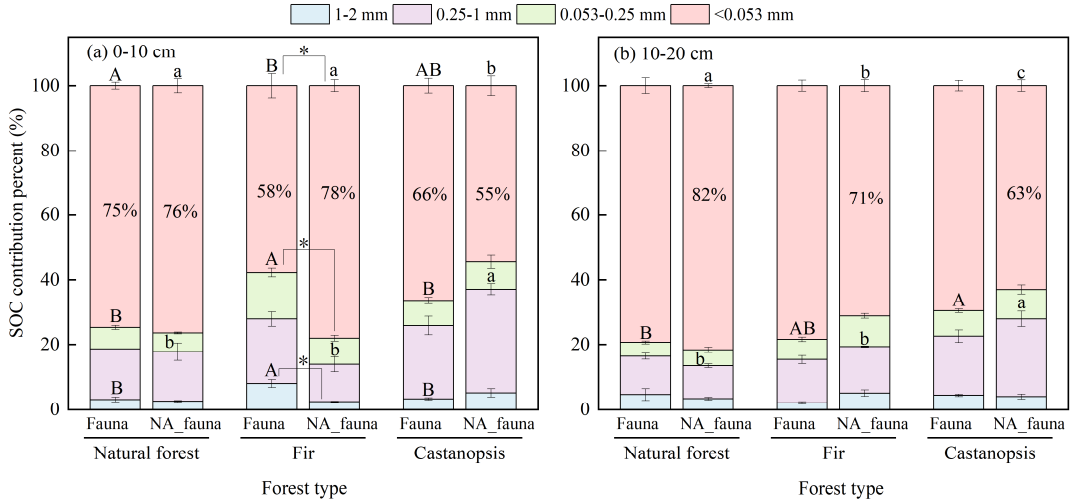

Figure 4. Effects of forest type and soil fauna treatment on the relative contribution of aggregate-associated SOC. Values are means ± standard error (n = 3). Different uppercase letters indicate significant differences among forest types under the fauna-access treatment, whereas different lowercase letters indicate significant differences among forest types under the fauna-exclusion treatment; Asterisks indicate significant differences between the fauna-access and fauna-exclusion treatments within the same forest type ($p < 0.05$).

3.3. Relationships between Soil Fauna Community and Aggregate-Associated SOC Properties

Soil fauna attributes exhibited distinct relationships with aggregate-associated SOC properties across the two soil layers (Figure 5). No significant correlations were observed between soil fauna attributes and aggregate mass proportions in either soil layer, whereas significant correlations were mainly detected for SOC concentration and relative SOC contribution. In the 0–10 cm layer, PR abundance was positively correlated with SOC concentration in the 0.25–1 mm fraction ($p < 0.05$), while total fauna abundance and PH abundance were negatively correlated with relative SOC contribution in the 0.053–0.25 mm fraction ($p < 0.01$). By comparison, relationships between soil fauna attributes and aggregate-associated SOC properties were more pronounced in the 10–20 cm layer. Total abundance, biomass, and OM abundance were generally positively correlated with SOC concentration and relative contribution in the 0.25–1 and 0.053–0.25 mm fractions. Notably, biomass was strongly positively correlated with relative SOC contribution in the 0.25–1 mm fraction ($p < 0.001$). Conversely, total abundance, biomass, and OM abundance were negatively correlated with SOC concentration and relative contribution in the <0.053 mm fraction.

3.4. Relationships between Environmental Factors and Aggregate-Associated SOC Properties

Redundancy analysis revealed exploratory patterns in the relationships between environmental variables and aggregate-associated SOC properties across soil depths (Figure 6). In the 0–10 cm layer, the RDA ordination suggested positive relationships between SOC concentration in the <0.053 mm fraction and soil moisture and soil P, whereas SOC concentration in the 0.25–1 mm fraction and its relative SOC contribution showed positive trends with litter N and litter mass. SOC concentration and aggregate mass proportion in the 0.053–0.25 mm fraction showed positive trends with pH, while the relative SOC contribution of this fraction showed a negative trend with soil moisture. In the 10–20 cm layer, SOC concentration in the <0.053 mm fraction showed a positive trend with soil moisture. SOC concentration and relative SOC contribution in the 0.25–1 mm fraction showed positive trends with litter N and litter mass, whereas those in the 0.053–0.25 mm fraction showed negative trends with soil moisture.

