

Effects of soil properties, stand structure, and species diversity on forest ecosystem carbon stocks in a cold- temperate watershed of northeastern China

Zhongzhou FAN

313671525@qq.com

Harbin Center for Integrated Natural Resources Survey, China Geological Survey

Chuanfang ZHOU

Harbin Center for Integrated Natural Resources Survey, China Geological Survey

Haifeng WEI

Harbin Center for Integrated Natural Resources Survey, China Geological Survey

Shaojie BIAN

School of Forestry, Northeast Forestry University

Qi GUO

Heilongjiang Forestry Research Institute

Yanfeng SUN

Harbin Center for Integrated Natural Resources Survey, China Geological Survey

Xuefeng TANG

Harbin Center for Integrated Natural Resources Survey, China Geological Survey

Xiaoyong WEI

Harbin Center for Integrated Natural Resources Survey, China Geological Survey

Yue MA

Harbin Center for Integrated Natural Resources Survey, China Geological Survey

Mingzhi SHI

Harbin Center for Integrated Natural Resources Survey, China Geological Survey

Feng JIANG

Harbin Center for Integrated Natural Resources Survey, China Geological Survey

Yuanyuan YAN

Harbin Research Institute of Forestry Machinery, State Forestry and Grassland Administration

Keywords: cold-temperate forest, carbon stock, soil carbon, stand structure, watershed

Posted Date: October 5th, 2026

DOI: <https://doi.org/10.21203/rs.3.rs-11014117/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License.

[Read Full License](#)

Additional Declarations: No competing interests reported.

Effects of soil properties, stand structure, and species diversity on forest ecosystem carbon stocks in a cold-temperate watershed of northeastern China

Zhongzhou FAN^{1,2}, Chuanfang ZHOU^{1,2,3*}, Haifeng WEI^{1,2*}, Shaojie BIAN⁴, Qi GUO⁵, Yanfeng SUN^{1,2}, Xuefeng TANG^{1,2}, Xiaoyong WEI^{1,2}, Yue MA^{1,2}, Mingzhi SHI^{1,2}, Feng JIANG^{1,2}, Yuanyuan YAN⁶

FAN Zhongzhou: 313671525@qq.com ([ORCID: 0009-0003-3459-5591](https://orcid.org/0009-0003-3459-5591))

*Correspondence:ZHOU Chuanfang: cfzhou1985@163.com;WEI Haifeng: weihafeng@mail.cgs.gov.cn

1. Harbin Center for Integrated Natural Resources Survey, China Geological Survey, Harbin 150086, Heilongjiang, China;

2. Observation and Research Station of Earth Critical Zone in Black Soil, Harbin, Ministry of Natural Resources, Harbin 150086, Heilongjiang, China;

3. School of Earth Sciences and Resources, China University of Geosciences, Beijing 100083, China;

4. School of Forestry, Northeast Forestry University, Harbin 150040, Heilongjiang, China;

5. Heilongjiang Forestry Research Institute, Harbin 150081, Heilongjiang, China;

6. Harbin Research Institute of Forestry Machinery, State Forestry and Grassland Administration, Harbin 150086, Heilongjiang, China

Abstract

Cold-temperate forests store large amounts of carbon, but the distribution of carbon among vegetation, litter, and soil pools remains poorly quantified at watershed scales. We assessed forest ecosystem carbon stocks in the Ergong River Basin of the Xiaoxing'an Mountains, northeastern China, using field measurements and forest inventory data. Carbon stocks were estimated for tree, shrub, herb, litter, and soil layers across four dominant forest types. Mantel tests, principal component analysis, and piecewise structural equation model-ing were used to identify the soil, stand, and diversity factors associated with carbon storage. Soil was the dominant carbon pool, accounting for 61.57-77.68% of total ecosystem carbon stocks, whereas tree biomass contributed 88.15% of vegetation carbon. Total ecosystem carbon stocks were highest in mixed conifer-broadleaf forest (231.42 Mg ha⁻¹), followed by larch forest (227.06 Mg ha⁻¹), birch forest (204.24 Mg ha⁻¹), and mixed broadleaf forest (187.54 Mg ha⁻¹). High total carbon stocks were concentrated mainly in low-elevation riparian zones, whereas high vegetation carbon densities occurred more often at higher elevations with weaker disturbance. Soil total carbon, nitrogen, organic carbon, phosphorus, and MnO were strongly associated with ecosystem carbon stocks. Mean diameter at breast height was the main correlate of vegetation carbon. The structural equation model indicated that soil total carbon had the strongest direct association with ecosystem carbon stocks, with additional associations linked to stand structure and species dominance. These findings indicate that carbon accumulation in cold-temperate watershed forests is closely associated with soil nutrient status and stand structural attributes. The results provide field-based evidence for forest carbon assessment and management in northeastern China.

Keywords: cold-temperate forest; carbon stock; soil carbon; stand structure; watershed

1. Introduction

Forest ecosystems are major terrestrial carbon reservoirs and therefore play a central role in regional carbon balance and climate-change mitigation (Pan et al. 2011; Wu et al. 2024). Forest carbon is distributed among vegetation, litter, and soil pools, but these pools respond differently to climate, topography, soil properties, and stand development (Jobbagy and Jackson 2000; Lal 2005; Wang et al. 2018). Soil organic carbon is often the largest and most persistent pool, whereas vegetation carbon is more directly linked to stand structure and biomass accumulation. Quantifying the partitioning of carbon among these components is essential for improving regional carbon accounting and forest management.

In China, ecological restoration, land-quality surveys, and natural forest conservation have increased attention to forest carbon sinks and their spatial drivers (Li et al. 2019; Wang et al. 2024; Xie et al. 2024; Yang et al. 2026). The Xiaoxing'an Mountains form an important cold-temperate forest region in northeastern China and contain extensive mixed conifer-broadleaf forests (Guan et al. 1997; Hu et al. 2015). Compared with warmer forest regions, these forests are characterised by slower litter decomposition, strong surface-soil carbon accumulation, and marked spatial heterogeneity in terrain and disturbance. These features make the region important for understanding how cold-temperate forests store carbon.

Previous work in the Xiaoxing'an Mountains has improved knowledge of individual carbon pools, including understory vegetation, litter, and soil carbon (Cai 2017; Fang et al. 2007; Hu et al. 2025; Lyu and Jia 2025; Zhang et al. 2017). However, fewer studies have integrated vegetation, litter, and soil pools within a watershed framework. This limitation is important because watershed processes connect vegetation, soil, hydrology, and topography, and can create spatial patterns that are not visible from single-pool assessments. The relative contributions of soil nutrients, stand structure, and biodiversity to total ecosystem carbon storage therefore remain insufficiently resolved.

