Research Square

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Gap-Size-Dependent Responses of Soil Organic Carbon Fractions in Natural Pinus koraiensis Forests of Northeast China

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Research Article

Keywords: canopy gap, Pinus koraiensis forest, soil organic carbon, physical fractions of organic carbon, carbon stability, carbon sequestration

Posted Date: November 2nd, 2026

DOI: https://doi.org/10.21203/rs.3.rs-11350895/v1

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Additional Declarations: No competing interests reported.

Abstract

Purpose

As a key forest management tool in near-natural forestry, canopy gaps offer significant potential to restore low-productivity forests. However, the effects of canopy gap size on soil organic carbon (SOC) and its physical fractions remain poorly understood. In this study, we investigated the responses of SOC and its physical fractions to canopy gaps of three sizes in natural Korean pine forests of northeastern China.

Methods

Soil samples were collected along a gradient extending from closed-canopy stands to gap edges, expanded gap zones, and gap centers. Soil organic carbon, particulate organic carbon (POC), and mineral-associated organic carbon (MAOC) were measured together with canopy closure, environmental variables and other soil conditions.

Results

The results showed that SOC per unit area decreased significantly in large and medium-sized gaps by 14.11% and 12.07%, respectively, relative to closed-canopy stands, whereas small gaps increased SOC by 26.49%. MAOC decreased from closed stands toward gap centers in large and medium-sized gaps but increased overall in small gaps. The relative contribution of MAOC to SOC increased with gap size. RDA and SEM analyses further revealed that canopy closure indirectly regulated SOC fractions through its effects on soil temperature, electrical conductivity, and pH.

Conclusions

Overall, this study elucidates the mechanisms by which gap formation enhances soil organic carbon stability and demonstrates the potential of small gaps to increase soil carbon sequestration. Therefore, integrating small-canopy-gap management into sustainable forest management practices may provide an effective approach to simultaneously enhance soil organic carbon stability and forest carbon sequestration.

1 Introduction

Climate change is one of the most significant environmental challenges facing humanity, largely driven by the increasing concentration of greenhouse gases in the atmosphere. Recent observations indicate that global mean temperatures rose sharply between 2023 and 2024, with the average temperature in 2024 exceeding pre-industrial levels by 1.5°C, thereby surpassing the critical threshold established under the 2015 Paris Agreement. Consequently, reducing greenhouse gas emissions and enhancing the carbon sequestration capacity of terrestrial ecosystems have become key strategies for climate change mitigation(Tollefson 2025).

Forest ecosystems are among the largest terrestrial carbon reservoirs, with forest soils storing more than 70% of terrestrial ecosystem carbon (Post et al. 1982). Therefore, improving forest soil carbon sequestration through sustainable forest management is widely regarded as an effective approach for enhancing ecosystem carbon sinks (Zhu et al. 2024). However, many plantations in China were established through large-scale clonal afforestation, resulting in reduced genetic diversity, simplified age structures, and limited natural regeneration due to the absence of canopy disturbances (Liu et al. 2018). To address these challenges, Liu et al. (2018) proposed incorporating canopy gaps into plantation management to promote near-natural succession processes and improve ecosystem functioning. Therefore, elucidating the effects of canopy gap formation on forest soil carbon sequestration and the mechanisms underlying these effects is critical for the rational planning and scientific implementation of canopy-gap management. This would provide a scientific basis for using canopy gaps to improve the productivity and ecological functioning of low-yield planted forests and degraded natural forests, ultimately enhancing their carbon sequestration potential.

Canopy gaps are openings in the forest canopy created by disturbances such as windthrow, fire, or tree mortality (Gorgens et al. 2023). As a natural component of forest dynamics, canopy gap formation plays a crucial role in forest regeneration (Gass and Hülsmann 2026), the maintenance of forest structure, and the conservation of biodiversity (Bast et al. 2026). Moreover, it enhances the ecological resilience of forest ecosystems (Ueta et al. 2026). By altering light availability, temperature regimes, and resource distribution patterns, canopy gaps create heterogeneous microenvironments that promote niche differentiation and species coexistence. These processes directly influence forest community succession and the development of biodiversity patterns (Luo et al. 2025). Consequently, canopy gaps are increasingly recognized as an important ecological feature that should be incorporated into planted forest management to support sustainable ecosystem functioning and biodiversity conservation.

Despite increasing recognition of their ecological importance, the effects of canopy gaps on forest soil carbon sequestration remain controversial. Several studies have reported positive effects of canopy gap formation on soil carbon accumulation. For example, Lyu et al. (Lyu et al. 2022) monitored soil properties in low-productivity pure stands of Chinese cypress (*Cupressus funebris*) following the creation of large canopy

gaps in the upper Yangtze River Basin, China. They found that soil carbon content was higher within the gaps and that microbial diversity and activity were significantly enhanced, suggesting that canopy gap formation can improve soil ecological functioning. Similarly, Liu et al. (Liu et al. 2018) observed that increasing gap size promoted microbial biomass in the organic soil layer, thereby improving soil carbon stability. In boreal forests, Ni et al. (Ni et al. 2015) reported that although winter snow accumulation in canopy gaps inhibited litter humification, elevated summer temperatures accelerated decomposition and humification processes, resulting in greater net soil carbon sequestration.

In contrast, other studies have documented negative impacts of canopy gaps on soil carbon pools. Li et al. (Li et al. 2025) reported that canopy gap formation reduced soil pH, accelerated soil organic carbon decomposition, and negatively affected microbial diversity. A similar meta-analysis also demonstrated that canopy gaps may decrease soil organic carbon stocks, particularly microbial carbon pools (Tong et al. 2024). These inconsistent findings suggest that the response of soil carbon to canopy gap formation is highly context-dependent and may be regulated by factors such as gap size, forest type, climatic conditions, and soil properties.

Among these factors, gap size appears to be particularly important. Amolikondori et al. (Amolikondori et al. 2022) found significant differences in soil organic carbon stocks among canopy gaps of different sizes, with larger gaps generally exhibiting greater carbon accumulation. In contrast, small gaps showed little difference from adjacent closed-canopy stands. These findings indicate that the influence of canopy gaps on soil carbon sequestration is strongly mediated by gap characteristics and associated environmental changes. Nevertheless, information on the spatial variation of soil organic carbon and its physical fractions across canopy gaps of different sizes in natural Korean pine (*Pinus koraiensis*) forests remains limited, particularly in northeastern China. This knowledge gap constrains our ability to accurately assess and predict the carbon sink function of these ecologically important forests.

To fill this knowledge gap, the present study examined canopy gaps of different sizes within natural Korean pine forests in northeastern China. Soil samples were collected along a gradient extending from closed-canopy stands to gap expansion zones, gap edges, and gap centers. By quantifying soil organic carbon (SOC) content, its physical fractions, and associated environmental variables, this study aims to answer the following questions: (1) Do SOC stocks differ significantly among canopy gaps of different sizes? (2) Do SOC physical fractions vary along the gradient from closed-canopy stands to expanding canopy gaps, gap edges, and gap centers? (3) What are the mechanisms through which environmental factors regulate SOC and its physical fractions following canopy gap formation?

2 Study Area and Research Methods

2.1 Overview of the Study Area

The study was conducted at Liuhe Forest Farm, Hailin City, Mudanjiang, Heilongjiang Province, China (130°31'–130°50'E, 48°03'–48°21'N), located on the southeastern slope of the Zhangguangcai Ridge, a branch of the Changbai Mountain Range. The terrain is characterized by low mountains and hilly landscapes, with a mean elevation of 801.03 m above sea level. The region experiences a temperate continental monsoon climate, with a mean annual temperature of 2.7°C and mean annual precipitation of approximately 555 mm, most of which occurs during summer and autumn. The dominant soil type is dark brown forest soil.