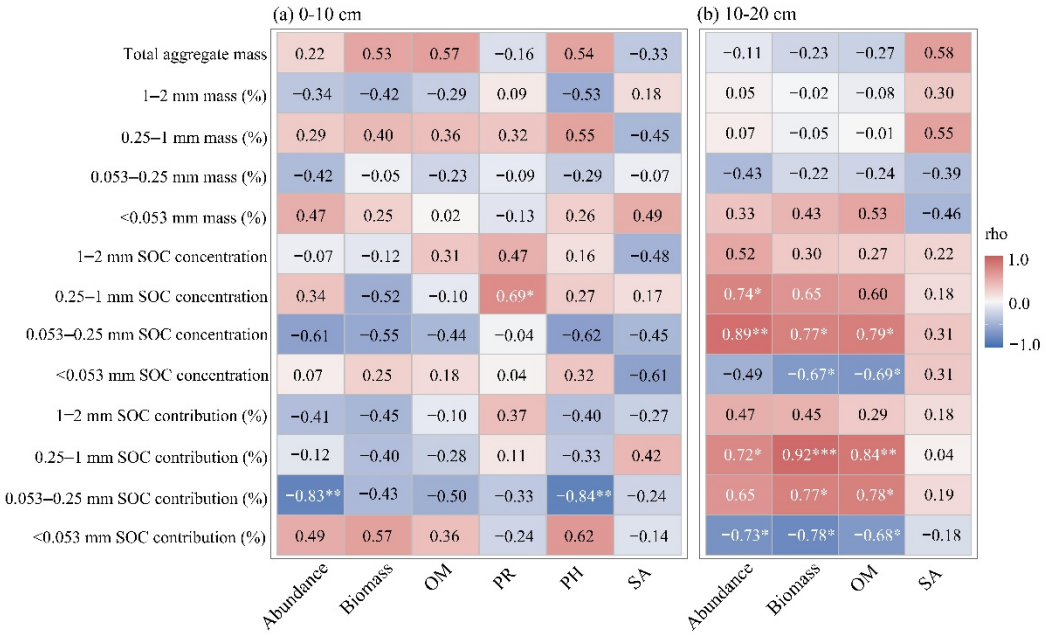

Figure 5. Relationships between soil fauna attributes and soil aggregate-related properties in the 0–10 cm (**a**) and 10–20 cm (**b**) soil layers. Analyses were conducted using samples from the fauna-access treatment only. Soil fauna variables included total abundance, biomass, and functional-group abundances. PR and PH were excluded from the 10–20 cm analysis because of insufficient non-zero observations. Asterisks indicate statistical significance: * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