Here, we used the Ergong River Basin in the Xiaoxing'an Mountains as a representative cold-temperate watershed to quantify forest ecosystem carbon stocks and their associated factors. Specifically, we aimed to: (1) estimate carbon stocks in vegetation, litter, and soil pools across dominant forest types; (2) characterise the spatial distribution of carbon stocks within the watershed; and (3) identify the major soil, stand, and biodiversity factors associated with carbon accumulation using Mantel analysis and piecewise structural equation modelling. By linking whole-ecosystem carbon

allocation with environmental and biotic correlates, this study provides evidence for forest carbon assessment and management in northeastern China.

2. Study region and data preprocessing

2.1. Study area

The study was conducted in the Ergong River Basin, Heihe City, in the northern Xiaoxing'an Mountains of northeastern China. The basin drains into the Heilongjiang (Amur) River and includes hilly upper reaches, valley zones, and alluvial plains. Forest vegetation is dominated by *Quercus* forests, birch forests, larch forests, mixed broadleaf forests, and mixed conifer-broadleaf forests, whereas cropland is distributed mainly along the middle and lower reaches. The region has a temperate continental monsoon climate, with a mean annual temperature of approximately 0–2 °C and mean annual precipitation of 450–500 mm. The terrain is typical of low mountain and hill landscapes, and the dominant soil type is dark brown forest soil.

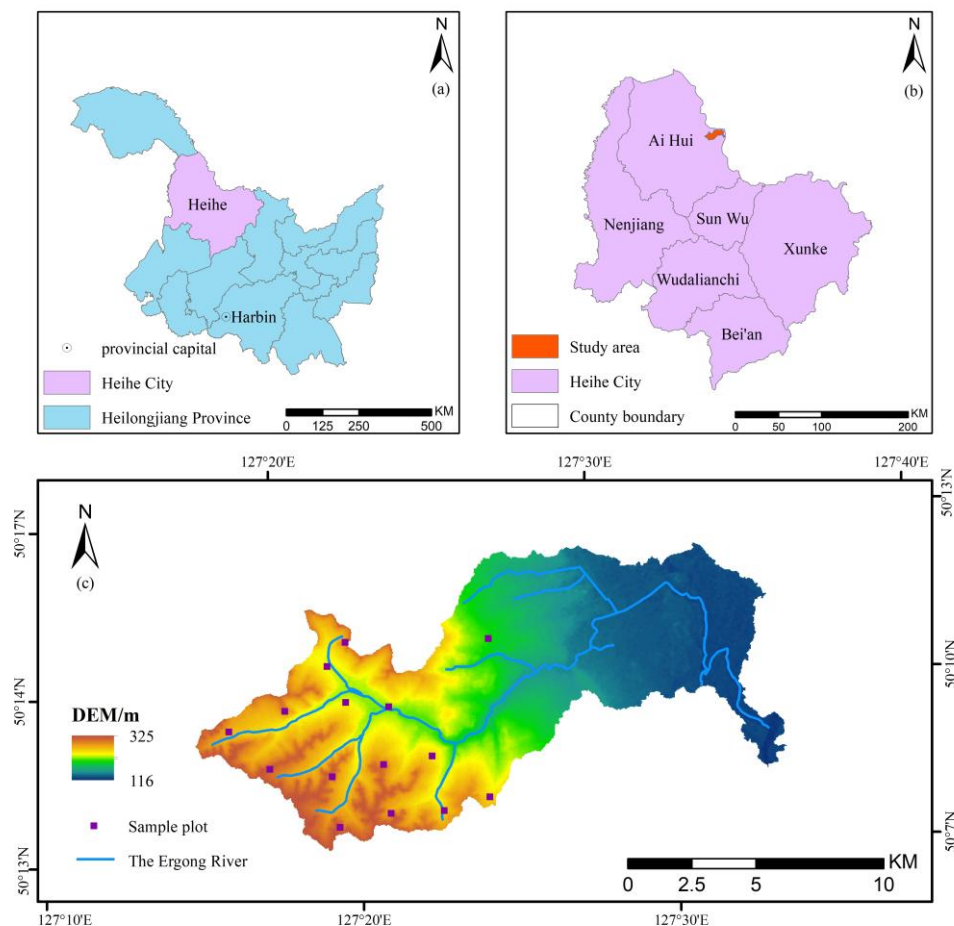


Figure 1. Schematic diagram of the study area

2.2. Data sources and field sampling

Field surveys were conducted in 2023 in forested areas of the Ergong River Basin. Based on the Third National Land Survey dataset, 15 plots were established using a systematic 2 km x 2 km grid. Each plot was a 0.06 ha rhombus-shaped tree plot. All trees with diameter at breast height (DBH) ≥ 5 cm were measured for DBH, height, and growth status. Plot centres were positioned using real-time kinematic surveying under the China Geodetic Coordinate System 2000, with positional accuracy within 1 m. Soil samples were collected at the plot centre from the A horizon and from 30 cm depth. Understory vegetation was surveyed using five 2 m x 2 m shrub subplots and five 1 m x 1 m herb subplots at the four corners and centre of each tree plot. In total, 75 shrub subplots and 75 herb subplots were surveyed for species composition, abundance, basal diameter, height, and coverage. Herbaceous biomass was harvested, oven-dried at 65 °C to constant mass, and weighed to 0.01 g. Soil bulk density was measured using the core method. Soil samples were air-dried, ground, and sieved before analysis. Of 54 geochemical indicators, 13 variables were used in this study: organic carbon (Corg), total carbon (TC), total nitrogen (N), total phosphorus (P), potassium (K), Al_2O_3 , CaO , Fe_2O_3 , FeO , MgO , MnO , SiO_2 , and TiO_2 .

2.3. Forest type classification

Forest types were classified from the Third National Land Survey dataset and verified during the 2023 field survey. Four dominant forest types were identified: birch forest, larch forest, mixed broadleaf forest, and mixed conifer-broadleaf forest. Birch forests were dominated by *Betula platyphylla*, and larch forests mainly consisted of *Larix spp.* plantations. Mixed broadleaf forests included *Betula platyphylla*, *Betula dahurica*, *Quercus mongolica*, *Populus davidiana*, *Tilia amurensis*, and *Acer mono*. Mixed conifer-broadleaf forests were dominated by *Larix gmelinii*, *Quercus mongolica*, and *Betula platyphylla*.