Natural Korean pine forests constitute the primary vegetation type in the Zhangguangcai Ridge region. The forest community is dominated by Korean pine (*Pinus koraiensis*), accompanied by species such as Ukurundu maple (*Acer ukurunduense*) and Tegmentosum maple (*Acer tegmentosum*). Other common canopy species include Korean fir (*Abies nephrolepis*), Jeju spruce (*Picea jezoensis*), and white birch (*Betula platyphylla*). The forest exhibits a complex community structure, high biodiversity, and considerable ecological and economic value.

2.2 Research Methods

2.2.1 Plot Establishment and Vegetation Survey

In May 2025, a permanent plot measuring 300 m × 100 m was established within a natural *Pinus koraiensis* forest in the study area. The plot was subdivided into 10 m × 10 m quadrats. All trees with a diameter at breast height (DBH) ≥ 2 cm were surveyed and tagged. For each tree, species identity, spatial coordinates, tree height, DBH, and abundance were recorded. Basic characteristics of the plot are presented in Table 1.

Table 1
Overview of the Model Home

Species	Number	Mean tree height/m	Mean diameter at breast height/cm
Abies nephrolepis	1766	7.80	8.07
Betula platyphylla	529	16.82	17.41
Tilia mandshurica	690	13.28	15.01
Picea jezoensis	802	5.96	6.16
Pinus koraiensis	558	7.76	8.80
Acer tegmentosum	665	9.34	8.07
Acer ukurunduense	595	8.19	5.32
Acer pictum	289	10.18	8.94
Tilia amurensis	247	10.93	10.44
Betula costata	127	18.19	20.20
Populus davidiana	102	12.67	11.46
Populus cathayana	28	21.86	33.99
Larix gmelinii	52	17.42	21.20
Ulmus pumila	47	9.58	9.22
Salix arbutifolia	36	11.41	12.94
Padus avium	32	7.32	11.11
Picea koraiensis	19	5.72	6.12
Sorbus pohuashanensis	10	9.53	8.88

2.2.2 Classification of Gap Sizes

Potential canopy gaps were initially identified in ArcGIS using spatial tree distribution data and tree height information collected during the vegetation survey. Following the method proposed by Zhu et al. (2015), two-thirds of the maximum tree height within the plot was used as the threshold canopy height for gap delineation. A total of 20 candidate canopy gaps were identified through spatial analysis and subsequently verified through field investigation.

Gap size was classified using the CTSG method (Zhu et al. 2015) according to Eq. (1):

$$R=\frac{D}{H} \quad (1)$$

where D represents the length of the major axis of the forest gap (m), and H denotes the mean height of the surrounding edge trees (m).

Based on the gap size ®, forest gaps were categorized into three classes: small gaps (0.49 < R < 1.00), medium gaps (1.00 < R < 2.00), and large gaps (2.00 < R < 3.49).

The dominant canopy height in the study area was 18 m. Accordingly, the corresponding major-axis length ranges were 8.82-18.00 for small gaps, 18.00–36.00 for medium gaps, and 36.00-62.82 for large gaps. Ultimately, three gaps from each size class were selected, resulting in a total of nine representative forest gaps. The basic characteristics of the different canopy-gap plots are summarized in Table 2.

Table 2
Basic characteristics of canopy gaps of different sizes

Item	Large gap	Medium gap	Small gap
Long-axis length (m)	36.97+/-1.72	26.26+/-2.43	17.00+/-1.51
Short-axis length (m)	23.40+/-2.19	14.83+/-2.50	12.97+/-2.18
Formation mode	Stem breakage	Stem breakage	Stem breakage
Regenerating trees	Manchurian fir, Acer tegmentosum, Tilia mandshurica, white birch, larch, poplar, Yezo spruce	Amur linden, Acer tegmentosum, Korean birch, white birch, Manchurian fir, Korean birch, Acer ukurunduense, Korean pine	Acer ukurunduense, small Manchurian fir, Manchurian fir, Acer mono

2.2.3 Forest Gap Gradient Design and Sampling Point Establishment

Based on the initial survey and previous findings indicating that canopy openings are more likely to form adjacent to existing gaps (Saha et al. 2023), three habitat zones were defined along the major axis of each forest gap. The area extending 10 m inward from the edge trees toward the closed forest was defined as the closed-canopy stand (CC). The area between the closed-canopy stand and the edge trees was designated as the gap edge, while the area between the edge trees and the gap center was defined as the expanded gap zone.

Along the major axis of each forest gap, a transect was established from the gap center to the closed-canopy stand. The transect was divided into ten equally spaced sampling gradients (G1–G10), with the closed-canopy stand (CC) serving as the control (Fig. 1). One sampling point was established at each gradient and within the closed-canopy stand, resulting in a total of 11 sampling points per gap.

2.2.4 Soil Sample Collection and Preparation

Soil sampling was conducted along the established gradients within the nine selected forest gaps. Sampling locations were positioned to avoid edge trees, fallen logs, mounds, depressions, and other microsites that could introduce local heterogeneity. Surface litter was carefully removed before sampling.

At each sampling point, soil samples were collected from the 0–20 cm mineral soil layer. Samples were placed in hard plastic containers and transported to the laboratory for processing. Eleven samples were collected from each forest gap, yielding 33 samples for each gap-size category and a total of 99 soil samples.

In the laboratory, a portion of each sample was air-dried at room temperature in a shaded environment. Plant roots, stones, and other debris were carefully removed. The samples were then ground and passed through a 100-mesh sieve before being stored in sealed polyethylene bags for subsequent analyses.

2.2.5 Soil Physicochemical Analyses

Soil total organic carbon (TOC) was determined using an Elementar Vario TOC Select analyzer (Vario TOC Select, Germany). Soil pH was measured using a pHS-25 pH meter (INESA Scientific Instrument Co., Ltd., China). Soil cation exchange capacity (CEC) was determined following standard laboratory procedures. Soil texture was analyzed using the pipette method and classified into sand (2–0.05 mm), silt (0.05–0.002 mm), and clay (< 0.002 mm) fractions (Svensson et al. 2022). Soil microbial diversity, fungal abundance and bacterial abundance were analyzed by metagenomics method.

The physical fractions of SOC were separated using the wet-sieving method (Breure et al. 2026). Briefly, 20 g of air-dried soil (< 2 mm) was placed in a 250-mL Erlenmeyer flask, and 100 mL of 5 g L^{-1} sodium hexametaphosphate solution was added. The suspension was manually shaken for 10–15 min and then placed on a reciprocating shaker (180 rpm) for 18 h. The dispersed sample was subsequently passed through a 0.053-mm sieve and rinsed with distilled water until the filtrate became clear.

The material retained on the sieve was separated into coarse particulate organic matter (Coarse POM, or CPOM, 0.25–2 mm) and fine particulate organic matter (Fine POM, or FPOM, 0.053–0.250 mm). These fractions were dried at 80°C for 12 h and weighed. The undersized fraction constitutes mineral-associated organic carbon (MAOC, < 0.053 mm), which was then dried in an oven (12 h). After drying and grinding, TOC was measured, and the percentage of MAOC relative to the total soil was calculated. The basic physicochemical properties of the test soils are shown in Table 3.