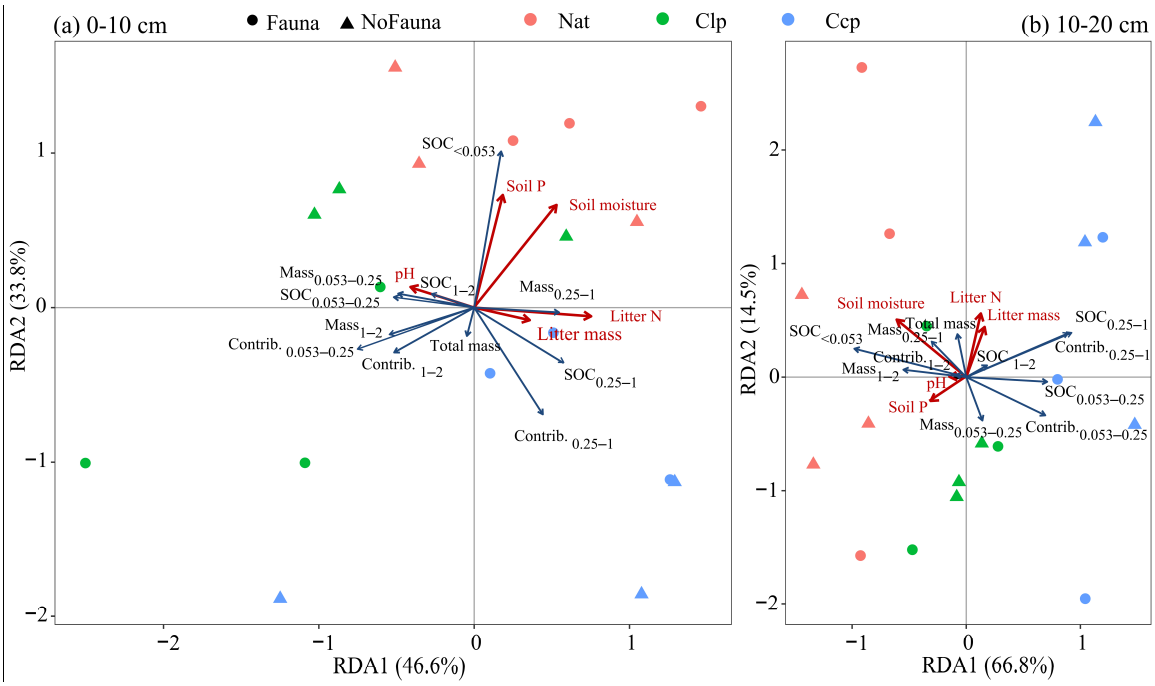

Figure 6. Redundancy analysis of environmental factors and aggregate-associated SOC properties in the 0–10 cm (**a**) and 10–20 cm (**b**) soil layers. Environmental variables included soil moisture, pH, soil P, litter mass, and Litter N. Red and blue arrows represent environmental and aggregate/SOC variables, respectively. Point colors indicate forest type and shapes indicate fauna treatment, which was included as a conditional variable in the partial RDA. Axis percentages indicate the constrained variation explained. Mass, aggregate mass proportion; Contrib., relative SOC contribution; Nat, natural forest; Clp, fir plantation; Ccp, Castanopsis plantation.

4. Discussion

Our results partially supported our hypotheses, showing that aggregate-associated SOC allocation varied among forest types, soil depths, and aggregate-size fractions, with responses to fauna access differing across forest

types. Forest type differences in aggregate mass distribution and SOC allocation were particularly pronounced within the 0–10 cm soil layer. This pattern may reflect greater inputs of fresh organic matter and higher soil fauna abundance in surface soils [17], whereas deeper soils generally receive less fresh carbon input and exhibit slower carbon turnover [13,14]. Under fauna access, the fir plantation had a higher proportion of 1–2 mm aggregates, whereas the natural forest showed a higher relative SOC contribution from the <0.053 mm fraction. Fine mineral particles play an important role in SOC stabilization and accumulation [39,40]. The effects associated with soil fauna access also varied markedly among forest types and aggregate-size fractions. Notably, soil fauna community attributes were not significantly correlated with aggregate mass proportions but showed depth- and fraction-specific associations with SOC concentration and relative SOC contribution, with stronger relationships generally observed in the 10–20 cm layer. This suggests that short-term fauna-associated responses were more evident in SOC allocation than in aggregate mass distribution.

Under fauna access, the fir plantation exhibited a higher proportion of the 1–2 mm fraction than the natural forest, whereas the proportions of the 0.25–1 mm and <0.053 mm fractions were significantly lower. Rather than indicating a general increase in macroaggregates, this pattern suggests a shift in aggregate mass distribution among size fractions in the fir plantation. Such differences may be related to variations in vegetation composition, litter inputs, soil nutrient availability, and biological activity among forest types [5,15–17], which can influence aggregate formation and turnover [5,41]. However, aggregate mass distribution did not directly correspond to SOC allocation. Despite the higher proportion of the 1–2 mm fraction in the fir plantation, the natural forest maintained higher SOC concentration and relative SOC contribution in the <0.053 mm fraction. This finding is broadly consistent with Dong et al. [5], who reported higher soil SOC concentrations and aggregate stability in natural forests than in fir plantations. The higher relative SOC contribution of the finest fraction in the natural forest may reflect differences in organic matter inputs and microbial processing, which are important processes in SOC formation [42]. Overall, these results highlight forest-specific differences in SOC allocation among aggregate-size fractions but do not provide direct evidence of differences in long-term SOC stabilization.

Soil fauna may influence SOC formation through decomposition and organic matter transformation [22,43]. In the present study, fauna access was associated with changes in aggregate-associated SOC, with responses varying among forest types and aggregate-size fractions. Specifically, in the 0–10 cm layer, fauna access increased SOC concentration in the 1–2 mm and 0.25–1 mm fractions of the fir plantation, whereas it decreased SOC concentration in the 1–2 mm fraction of the castanopsis plantation. These contrasting responses suggest that fauna-associated changes in SOC allocation depend on forest type and aggregate size. Such variation may be related to the effects of soil fauna on organic matter processing through litter fragmentation, feeding, excretion, bioturbation, and interactions with microorganisms, which may influence aggregate formation and turnover [22,23,44]. Notably, soil fauna community attributes were not related to aggregate mass proportions but were associated with SOC concentration and relative SOC contribution, particularly in the 10–20 cm layer, suggesting that short-term fauna-associated responses were expressed mainly through SOC redistribution rather than detectable changes in aggregate mass distribution. These relationships may also be influenced by differences in soil fauna composition and resource availability among forest types. Litter quality and nutrient availability may influence soil fauna biomass [28], while variation in prey availability may affect higher trophic levels through trophic interactions within soil food webs [45]. Such trophic interactions may provide one possible ecological explanation for the varying associations between soil fauna functional groups and aggregate-associated SOC properties observed in this study.