2.4 Carbon stock estimation

2.4.1 Vegetation and litter carbon density

Forest vegetation was divided into tree, shrub, and herb layers. Carbon density (Mg ha^{-1}) was calculated from biomass per unit area and the corresponding carbon conversion coefficient. Tree carbon fractions followed the species-specific values in Table 1, and a coefficient of 0.4412 was used for shrub and herb layers. Tree biomass was estimated

using species-specific allometric equations developed for forest stands in Heilongjiang Province (Jia 2014). Individual-
tree biomass was summed to obtain plot-level tree biomass. The general form of the allometric model is as follows:

$$W_s = c_0 D^{b_0} / (1 + r_2 D^{k_2} + r_3 D^{k_3} + r_4 D^{k_4}) \quad (1)$$

$$W_b = c_0 r_2 D^{k_2+b_0} / (1 + r_2 D^{k_2} + r_3 D^{k_3} + r_4 D^{k_4}) \quad (2)$$

$$W_l = c_0 r_3 D^{k_3+b_0} / (1 + r_2 D^{k_2} + r_3 D^{k_3} + r_4 D^{k_4}) \quad (3)$$

$$W_r = c_0 r_4 D^{k_4+b_0} / (1 + r_2 D^{k_2} + r_3 D^{k_3} + r_4 D^{k_4}) \quad (4)$$

$$W_{tree} = W_s + W_b + W_l + W_r \quad (5)$$

where W_s 、 W_b 、 W_l 、 W_r 、 and W_{tree} represent the biomass of stem, branch, leaf, root , and tree (kg), respectively; D
is the diameter at breast height (cm); and c_0 、 b_0 、 r_2 、 k_2 、 r_3 、 k_3 、 r_4 and k_4 are species-specific model parameters,
as listed in Table 1 .

Table 1. Parameter estimates of biomass models for different tree species

Tree species (group)	Parameter								Carbon content
	c_0	b_0	r_2	k_2	r_3	k_3	r_4	k_4	
<i>Tilia amurensis</i>	0.3025	2.1117	0.0027	1.1750	0.6256	-0.9893	1.1161	-0.4433	0.4412
<i>Quercus mongolica</i>	0.1893	2.3520	0.0094	1.1166	0.0047	0.7604	0.2471	0.1265	0.4673
<i>Acer mono</i>	0.3987	2.1092	2.2662	-0.6941	1.2319	-1.0653	0.1739	0.2938	0.4412
<i>Populus davidiana</i>	0.0762	2.5669	0.0000	3.7653	0.0320	-0.0255	0.0339	0.5498	0.4538
<i>Betula dahurica</i>	0.0427	2.7692	0.0034	1.4152	0.0028	0.9926	0.3631	-0.0561	0.4594
<i>Betula platyphylla</i>	0.3124	2.1983	0.0140	0.9187	0.0699	-0.1336	0.0315	0.7762	0.4594
<i>Larix gmelinii</i>	0.2693	2.1905	0.0011	1.4213	0.0314	0.0086	0.1904	0.2223	0.5095
<i>Larix spp.</i>	0.1988	2.3010	0.1212	-0.0206	0.5378	-0.8716	0.4009	-0.0326	0.5095

Shrub biomass was estimated using an allometric model developed for shrubs in the Xiaoxing'an Mountains (Fan
et al. 2011). Mean shrub height in each subplot was used as the model input. Estimated biomass was multiplied by
shrub coverage to obtain plot-level shrub biomass. Shrub carbon density was then calculated by dividing biomass by
plot area and multiplying by the carbon conversion coefficient.

$$W_{shrub} = 0.0151 \times h + 1.2618 \quad (6)$$

In the model, W_{shrub} represents the biomass of the shrub layer, h represents the mean shrub height (m).

For the herb layer, aboveground biomass harvested from each subplot was converted to biomass per unit area.
Mean subplot biomass was used to represent herb-layer biomass at the plot scale, and carbon density was calculated
using the corresponding carbon conversion coefficient.

Litter carbon density was estimated using forest-type litter coefficients from the Guidelines for Carbon Accounting in Forest Ecosystems (LY/T 2988-2018) and regional litter biomass evidence from the Xiaoxing'an Mountains (Zhang et al. 2015) (Table 2). DF denotes the ratio of litter biomass to aboveground biomass (%).

$$W_{litter} = (W_{tree} + W_{shrub} + W_{herb}) \times DF_{litter} \quad (7)$$

Where DF_{litter} represents the proportion of litter biomass to aboveground biomass (%).

Table 2. Proportion of litter biomass to aboveground biomass across different forest types

Forest type	Estimated value (%)	Sample size (n)	Standard deviation	95% confidence interval	
				Lower	Upper
Birch forest	22.976	15	0.363	0.624	45.328
Mixed broadleaf forest	11.414	31	14.111	6.238	16.590
Larch forest	26.997	22	24.610	16.085	37.909
mixed conifer–broad- leaf forest	12.077	6	7.275	4.442	19.711

2.4.2 Soil carbon density

Soil organic carbon (SOC) content was determined using potassium dichromate oxidation with external heating, and soil bulk density was measured using the core method (Zi et al. 2016). The volume fraction of coarse fragments (> 2 mm) was determined by sieving. Soil carbon density was estimated from SOC content, bulk density, soil depth, and gravel fraction for each soil layer (You et al. 2018).

$$SOC = \sum_i^k SOC = \sum_i^k C_i \times D_i \times E_i \times \frac{(1 - G_i)}{10} \quad (8)$$

where SOC is the soil organic carbon density ($Mg\ ha^{-1}$), k is the number of soil layers, C_i is the soil organic carbon content of the i -th layer ($g\ kg^{-1}$), D_i is the soil bulk density of the i -th layer ($g\ cm^{-3}$), E_i is the thickness of the soil layer, and G_i is the volumetric proportion of gravel with a diameter $\geq 2\ mm$ (%).

2.5 Species diversity indices

Three diversity indices were calculated from the field survey data to characterise community composition: the Shannon-Wiener diversity index (H), Pielou's evenness index (J), and Simpson's dominance index (D) (Su et al. 2017).

$$D = \ln \left[\sum_{i=1}^S \left(\frac{N_i}{N} \right)^2 \right] \quad (9)$$

$$H = - \sum_{i=1}^S (P_i \ln P_i) \quad (10)$$

$$J = H / \ln S \quad (11) \quad 138$$

where N_i is the number of individuals of the i -th species, N is the total number of individuals, S is the total number of species, and P_i represents the proportion of individuals of the i -th species relative to the total number of individuals. 139 140

2.6 Statistical analysis 141

Principal component analysis (PCA) was conducted in Origin 2024 to visualise multi-variate relationships among carbon stocks, soil properties, and community characteristics. Variables were centred and standardised before PCA, and the analysis was based on the correlation matrix. Other statistical analyses were performed in R version 4.3.3. Mantel tests were conducted using the linkET package with 9999 permutations to evaluate relationships among environmental variables, community characteristics, and carbon pools. Piecewise structural equation modelling (SEM) was implemented using the piecewiseSEM package to assess direct and indirect associations among soil properties, stand structure, biodiversity, and ecosystem carbon storage. Because the plot-level sample size was limited ($n = 15$), PCA, Mantel tests, and SEM were used as exploratory tools to identify coherent association patterns rather than to make broad causal inference. Candidate SEM variables were selected from ecologically interpretable factors supported by correlation and Mantel analyses, and the number of paths was kept low relative to the sample size. Linear mixed-effects models were first constructed and then incorporated into the piecewise SEM framework. Model fit was evaluated using Fisher's C statistic and Shipley's d-separation test. The final model showed good fit to the observed data (Fisher's $C = 12.57$, $df = 18$, $P = 0.817$), but the path coefficients should be interpreted as plot-scale associations that require validation with larger and re-peated plot networks. 142 143 144 145 146 147 148 149 150 151 152 153 154 155