Table 3
Basic Physical and Chemical Properties of the Test Soil

Item	Cannopy gap size	CC	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10
pH	BG	5.21 ± 0.28b	5.40 ± 0.05ab	5.65 ± 0.03ab	5.62 ± 0.05ab	5.67 ± 0.11a	5.58 ± 0.10ab	5.56 ± 0.03ab	5.53 ± 0.16ab	5.82 ± 0.17a	5.58 ± 0.12ab	5.5 ± 0.12ab
	MG	5.59 ± 0.05a	5.67 ± 0.07a	5.77 ± 0.14a	5.54 ± 0.27a	5.83 ± 0.25a	5.62 ± 0.13a	5.57 ± 0.10a	5.61 ± 0.03a	5.71 ± 0.15a	5.72 ± 0.04a	5.69 ± 0.12a
	SG	5.49 ± 0.09a	5.72 ± 0.02a	5.57 ± 0.12a	5.39 ± 0.09a	5.42 ± 0.16a	5.52 ± 0.14a	5.45 ± 0.06a	5.59 ± 0.09a	5.54 ± 0.09a	5.57 ± 0.13a	5.51 ± 0.13a
EC	BG	102.4 ± 19.31a	78.70 ± 14.97ab	70.23 ± 10.70ab	62.13 ± 2.23ab	55.10 ± 1.84b	60.80 ± 11.45ab	60.83 ± 8.49ab	71.97 ± 15.69ab	55.77 ± 17.75b	64.67 ± 6.96ab	65.23 ± 15.95ab
	MG	70.93 ± 10.71a	59.57 ± 12.83a	75.63 ± 10.10a	80.00 ± 6.01a	68.30 ± 4.69a	74.10 ± 8.28a	80.83 ± 20.02a	79.27 ± 10.53a	78.87 ± 14.62a	75.27 ± 10.83a	77.90 ± 11.85a
	SG	72.33 ± 6.60a	79.23 ± 28.42a	96.17 ± 11.10a	82.20 ± 20.33a	88.77 ± 12.68a	119.43 ± 26.49a	111.03 ± 26.69a	132.47 ± 9.77a	100.5 ± 1.79a	109.10 ± 32.19a	98.80 ± 16.25a
Sand	BG	51.12 ± 7.19a	33.30 ± 11.85ab	15.42 ± 16.60b	32.77 ± 3.27ab	31.34 ± 6.28ab	27.81 ± 3.88ab	32.87 ± 0.70ab	33.34 ± 5.36ab	47.14 ± 8.75a	37.06 ± 9.43ab	42.00 ± 9.41ab
	MG	45.34 ± 5.49a	44.45 ± 2.82ab	43.73 ± 1.10ab	40.60 ± 1.90abc	40.00 ± 1.19abc	40.53 ± 3.27abc	42.29 ± 4.05abc	36.89 ± 4.58abc	34.43 ± 2.96bc	32.05 ± 1.79c	35.20 ± 0.68abc
	SG	38.89 ± 3.28ab	34.19 ± 5.73ab	43.13 ± 1.12a	39.41 ± 3.87ab	33.22 ± 4.98ab	38.73 ± 3.92ab	35.37 ± 5.05ab	39.84 ± 0.72a	37.42 ± 1.57ab	37.39 ± 3.44ab	27.33 ± 1.47b
Silt	BG	23.24 ± 3.90b	44.07 ± 15.18ab	56.90 ± 14.70a	23.87 ± 4.17b	27.23 ± 2.72b	40.16 ± 11.39ab	28.43 ± 3.27ab	18.79 ± 8.48b	14.71 ± 3.81b	20.98 ± 10.51b	26.09 ± 7.94b
	MG	33.00 ± 2.73a	28.97 ± 2.63a	32.35 ± 2.21a	32.70 ± 1.44a	27.51 ± 0.97a	32.67 ± 2.65a	32.36 ± 2.09a	33.05 ± 3.71a	33.39 ± 0.69a	34.30 ± 4.14a	29.80 ± 1.51a
	SG	31.01 ± 2.15ab	34.23 ± 3.79ab	31.02 ± 1.16ab	28.79 ± 3.66b	33.85 ± 4.14ab	35.63 ± 2.70ab	38.31 ± 1.41a	34.32 ± 0.97ab	27.52 ± 2.24b	35.06 ± 1.01ab	34.99 ± 2.62ab
Clay	BG	25.64 ± 6.35b	22.63 ± 5.39b	27.68 ± 4.90ab	43.36 ± 7.45ab	41.43 ± 3.57ab	32.03 ± 11.77ab	38.70 ± 3.95ab	47.87 ± 7.11a	38.15 ± 5.43ab	41.96 ± 4.78ab	31.91 ± 1.68ab
	MG	21.66 ± 2.83d	26.58 ± 0.99bcd	23.93 ± 2.74cd	26.70 ± 0.46bcd	32.49 ± 1.45ab	26.80 ± 5.39bc	25.36 ± 2.23bcd	30.07 ± 1.32abc	32.18 ± 2.33abc	33.65 ± 2.65ab	35.01 ± 0.85a
	SG	30.10 ± 2.43ab	31.58 ± 3.32ab	25.84 ± 0.20b	31.79 ± 2.63ab	32.93 ± 0.86ab	25.64 ± 5.49b	26.32 ± 4.04b	25.84 ± 1.19b	35.06 ± 3.74ab	27.55 ± 4.26ab	37.68 ± 1.16a

Note: EC: electrical conductivity

2.2.6 Canopy Structure Characterization and Microenvironmental Monitoring

Canopy structure was assessed using hemispherical imaging technology. Images were acquired using a Canon EOS 50D digital camera equipped with a Sigma EX DG 8-mm fisheye lens (Beijing Havesting Technology Co., Ltd., China) mounted on a tripod at a height of 1.5 m above ground level. Five randomly selected points were photographed along each transect, and the resulting images were analyzed to obtain canopy structural parameters (Jonckheere et al. 2004).

Soil temperature was continuously monitored throughout the 2025 growing season using a HOBO data logger (Onset Computer Corporation, USA) installed at a depth of 10 cm. Variations in canopy closure and soil temperature across different forest gap positions are presented in Figs. 2(a) and 2(b).

2.2.7 Estimation of Soil Organic Carbon Content per Unit Area

Using the closed-canopy stand (CC) as the control, spatial variations in soil organic carbon content per unit area were analyzed across the sampling gradients for different gaps (Fig. 3a). Cubic spline interpolation (Amirzehni et al. 2023) combined with numerical integration was employed to estimate the total soil organic carbon variation along the entire forest-gap transect (Fig. 3b). The integrated value was divided by the total transect length (0.5*D + 10 m) to obtain the average soil organic carbon variation per unit area across the forest-gap gradient.

2.2.8 Statistical Analyses

Data were initially organized using Microsoft Excel 2021. One-way analysis of variance (ANOVA) followed by Tukey's honestly significant difference (HSD) post hoc test, was performed in SPSS to evaluate differences in soil physicochemical properties and soil organic carbon fractions among treatments ($\alpha = 0.05$).

All data were normalized by Z-score before analysis. Pearson correlation analysis was conducted to investigate the relationships between SOC, its components, and environmental variables. Origin 2026 was used to plot mean charts and correlation heatmaps, with results expressed as mean ± standard error (SE).

Redundancy Analysis (RDA) was applied to assess the comprehensive effects of environmental factors on SOC components. Structural equation modeling (SEM) was performed using Smart PLS 4.1 to quantify both direct and indirect effects of environmental factors on soil organic carbon fractions and to identify the key mechanisms regulating soil organic carbon dynamics under forest-gap disturbance.

3 Results

3.1 Effects of Forest Canopy Gaps of Different Sizes on Soil Organic Carbon Content

As shown in Fig. 4, soil organic carbon (SOC) generally decreased in large and medium-sized canopy gaps compared with closed-canopy stands, whereas SOC increased in small canopy gaps, reaching its highest value in the transition zone between the gap edge and the expanded gap area. Using a combination of cubic spline interpolation and numerical integration to calculate the area under the curve, SOC per unit area was found to decrease significantly in large and medium-sized canopy gaps by 14.11 ± 8.45% and 12.07 ± 2.74%, respectively, relative to closed stands. In contrast, small canopy gaps exhibited a significant increase in SOC per unit area, with an average increase of 26.49 ± 11.70%.