Moreover, previous studies have reported differences in aggregate-associated SOC distribution among vegetation types [46,47], suggesting that vegetation characteristics and associated soil conditions may contribute to these patterns. In this study, exploratory RDA suggested potential relationships between aggregate-associated SOC properties and soil moisture, pH, soil P, litter N, and litter mass, with patterns varying across soil depths and aggregate-size fractions. Differences in litter inputs and quality may influence microbial processing and SOC formation [42]. These processes may contribute to variation in aggregate-associated SOC, as physical and biochemical transformations are involved in SOM formation and transformation within soil aggregates [48]. However, several limitations warrant consideration. Differences in mesh size may have influenced not only soil fauna access but also root and fungal hyphal ingrowth, water exchange, and dissolved organic matter transport. Incomplete fauna recolonization and the limited extraction efficiency of Tullgren funnels may also have affected estimates of the soil fauna community. Thus, treatment differences should be interpreted as responses associated with the experimental manipulation of fauna access rather than effects exclusively attributable to soil fauna. In addition, forest type differences may reflect combined variation in vegetation, stand age, litter characteristics, and soil conditions. Finally, given the six-month duration and the lack of direct measurements of SOC turnover-related processes, our results primarily reflect differences in aggregate-associated SOC distribution observed over the

experimental period rather than long-term SOC stabilization. Future studies should combine longer-term experiments, improved exclusion designs, and process-based measurements to better clarify the role of soil fauna in forest SOC dynamics.

5. Conclusions

Aggregate-associated SOC allocation varied among forest types, while responses associated with soil fauna access differed among forest types, aggregate-size fractions, and soil depths. Forest type differences were most pronounced in the 0–10 cm layer, where the natural forest showed higher SOC concentration in the <0.053 mm fraction than both plantations and a higher relative SOC contribution from this fraction than the fir plantation. Fauna-access treatments were associated with contrasting differences in SOC concentration among forest types and aggregate-size fractions. Soil fauna community attributes showed significant correlations with SOC concentration and relative SOC contribution in specific aggregate-size fractions, but not with aggregate mass proportions. Exploratory RDA also suggested potential relationships between aggregate-associated SOC properties and soil moisture, pH, soil total P, litter N, and litter mass. Overall, these findings highlight forest-type differences in aggregate-associated SOC distribution and its associations with soil fauna community attributes over the six-month experimental period. Longer-term studies are needed to determine whether these patterns translate into differences in SOC persistence.

Supplementary Materials

The additional data and information can be downloaded at: https://media.sciltp.com/articles/others/26112316 20304544/SE-26060033-SI.pdf. Table S1: Site characteristics and stand attributes of the natural forest, castanopsis plantation, and fir plantation. Table S2: Soil physicochemical properties, litter characteristics, and soil fauna attributes under fauna-access and fauna-exclusion treatments across three forest types. Table S3: Soil fauna taxonomic groups and functional groups in different forests. Table S4: Two-way ANOVA results for the interactive effects of forest type and soil fauna treatment on aggregate mass proportion, aggregate-associated SOC concentration, and relative SOC contribution.

Author Contributions

F.W.: Conceptualization, methodology, writing—review and editing; H.W.: Investigation, formal analysis, writing—original draft preparation; L.Z.: Investigation; J.Y.: Investigation; J.L.: Investigation. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement

Data are available from the Figshare repository at https://doi.org/10.6084/m9.figshare.35039290 (Wen et al., 2026).

Conflicts of Interest

The authors declare no conflict of interest. Given the role as Editorial Board Member, Fuzhong Wu had no involvement in the peer review of this paper and had no access to information regarding its peer-review process. Full responsibility for the editorial process of this paper was delegated to another editor of the journal.

Use of AI and AI-Assisted Technologies

AI tools were utilized for language editing of this paper.

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