3. Results 156

3.1 Carbon stocks among forest ecosystem components 157

Total ecosystem carbon stocks differed among the four forest types. The order was mixed conifer-broadleaf forest (231.42 Mg ha⁻¹) > larch forest (227.06 Mg ha⁻¹) > birch forest (204.24 Mg ha⁻¹) > mixed broadleaf forest (187.54 Mg ha⁻¹) (Table 3; Fig. 2). Soil was the largest carbon pool in all forest types, accounting for 77.68% of total carbon in mixed conifer-broadleaf forest, 71.70% in mixed broadleaf forest, 68.98% in birch forest, and 61.57% in larch forest. Vegetation was the second largest pool, contributing 20.81%, 24.80%, 22.10%, and 30.84% in mixed conifer-broadleaf, mixed broadleaf, birch, and larch forests, respectively. Litter accounted for 1.51-8.92% of ecosystem carbon stocks. 158 159 160 161 162 163

Table 3. Carbon contents of the vegetation layer, litter layer, and soil layer

Mg ha⁻¹

Layer	Birch forest	Mixed broadleaf forest	Larch forest	Mixed conifer–broadleaf forest
Tree layer	42.59±9.28	36.73±5.93	63.09±18.9	42.56±10.21
Shrub layer	1.71±0.59	9.4±8.37	6.22±5.92	5.09±2.78
Herb layer	0.84±0.47	0.38±0.45	0.72±0.93	0.51±0.19
Litter layer	18.22±3.32	6.56±0.99	17.23±5.41	3.5±0.6
Soil A horizon	117.55±7.25	89.17±38.38	116.75±35.22	130.06±48.21
Soil B horizon	23.33±2.11	45.3±39.59	23.05±10.62	49.7±41.86

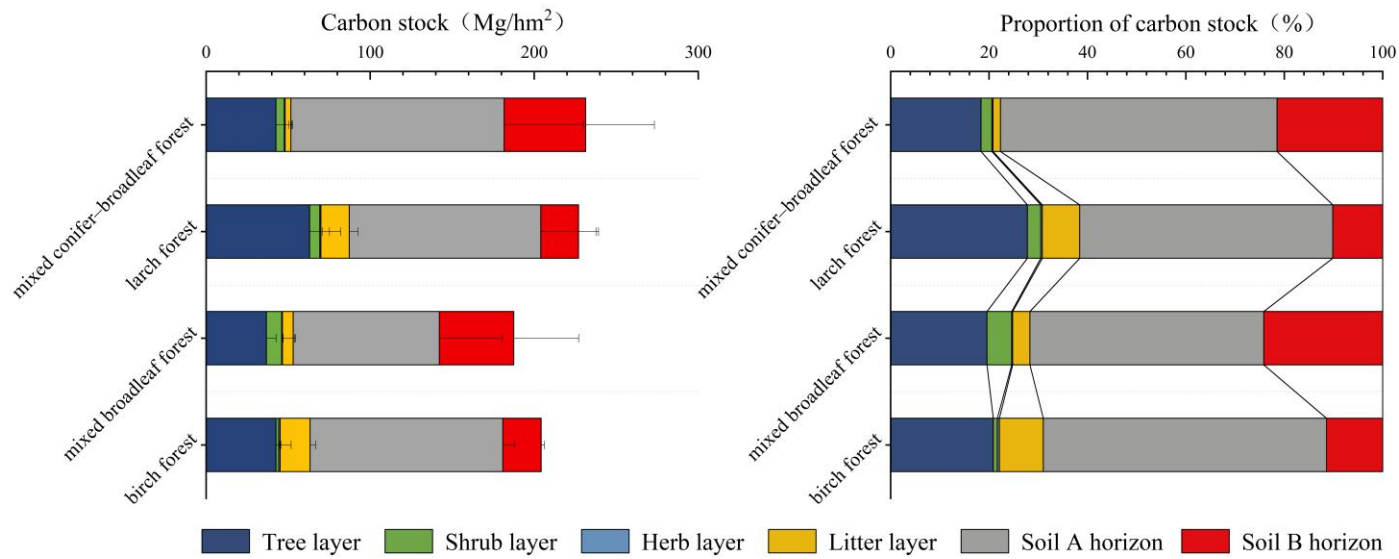


Figure 2. Carbon storage of different forest ecosystems and the proportion of carbon storage in each layer

Within the vegetation pool, tree biomass contributed most of the vegetation carbon stock (88.15%; mean, 46.24 Mg ha⁻¹). Shrub and herb layers contributed 10.68% (5.61 Mg ha⁻¹) and 1.17% (0.61 Mg ha⁻¹), respectively (Fig. 3). Soil carbon stocks decreased with increasing soil depth. The A horizon accounted for 72.35% of soil carbon in mixed conifer-broadleaf forest, 83.51% in larch forest, 66.31% in mixed broadleaf forest, and 83.44% in birch forest.