3.2 Effects of Forest Canopy Gaps on Organic Carbon Fractions

Canopy gaps significantly affected the concentrations of SOC fractions (Fig. 5). Overall, free particulate organic carbon (fPOC) concentrations were relatively low in large, medium, and small canopy gaps (SG: 3.01–7.06 g/kg, MG: 3.89–10.06 g/kg, BG: 3.62–9.62 g/kg), with peak values occurring in the transition zone between the gap edge and the expanded gap area.

The concentrations of coarse particulate organic carbon (cPOC) and particulate organic carbon (POC) at sampling points G5-G10 followed the order: large gaps (cPOC: 8.03–19.63 g/kg; POC: 13.26–26.39 g/kg) < medium gaps (cPOC: 12.67–32.81 g/kg; POC: 16.56–38.79 g/kg) < small gaps (cPOC: 16.13–33.72 g/kg; POC: 19.28–39.63 g/kg). Within each canopy-gap size category, the spatial patterns of CPOC and POC were largely consistent. Specifically, large canopy gaps exhibited an initial increase followed by a decrease, medium gaps displayed a bimodal distribution, and small gaps showed an initial decrease followed by an increase. POC concentrations were highest in the transition zone between the gap edge and the expanded gap area and lowest at the center of the forest gap.

Mineral-associated organic carbon (MAOC) concentrations generally decreased across large and medium-sized canopy gaps, except at sampling point G6, with average concentrations ranging from 14.94 to 58.89 g/kg and 12.37 to 49.14 g/kg, respectively. In contrast, MAOC concentrations in small canopy gaps ranged from 21.73 to 51.92 g/kg and showed an overall upward trend, peaking at G6.

3.3 Contribution of Organic Carbon Fractions to SOC

The contributions of different organic carbon fractions to SOC varied among canopy gaps of different sizes (Fig. 6). MAOC accounted for the largest proportion of SOC, whereas fPOC contributed the smallest proportion. Analysis of the average contribution rates across all sampling locations within each gap size revealed that the relative contributions of MAOC and fPOC increased with gap size (MAOC: SG 50.17%, MG 57.13%, BG 63.80%; fPOC: SG 8.47%, MG 10.32%, BG 11.29%). In contrast, the relative contributions of POC and cPOC to SOC decreased with increasing canopy-gap size (POC: SG 49.83%, MG 42.91%, BG 36.20%; cPOC: SG 41.37%, MG 32.59%, BG 24.92%).

Spatially, all carbon fractions exhibited similar distribution patterns, with the most pronounced changes occurring at the forest gap edge.

3.4 Main Drivers of Variation in Soil Organic Carbon Fractions

Redundancy analysis (RDA) explained 87.75% of the total variation in soil carbon fractions (Fig. 7a), indicating that the selected environmental variables effectively accounted for changes in SOC fractions. Among the response variables, POC, cPOC, POC/SOC, and cPOC/SOC were strongly associated with the first RDA axis, while MAOC, MAOC/SOC, SOC, and fPOC/SOC were more strongly associated with the second axis. Among the explanatory variables, electrical conductivity (EC) and silt content contributed most to the first axis, whereas soil temperature (ST), pH, and the Simpson diversity index contributed most to the second axis.

Further analysis integrating correlation analysis (Figs. 7b and 7c) with structural equation modeling (SEM; Fig. 7d) revealed that POC and cPOC were significantly positively correlated with EC and highly significantly negatively correlated with clay content. MAOC was significantly positively correlated with bacterial abundance. The SEM results further indicated that ST and canopy closure indirectly influenced the formation of POC and MAOC by regulating EC and pH, thereby affecting SOC accumulation.

4 Discussion

4.1 Variability in Soil Organic Carbon Content and Stability Following the Formation of Canopy Gaps of Different Sizes

Our results demonstrated that SOC content decreased in large and medium-sized canopy gaps but increased in small canopy gaps (Fig. 4). This pattern is consistent with previous studies indicating that canopy gap formation modifies understory environmental conditions by increasing light availability and soil temperature (Muscolo et al. 2014). These changes can stimulate microbial activity, root growth, and plant diversity (Terborgh et al. 2017), thereby enhancing the potential for soil carbon sequestration (Jia et al. 2021; Lange et al. 2015). Similarly, Yu et al. (Yu et al. 2018) and Tafesse et al. (Tafesse et al. 2025) reported that both artificial and natural canopy gaps supported greater cover, biomass, abundance, and diversity of understory shrubs and herbs than closed-canopy stands. Furthermore, Li et al. (Li et al. 2025) found that small canopy gaps significantly increased species and functional diversity in forests with complex topography, thereby enhancing ecosystem resilience. Collectively, these findings suggest that small canopy gaps promote plant functional diversity and facilitate long-term soil carbon sequestration (Tong et al. 2024).

However, our results differ from those reported by Amolikondori et al. (Amolikondori et al. 2022), who observed no significant change in SOC content between canopy gaps and closed stands following gap formation. This discrepancy may be attributed to differences in forest type and environmental conditions. While the present study was conducted in a mixed coniferous–broadleaf forest within the northeastern temperate broadleaf and red pine forest region, their study was conducted in a temperate broadleaf forest. Variations in vegetation composition, climate, and soil properties can substantially influence SOC dynamics and ecosystem responses to disturbance (Doetterl et al. 2025).

Evaluating carbon sink functions solely based on carbon content often overlooks carbon dynamics. Scharenbroch's study demonstrated that canopy gap formation reduces labile soil organic fractions, alleviates soil carbon saturation pressure, and enhances SOC stability, ultimately promoting net carbon sequestration processes (Scharenbroch and Bockheim 2008). These findings suggest that assessments of soil carbon sequestration should place greater emphasis on changes in SOC stability rather than carbon content alone.

Carbon stability, also referred to as carbon persistence, is a key determinant of long-term soil carbon sequestration. The intrinsic mechanisms governing soil carbon stability primarily include three aspects: the inherent biochemical resistance of organic carbon to microbial decomposition, microbial carbon use efficiency, and aggregate protection mechanisms (Zhou et al. 2022). Mineral-associated organic carbon (MAOC) represents a relatively stable carbon pool within SOC fractions. It is less susceptible to microbial decomposition and mineralization due to strong chemical bonding with mineral surfaces and physical protection within soil aggregates. As a result, MAOC can maintain a relatively high proportion of soil carbon even under canopy-gap disturbances that alter soil hydrothermal conditions (Yan et al. 2025), thereby supporting soil carbon sequestration in forest-gap ecosystems (Cheng et al. 2025).

Accordingly, the analysis of organic carbon fraction contributions in this study indicated that large canopy gaps exhibit the highest carbon stability, while small canopy gaps show the lowest (Fig. 6). This pattern is consistent with previous studies (Ni et al. 2016), which suggest that increasing canopy gap size is associated with enhanced soil microbial activity and altered microbial community structure, thereby enhancing soil carbon stability. Hou et al. (Hou et al. 2025) further reported that canopy gaps significantly increase bacterial and fungal abundances, with bacterial abundance peaking in large gaps, and simultaneously promote stochastic assembly processes and reduce the complexity of soil microbial co-occurrence networks.