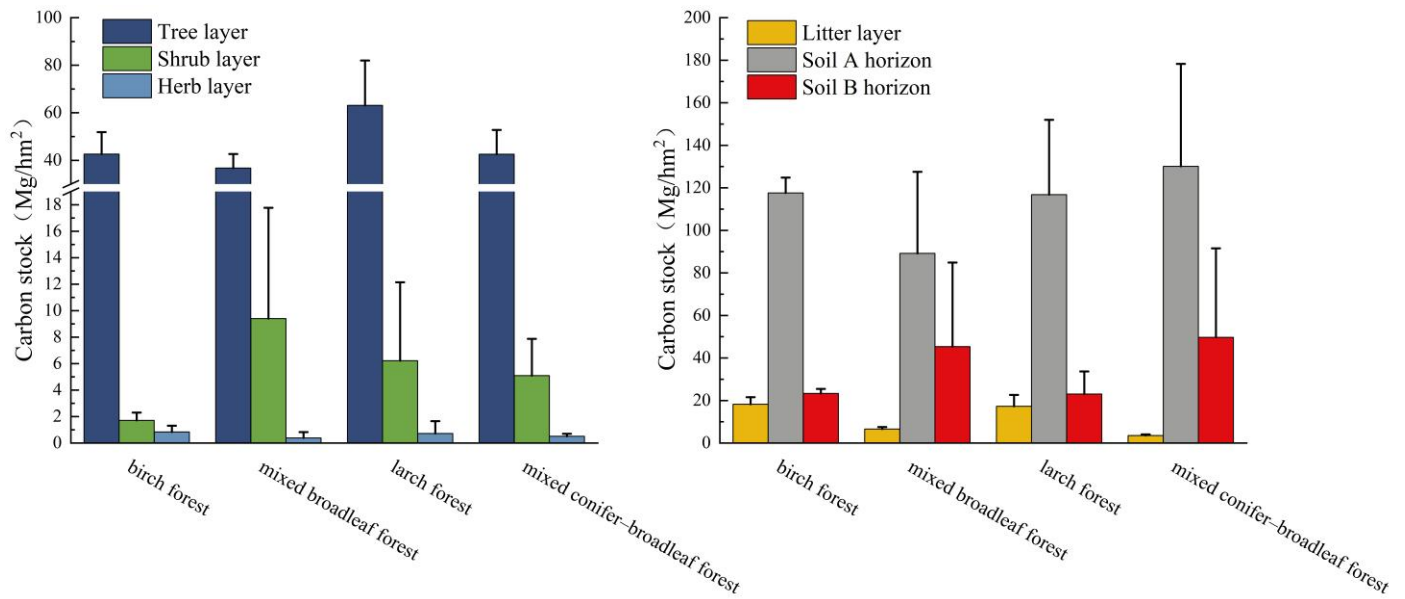


Figure 3. Carbon storage characteristics of different layers in different forest ecosystems

3.2 Spatial patterns of carbon stocks

Forest ecosystem carbon stocks showed clear spatial heterogeneity across the Ergong River Basin (Fig. 4). Areas with high ecosystem carbon stocks ($> 200 \text{ Mg ha}^{-1}$) were concentrated mainly in the western part of the study area and near low-elevation riparian zones. Medium-high carbon stocks ($180\text{--}200 \text{ Mg ha}^{-1}$) occurred across different elevation gradients, whereas low carbon stocks ($< 180 \text{ Mg ha}^{-1}$) were mainly distributed in the central part of the basin. Tree-layer carbon stocks were generally higher in high-elevation areas, while soil carbon stocks were concentrated mainly in low-elevation riparian zones. No clear spatial pattern was observed for shrub, herb, or litter carbon stocks.

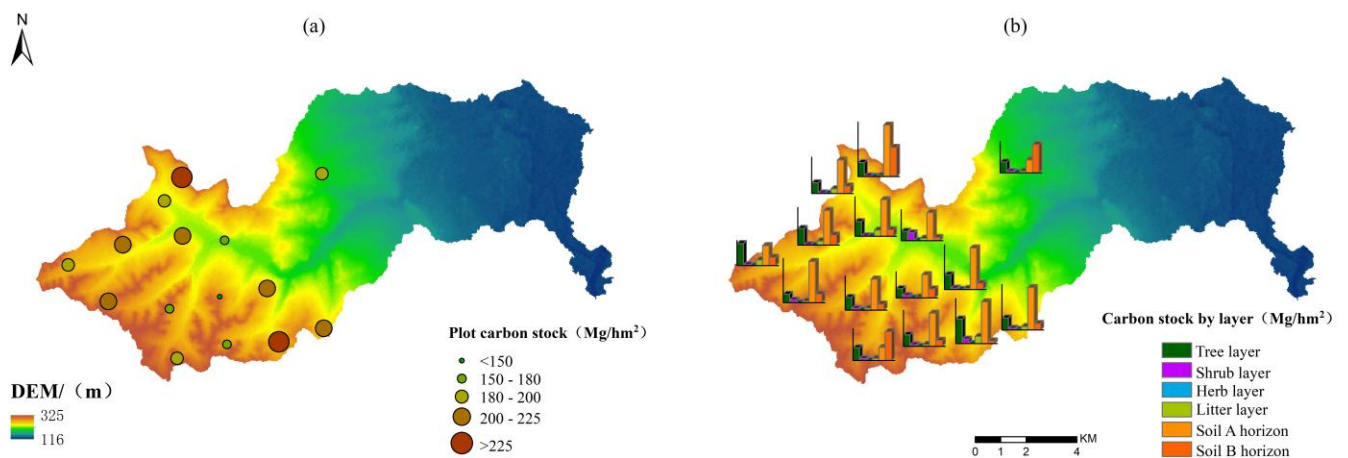


Figure 4. Spatial distribution of forest ecosystem carbon storage in the Ergong River Basin

3.3 Relationships between carbon stocks and environmental factors

Mantel tests showed that ecosystem total carbon stock (ETCS) was strongly associated with soil N, Corg, TC, P, and MnO (Fig. 5). Soil total carbon stock (STCS) was associated with the same soil variables and with Simpson's dominance index (D). Vegetation total carbon stock (VTCS) showed a significant relationship only with mean DBH. ETCS was positively related to N, Corg, and TC ($P < 0.01$) and to P and MnO ($P < 0.05$). STCS was positively related to N, Corg, and TC ($P < 0.01$) and to P, MnO, and D ($P < 0.05$). VTCS was positively related to DBH ($P < 0.01$). Variables significantly related to carbon stocks generally had Mantel correlation coefficients ≥ 0.4 .