In this study, standardized values and arithmetic means of soil fungal abundance, bacterial abundance, and fungal-to-bacterial ratios were calculated across all independent sampling points along the canopy gap gradient. The results showed that mean bacterial abundance, fungal abundance, and fungal-to-bacterial ratio in large gaps (6.195%; 2.551%; 41.18%) were slightly higher than those in medium (6.189%; 2.483%; 40.11%) and small gaps (6.187%; 2.491%; 40.23%). Compared with bacteria, fungal hyphae have stronger capacities for organic matter decomposition and mineral adsorption (Wang et al. 2017). Increased fungal abundance can accelerate the decomposition and transformation of exogenous organic carbon inputs, including plant residues, litter, and root exudates (Tunlid et al. 2022), and simultaneously promote the formation of stable organic-mineral complexes with soil colloids, thereby enhancing soil carbon sequestration potential via multiple pathways.

Although large canopy gaps are associated with more stable carbon pools, reduced litter input and accelerated organic matter mineralization may lead to a decline in total SOC content (Zhang et al. 2024). In contrast, the microenvironment of small canopy gaps closely resembles that of closed-canopy stands (De Frenne et al. 2021). Although MAOC accumulation is relatively high, it is accompanied by rapid inputs of easily decomposable organic carbon fractions, resulting in higher proportions of particulate organic carbon (POC) and elevated total organic carbon (TOC). This increase in TOC may dilute the relative contribution of MAOC, thereby making the carbon pool more sensitive to environmental fluctuations (Liang et al. 2025).

4.2 Effects of Forest Canopy Gaps on SOC Fractions and Their Relative Contributions

POC primarily originates from undecomposed or partially decomposed plant litter and root residues and is formed through biological fragmentation and decomposition processes in soil. In contrast, MAOC is generated through the adsorption of plant-derived soluble organic compounds onto mineral surfaces and the chelation of microbial metabolites, resulting in stable organo-mineral complexes associated with iron and aluminum oxides and clay minerals (Cotrufo et al. 2015; von Lützow et al. 2006). The heterogeneous microenvironment created by canopy gaps leads to pronounced spatial variation in SOC fractions. In the present study, both POC and MAOC concentrations reached their highest values at canopy gap edges and in expanded gap areas across all gap sizes (Fig. 5), and their contributions also varied significantly among locations (Fig. 6).

Previous studies have shown that the microenvironment at canopy gap edges resembles that of closed-canopy stands, supporting higher fungal activity and enhanced fine-root decomposition (Liao et al. 2024). These processes promote the rapid accumulation of active POC while simultaneously facilitating the formation of stable MAOC, thereby shaping the spatial distribution patterns of SOC fractions at the forest-gap scale. In addition, canopy gap edges often exhibit pronounced growth-release effects in residual trees (Zald et al. 2022), which help maintain high fine-root turnover and litter inputs (Saha et al. 2023). The decomposition of these organic materials releases substantial amounts of base cations, buffering soil acidity and maintaining high soil electrical conductivity (Desie et al. 2021). These conditions favor the formation and stabilization of soil microaggregates (Tang et al. 2022), thereby enhancing the accumulation and preservation of both POC and MAOC (Lugato et al. 2021).

The relative contributions of POC fractions varied significantly across canopy gaps of different sizes. Overall, the contribution of free particulate organic carbon (fPOC) increased with increasing gap size but remained the smallest fraction of the SOC pool, whereas the contribution of coarse particulate organic carbon (cPOC) showed the opposite trend (Fig. 6). This pattern is consistent with the distinct formation mechanisms of these fractions. cPOC mainly consists of partially decomposed plant residues, fine-root debris, and litter fragments (Witzgall et al. 2021), whereas fPOC is composed of smaller organic particles generated during microbial fragmentation and early-stage decomposition. Owing to their relatively complex chemical composition and slower turnover rates, fPOC particles are continuously utilized and mineralized by microorganisms, limiting their accumulation in soil (Angst et al. 2021). Consequently, cPOC contributes a substantially larger proportion of total POC than fPOC, and plays a dominant role in POC composition (Elias et al. 2024).

Spatially, both cPOC and fPOC exhibited similar distribution patterns within canopy gaps. Their contribution rates were highest at gap edges and in expanded gap areas and gradually declined toward the gap centers. This pattern is likely attributable to the accumulation of dead branches, leaves, and litter along gap edges and expanding gap zones. These areas generally support moderate vegetation cover and vigorous growth of understory shrubs and herbaceous plants, which increase aboveground litter deposition and belowground root inputs, providing abundant substrates for the formation of cPOC and fPOC (Zhang et al. 2024). In contrast, gap centers experience greater light availability and higher soil temperatures, which stimulate microbial activity and accelerate the decomposition and mineralization of particulate organic carbon (Lyu et al. 2022). Moreover, the relatively sparse vegetation cover in gap centers reduces organic matter inputs, thereby limiting the accumulation of both cPOC and fPOC (Gao et al. 2023), resulting in lower contribution rates of these fractions.

4. 3 Methodological and Experimental Design Limitations

To accurately quantify changes in soil organic carbon (SOC) content across canopy gaps of varying sizes, this study employed a gradient sampling approach combined with cubic spline interpolation and numerical integration to calculate the cumulative change in SOC throughout the entire gap area (i.e., the net area under the curve) (Amirzehni et al. 2023). The cubic spline interpolation method effectively captures the highly nonlinear and spatially heterogeneous characteristics of environmental data. In contrast, the traditional trapezoidal rule assumes linear variation between adjacent points and fails to account for spatial continuity, while global high-order polynomial fitting is susceptible to edge oscillations and overfitting, potentially resulting in substantial distortions of the underlying spatial patterns. In highly heterogeneous environments such as canopy gaps, combining cubic spline interpolation and numerical integration enables more accurate quantification of spatially distributed variables within the gap area (Ehbrecht et al. 2021).

Furthermore, since this study is based on a single sampling event during the growing season, the spatial patterns obtained represent only the transient state following gap formation and cannot distinguish between long-term cumulative effects and the immediate impacts of short-term

environmental fluctuations at the time of sampling (Liu et al. 2018; Mueller et al. 2022). Additionally, the environmental factors selected in this study were limited to conventional indicators—such as canopy closure, soil temperature, pH, and electrical conductivity—and did not include potentially important drivers, such as litter chemical composition and light quality (Cheng et al. 2025), which, to some extent, limits our ability to draw causal inferences regarding the underlying mechanisms (Schmidt et al. 2011). Despite these limitations, the clear spatial differentiation in carbon fractions among forest gaps of different sizes revealed here nevertheless provides testable empirical evidence and a theoretical reference for understanding the response of temperate forest soil carbon pools to disturbance.

5 Conclusions

Small canopy gaps in Natural *Pinus koraiensis* Forests of Northeast China promote the synergistic accumulation of total soil organic carbon (SOC) and stable carbon pools by maintaining a relatively moderate microenvironment, thereby exhibiting considerable carbon sink potential. Among the SOC fractions, mineral-associated organic carbon (MAOC), which represents the most stable component of soil carbon (Georgiou et al. 2022), showed an increasing trend in small canopy gaps. This pattern may result from the moderate microenvironmental disturbance associated with small gaps, which preserves the high litter and fine-root carbon inputs characteristic of closed-canopy stands (Gao et al. 2023), while providing favorable light, temperature, and moisture conditions that promote plant residue turnover and microbial activity (Lyu et al. 2022).

These findings underscore the important role of small canopy gaps and their edge transition zones in maintaining soil carbon stability and enhancing forest carbon sink functions. From a forest management perspective, the creation and maintenance of appropriately sized small canopy gaps should be considered as a near-natural management strategy in both planted and natural forests, with particular attention given to the conservation and utilization of gap-edge habitats. This study provides a theoretical foundation for the sustainable management of temperate forests to maximize soil carbon sequestration. Future research should integrate additional processes, such as soil respiration and litter decomposition, to further elucidate the mechanisms governing carbon cycling within canopy-gap environments.