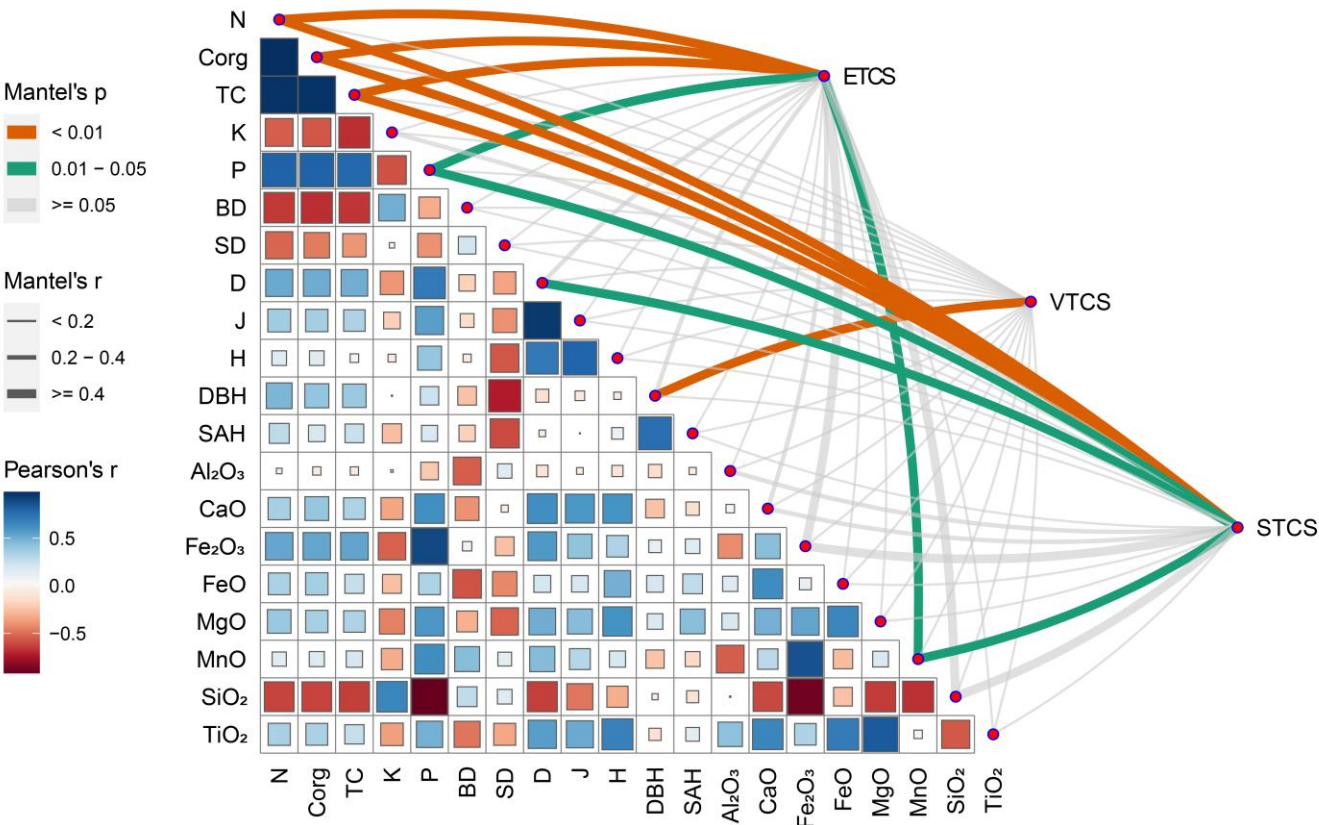


Figure 5. Mantel analysis of relationships between forest ecosystem carbon storage and environmental factors

Note: ETCS. ecosystem total carbon stock; VTCS. vegetable total carbon stock; STCS. soil total carbon stock; BD. bulk density; SD. stand density; DBH. diameter at breast height; SAH. stand average height.

PCA was used to further examine relationships between soil nutrient status, community characteristics, and ecosystem carbon storage (Fig. 6). PC1 and PC2 explained 48.6% and 20.0% of the total variance, respectively. Corg, N, P, and TC loaded mainly along PC1, indicating that soil nutrient status was a major gradient associated with carbon-stock variation.

The PCA ordination separated several plots by forest type and site conditions. Closely grouped plots had similar soil properties and stand characteristics, whereas separated plots indicated stronger environmental heterogeneity. Overall, variation in ecosystem carbon stocks was associated with both soil nutrient status and community structure.

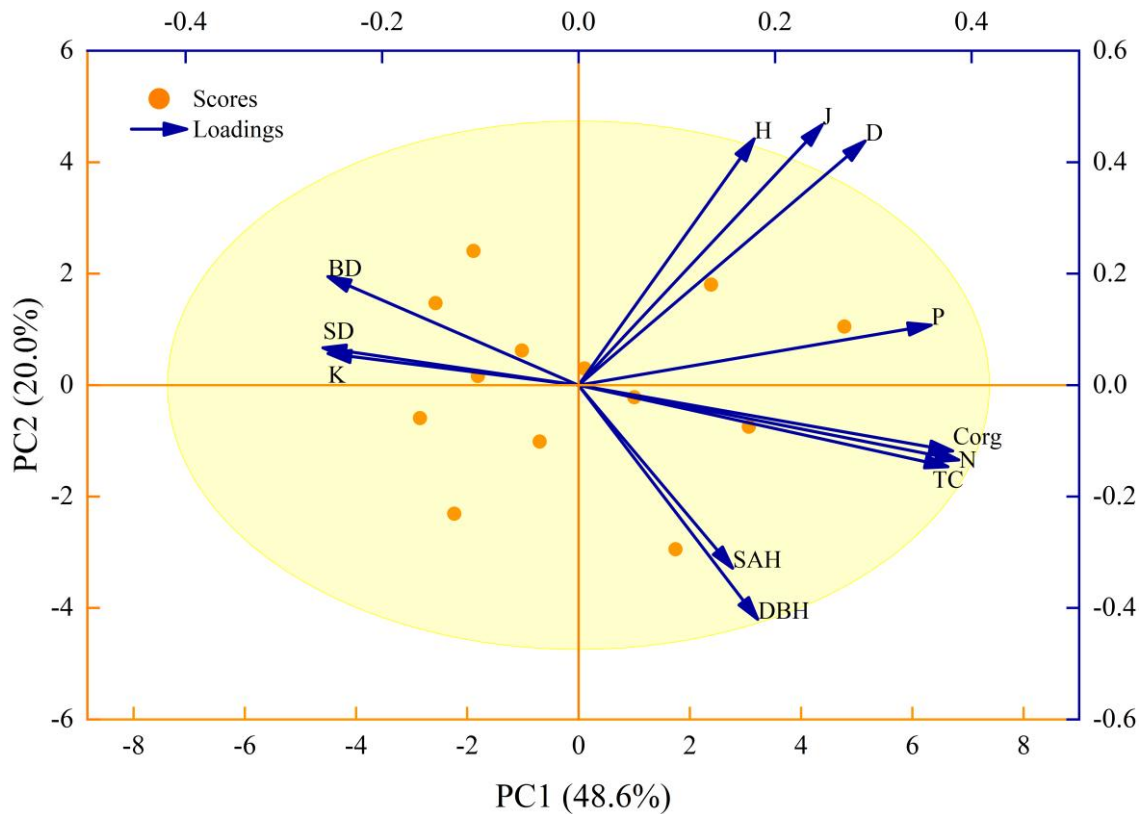


Figure 6. Principal component analysis of forest ecosystem carbon storage in relation to soil nutrient levels and community characteristics

Note: PC1, the first principal component; PC2, the second principal component.

3.4 Direct and indirect drivers of ecosystem carbon stocks

Piecewise SEM was used to assess direct and indirect associations between environmental variables and ETCS (Fig. 7), following its increasing use for evaluating linked stand, soil, and carbon-sink factors in forest studies (Mei et al. 2024). The model was simplified by removing non-significant paths and showed good fit (Fisher's $C = 12.566$, $df = 18$, $P = 0.817$). The coefficients of determination indicated strong explanatory power for ETCS and soil TC ($R^2 = 0.95$), with lower explanatory power for D ($R^2 = 0.27$) and DBH ($R^2 = 0.40$).