Declarations

Author contributions

Yu Pan: Investigation, Formal analysis, Data Curation, Writing–Original Draft, Visualization; Wenbiao Duan: Writing–Review & Editing, Supervision, Resources; Xinyi Xiong: Investigation, Formal analysis, Visualization; Liming Chen: Resources, Project Administration; Yafei Wang: Conceptualization, Writing–Review & Editing, Project Administration, Funding Acquisition; Lixin Chen: Project Administration, Writing–Review & Editing; Yanfei Li: Investigation

Funding

This research was funded by the Postdoctoral Project of Heilongjiang Province (LBH-Z24058) and General Program of National Natural Science Foundation of China 31770656 and 31670627

Data availability

The data that support the findings of this study are openly available in Zenado at https://doi.org/10.5281/zenodo.20653447.

Conflict of interest The authors declare no conflicts of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript; or in the decision to publish the results.

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Figures

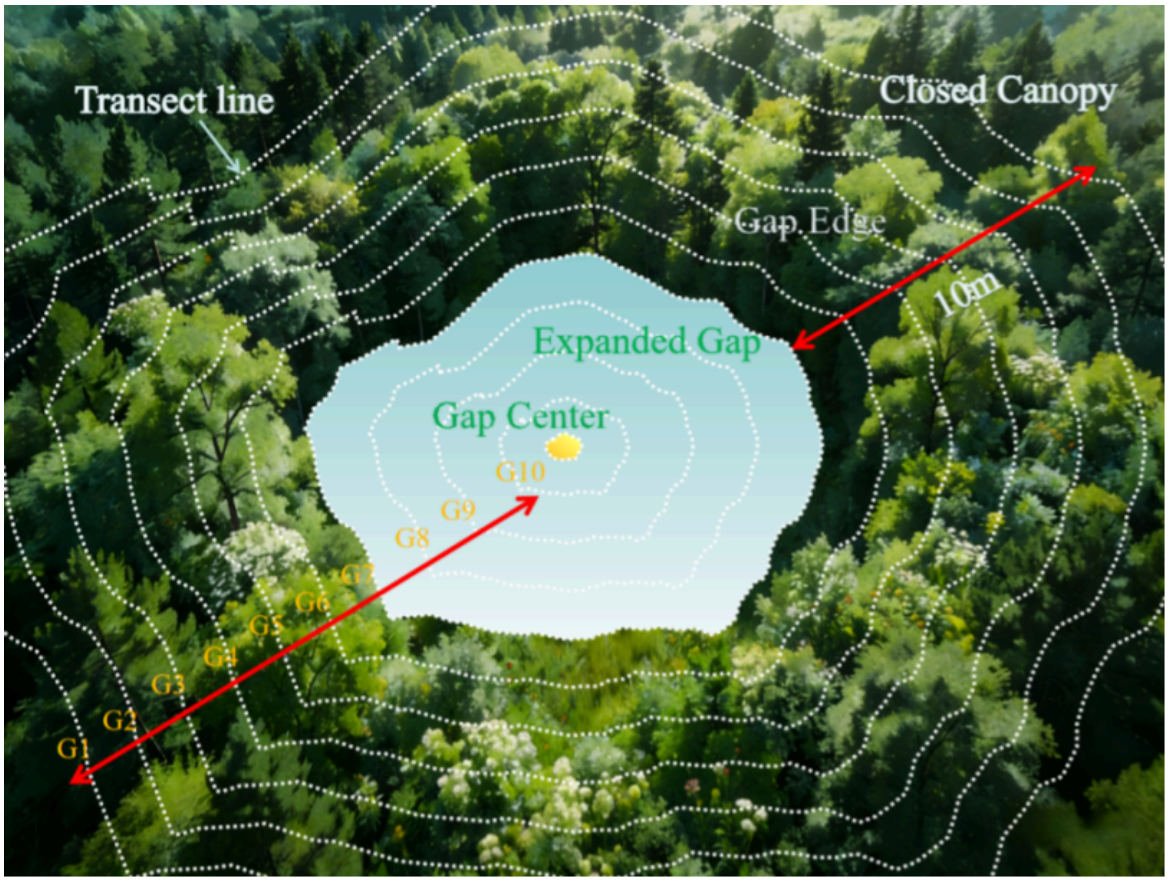


Figure 1

Schematic illustration of forest gap zones and transect layout

Note: The figure illustrates the gradient sampling design within forest gaps, including the gap center, expanded gap, gap edge, and closed canopy zones. The transect line represents the sampling pathalong which ten sampling points (G1–G10) were sequentially established from the closed canopy toward the gap center. The closed canopy area, located more than 10 m from the gap edge, served as the control (CC).

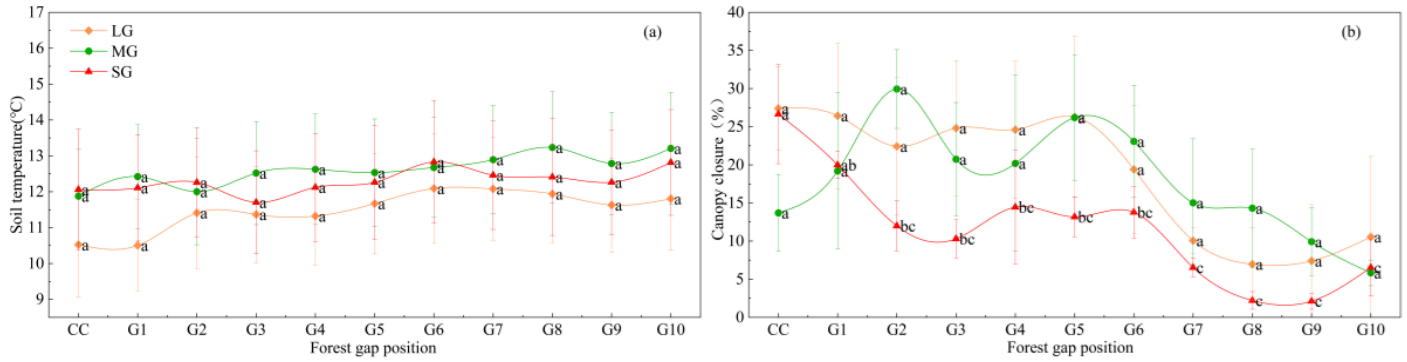


Figure 2

Soil temperature (a) and canopy closure (b) at different positions within forest gaps

Note: CC, closed canopy stand; G1–G10, ten gradient sampling points within the forest gap; BG, large gap; MG, medium gap; SG, small gap.