Soil TC had the strongest positive direct effect on ETCS (standardised coefficient = 0.63, $P < 0.001$). DBH also had a positive effect on ETCS (0.33, $P < 0.01$), whereas D had a negative effect (-0.2443, $P < 0.05$). Soil MnO had a positive effect on ETCS (0.49, $P < 0.001$). Soil N was indirectly associated with ETCS through relationships with D (0.52) and DBH

(0.73), while soil TC was associated with Corg (0.51) and N (0.47). These results indicate that soil properties and stand structure jointly explained variation in forest ecosystem carbon storage.

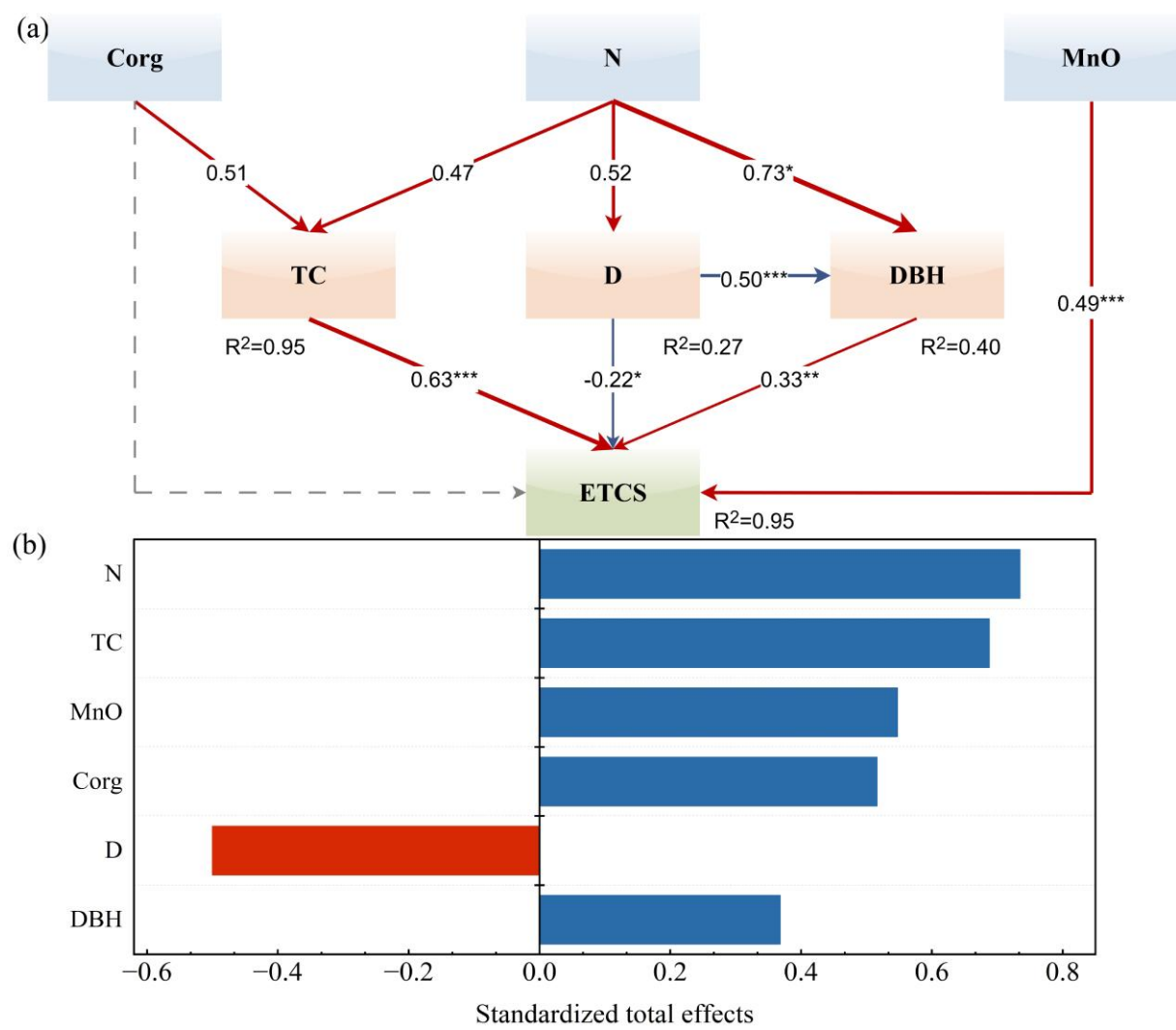


Figure 7. Structural equation model paths of factors influencing forest ecosystem carbon storage

Figure caption: In panel (a), solid lines indicate significant pathways ($P < 0.05$), whereas dashed lines denote non-significant pathways. Arrow directions represent causal relationships, and arrow thickness reflects the magnitude of the path coefficients. The values adjacent to the arrows represent standardized path coefficients; red indicates positive effects and blue indicates negative effects. The significance levels of each predictor are denoted as * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$. Panel (b) presents the standardized total effects of each driving factor on ETCS derived from the SEM.

4 Discussion

4.1 Carbon allocation among forest ecosystem pools

This study quantified whole-ecosystem carbon stocks across vegetation, litter, and soil pools in a cold-temperate watershed of northeastern China. Soil was the dominant carbon pool in all forest types, contributing 61.57-77.68% of total ecosystem carbon stocks, consistent with evidence that plant and soil carbon pools may respond differently across

forest ecosystems (Terrer et al. 2021). This pattern is consistent with the recognised role of forest soils as long-term carbon reservoirs (Jobbagy and Jackson 2000; Lal 2005; Hu et al. 2015). The large contribution of surface soil also reflects the cold climate of the Xiaoxing'an Mountains, where low temperatures can slow organic matter decomposition and favour carbon accumulation in the A horizon. Vegetation formed the second largest pool, and tree biomass accounted for 88.15% of vegetation carbon. This result confirms that stand structure remains central to aboveground carbon storage even where soil carbon dominates whole-ecosystem stocks.

Carbon stocks differed among forest types, with the highest ecosystem carbon stocks in mixed conifer-broadleaf forests. This pattern may reflect combined effects of species composition, stand development, and litter quality. Coniferous species generally decompose more slowly than many broadleaf species, which can favour carbon retention (Wang et al. 2022). At the same time, many broadleaf stands in the study area were young or middle-aged and had relatively low stem volume and biomass, a pattern consistent with regional evidence that stand type and development stage influence forest carbon density (Xu et al. 2024a; Ye et al. 2025; Zhao et al. 2025). These differences indicate that forest-type effects on carbon storage should be interpreted through both species identity and stand developmental stage.