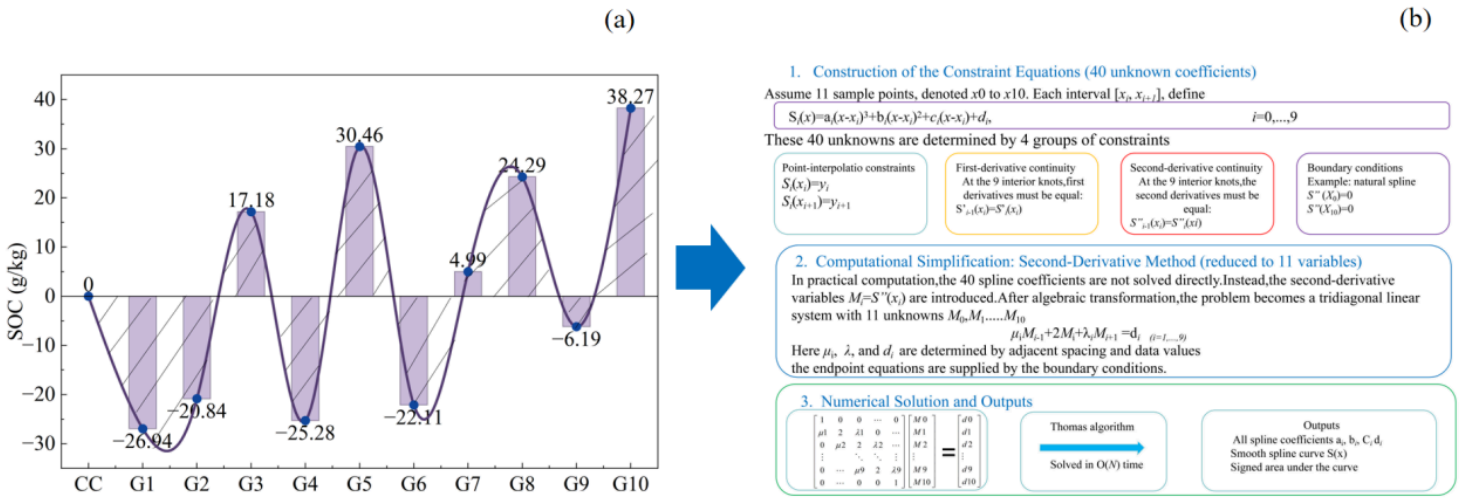


Figure 3

Schematic diagram of cubic spline interpolation

Note: CC, closed canopy stand; G1–G10, ten gradient sampling points within the forest gap.

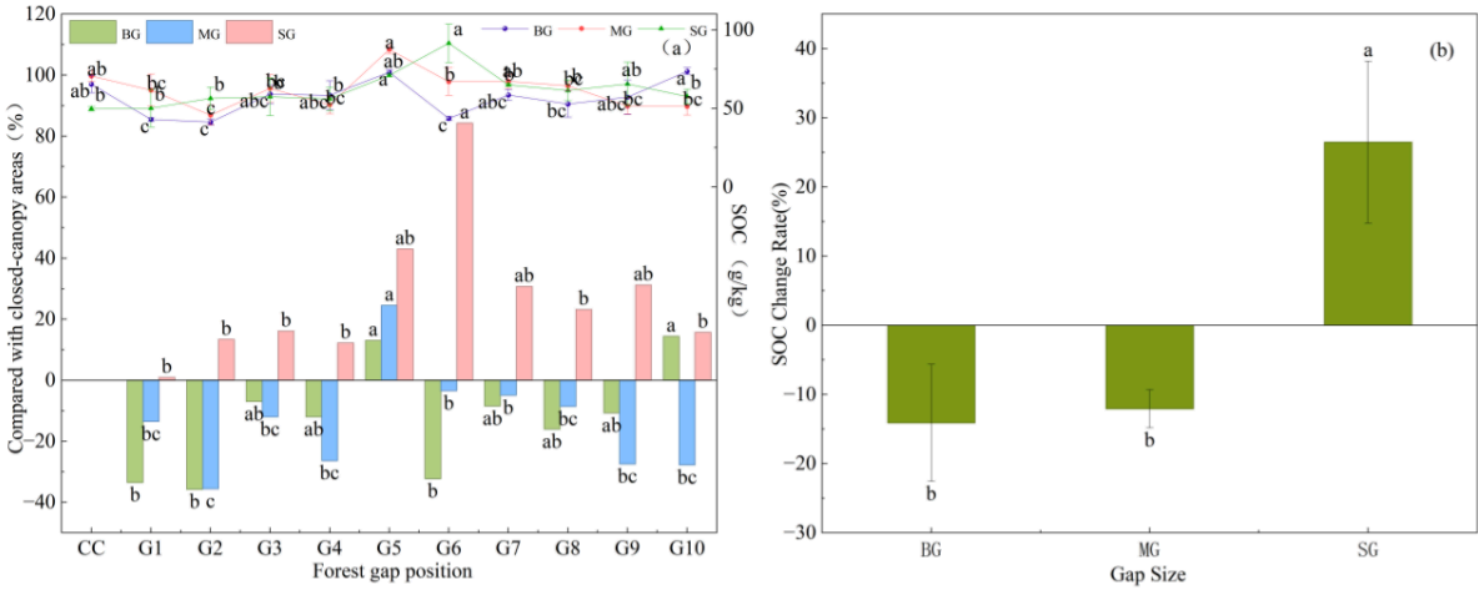


Figure 4

Effects of forest gaps on soil organic carbon content

Note: CC, closed canopy stand; G1–G10, ten gradient sampling points within the forest gap; BG, large gap; MG, medium gap; SG, small gap.

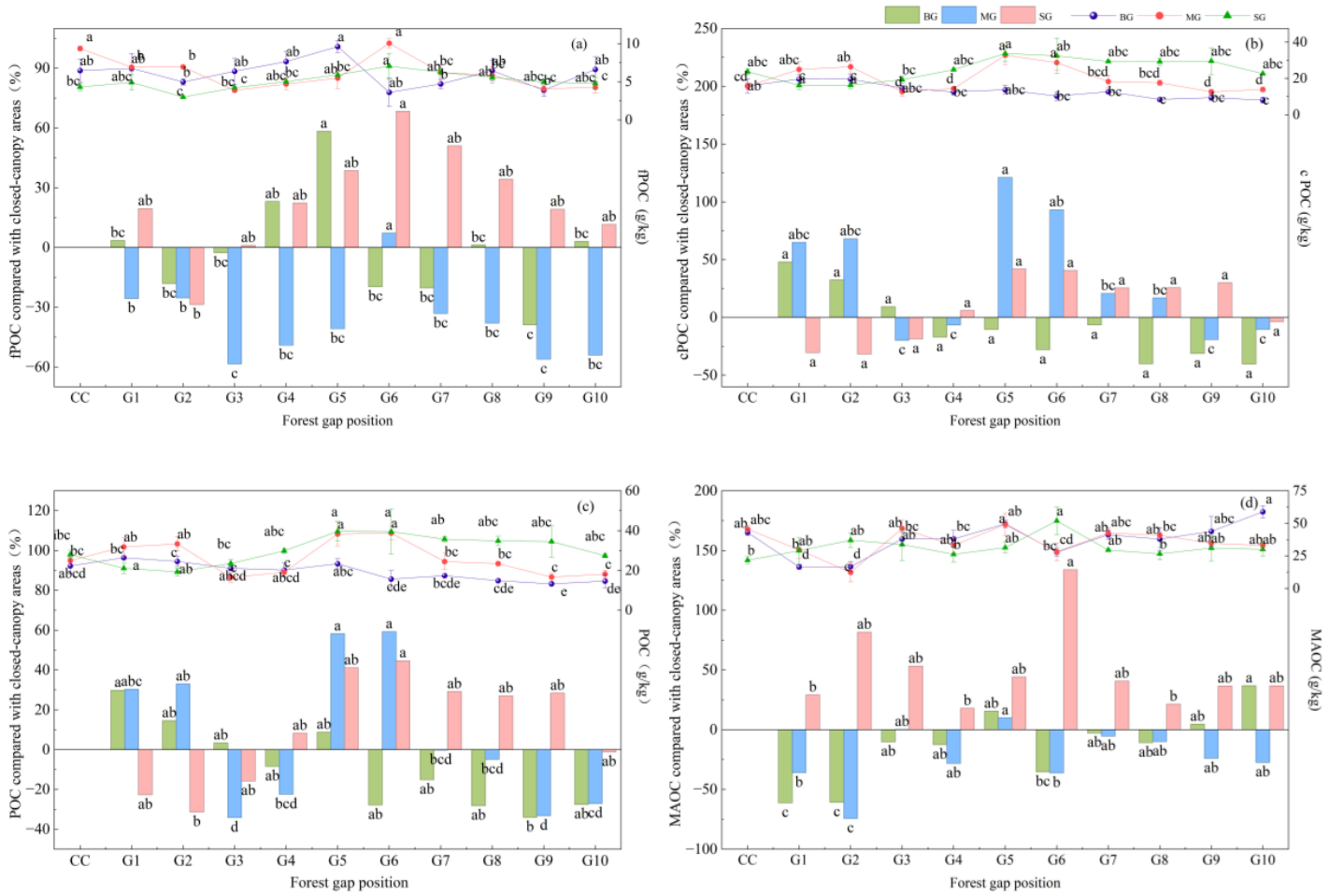


Figure 5

Effects of different positions within forest gaps on soil organic carbon fractions

Note: CC, closed canopy stand; G1–G10, ten gradient sampling points within the forest gap; BG, large gap; MG, medium gap; SG, small gap.

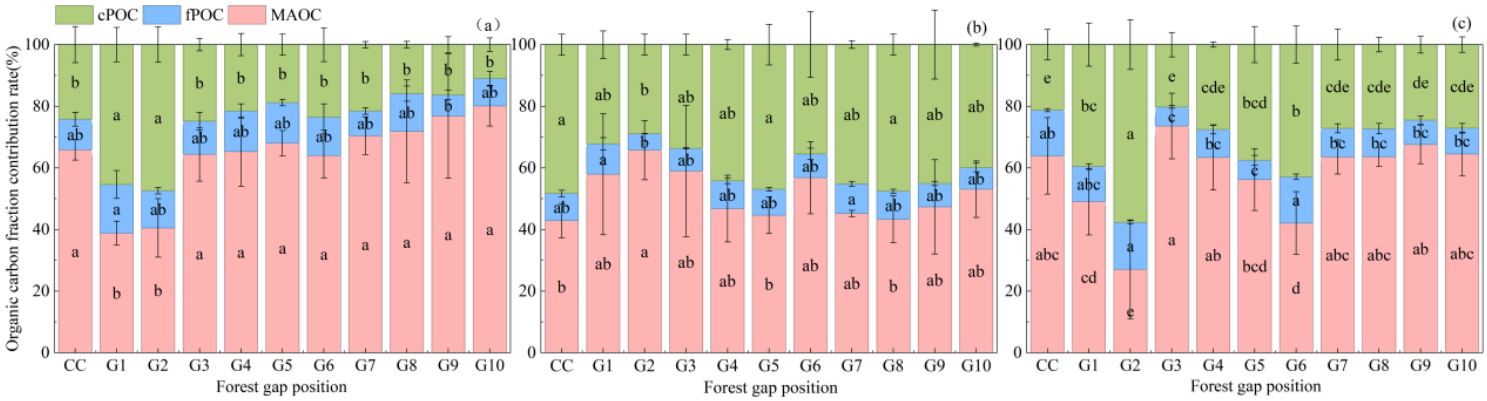


Figure 6

Contribution rates of carbon fractions at different positions within forest gaps

Note: CC, closed canopy stand; G1–G10, ten gradient sampling points within the forest gap; (a) large gap, (b) medium gap, and (c) small gap.

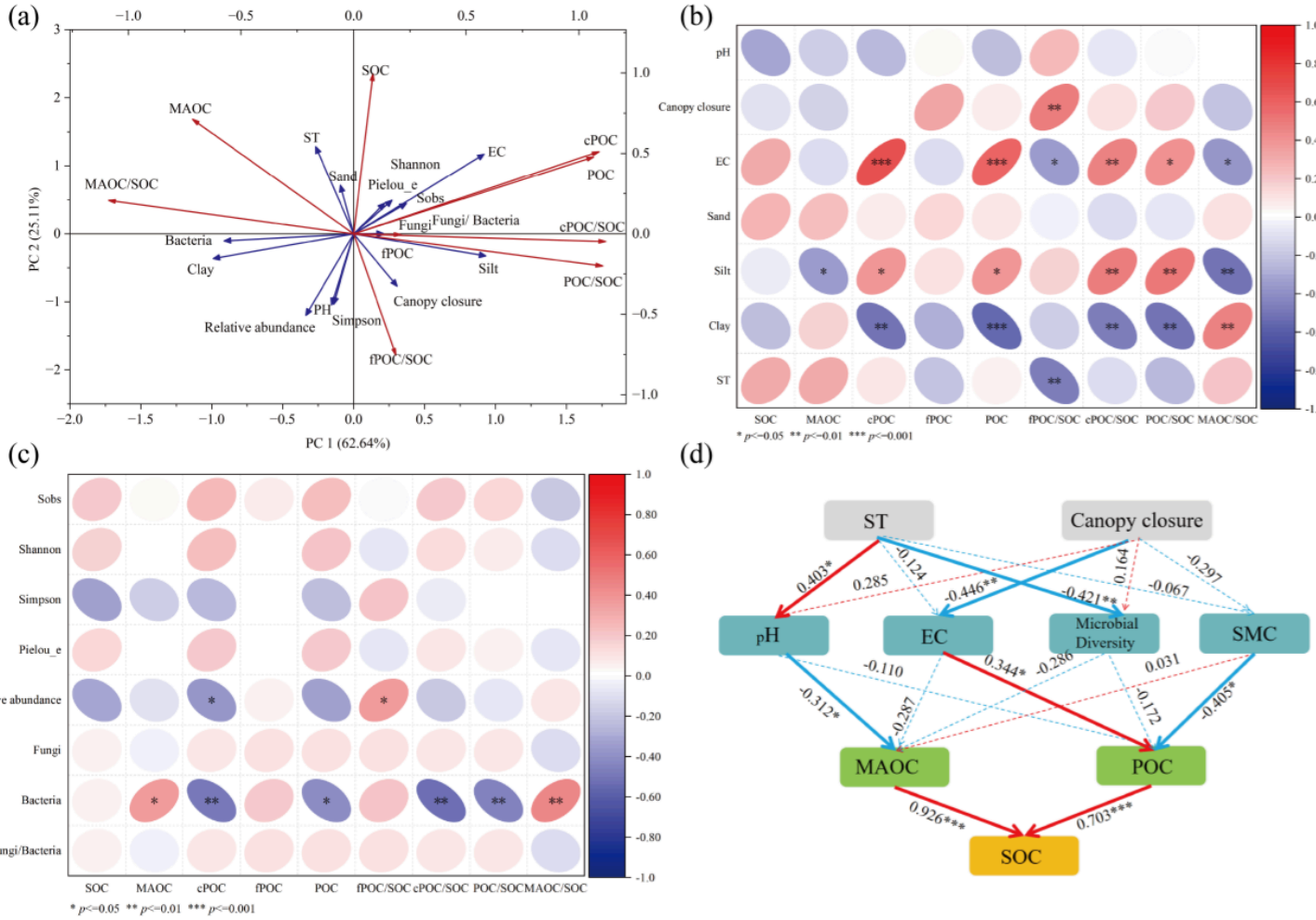


Figure 7

Correlation analysis and structural equation modeling of soil organic carbon and its fractions in relation to environmental factors

Note: fPOC, fine particulate organic carbon; cPOC, coarse particulate organic carbon; POC, particulate organic carbon; MAOC, mineral-associated organic carbon; SOC, soil organic carbon; EC, electrical conductivity; ST, soil temperature; SMC, soil mechanical composition. * and ** indicate significance at the 0.05 and 0.01 levels, respectively.