The spatial pattern of carbon stocks also highlights the importance of watershed context. High ecosystem carbon stocks were concentrated mainly near low-elevation riparian zones, whereas high tree-layer carbon stocks occurred more often at higher elevations with weaker disturbance. This contrast suggests that soil moisture and nutrient accumulation may enhance soil carbon in riparian areas, while reduced disturbance may favour vegetation carbon accumulation in upland forests. The finding is relevant for watershed-scale carbon management because the locations of high soil carbon and high vegetation carbon do not fully overlap.

4.2 Soil controls on ecosystem carbon storage

Soil variables were the strongest correlates of total ecosystem carbon storage. Mantel analysis linked ETCS with N, Corg, TC, P, and MnO, and the SEM identified soil TC as the strongest direct correlate. These results suggest that nutrient availability and soil organic matter status are jointly associated with carbon accumulation in the study area. Nitrogen may affect carbon storage by altering plant growth, litter production, microbial activity, and SOC stabilisation (Liu et al. 2024; Sha et al. 2022; Su et al. 2024). In this study, soil N was also indirectly associated with carbon stocks through

DBH and species dominance, indicating that soil fertility may influence carbon storage partly through stand development.

The positive association between MnO and ETCS suggests an additional mineral-related influence on carbon storage. Multivalent metal oxides can contribute to organo-mineral associations and affect soil carbon turnover and stabilisation (Xu and Tsang 2024b). However, the present study identifies statistical associations rather than experimentally verified mechanisms. Experimental or process-based studies would be needed to test whether Mn-related mineral protection directly increases carbon persistence in these forest soils.

4.3 Stand structure, biodiversity, and interpretation boundaries

Stand structure was most clearly linked to vegetation carbon. VTCS was significantly associated with mean DBH, and SEM showed a positive effect of DBH on ETCS. This result agrees with the expectation that larger trees contribute disproportionately to forest biomass and carbon storage (Lan et al. 2019; Wei et al. 2014). The PCA distribution of DBH and stand height may also reflect differences in stand developmental stage among plots. Therefore, variation in forest age structure is likely to be an important background factor when comparing carbon stocks among forest types.

The biodiversity-carbon relationship was more complex. Although biodiversity is often positively associated with ecosystem productivity through complementary resource use (Ali and Mattsson 2017; Sanaei et al. 2021), Simpson's dominance index showed a negative effect on ETCS in the SEM. This pattern may reflect successional stage and community composition rather than a simple diversity effect. Forests dominated by pioneer species such as *Betula platyphylla* are often associated with early succession in the study region. As succession proceeds, changes in competition, stand density, and biomass allocation may alter the relationship between species composition and carbon storage. These results should be interpreted cautiously because the study used 15 plots within one watershed and measured associations at one survey period.

5 Conclusions

This study assessed vegetation, litter, and soil carbon stocks in a cold-temperate watershed forest ecosystem in the Xiaoxing'an Mountains. Soil was the largest carbon pool in all forest types, and tree biomass dominated vegetation carbon. Mixed conifer-broadleaf forests had the highest total ecosystem carbon stocks, followed by larch, birch, and

mixed broadleaf forests. Spatially, high ecosystem carbon stocks occurred mainly in low-elevation riparian zones, whereas higher tree-layer carbon stocks were more common at higher elevations.

Soil nutrient status was the main factor associated with ecosystem carbon storage. TC, N, Corg, P, and MnO were strongly related to total ecosystem carbon stocks, while vegetation carbon was mainly associated with DBH. The SEM further indicated that soil TC had the strongest direct effect on ETCS, with additional contributions from DBH, MnO, and species dominance.

Together, these findings indicate that carbon accumulation in cold-temperate watershed forests is associated with soil properties, stand structure, and community composition. The results provide field-based evidence for carbon-stock assessment and forest management in northeastern China. Because the analysis is based on one watershed and 15 field plots, broader regional inference should be tested with larger plot networks and repeated surveys.

Author contributions

Conceptualization, F.Z.Z.; methodology, F.Z.Z.; data analysis, F.Z.Z., B.S.J. and G.Q.; investigation, F.Z.Z., W.X.Y, M.Y., S.M.Z., and J.F.; writing—original draft preparation, F.Z.Z.; writing—review and editing, F.Z.Z., S.Y.F. and T.X.F.; supervision, F.Z.Z.; project administration, Z.C.F. and W.H.F.; formal analysis, F.Z.Z.; funding acquisition, W.H.F.; resources, Y.Y.Y.; data curation, F.Z.Z.; All authors have read and agreed to the published version of the manuscript.

Project funding

This study was supported by the China Geological Survey through the projects “Comprehensive Survey of Natural Resources in the Heihe Area of the Xiaoxing’an Mountains” (Grant No. DD20230504) and “1:50,000 Applied Geological Survey of Four Map Sheets Including Shenwucheng in the Changbai Mountain Area, Jilin Province” (Grant No. DD202606301603).

Data availability

The datasets generated and analysed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Conflict of interest

The authors declare that they have no conflict of interest.

References

- Ali A, Mattsson E (2017) Individual tree size inequality enhances aboveground biomass in homegarden agroforestry systems in the dry zone of Sri Lanka. *Sci Total Environ* 575:6–11. <https://doi.org/10.1016/j.scitotenv.2016.10.022>

- Cai HY (2017) Carbon storage and productivity for typical forest ecosystems in Xiaoxing'an Mountains, China. Dissertation, Northeast Forestry University. 308
309
- Fan WY, Zhang HY, Yu Y et al (2011) Comparison of three models of forest biomass estimation. *Chin J Plant Ecol* 35(4):402-410. 310
<https://doi.org/10.3724/SP.J.1258.2011.00402> 311
- Fang JY, Guo ZD, Piao SL et al (2007) Estimation of terrestrial vegetation carbon sink in China from 1981 to 2000. *Sci China Ser D Earth Sci* 37(6):804-812. <https://doi.org/10.1007/s11430-007-0049-1> 312
313
- Guan WB, Chen T, Dong YJ et al (1997) Vegetation diversity in northeastern China I. Diversity of vertical vegetation composition 314
in cold temperate coniferous forest region. *Chin J Appl Ecol* 8(5):465-470. 315
- Hu HQ, Luo BZ, Wei SJ et al (2015) Biomass carbon density and carbon sequestration capacity in seven typical forest types of the 316
Xiaoxing'an Mountains, China. *Chin J Plant Ecol* 39(2):140-158. <https://doi.org/10.17521/cjpe.2015.0014> 317
- Hu JT, Liu JG, Wang CK et al (2025) Differentiation of forest carbon density and its influencing factors at different latitudes in the 318
Xiaoxing'an Mountains. *Acta Ecol Sin* 45(23):11763-11776. 319
- Jia WW (2014) Forest biomass and carbon storage of different forest stand types in Northeast China. Heilongjiang Science and 320
Technology Press, Harbin. 321
- Jobbagy EG, Jackson RB (2000) The vertical distribution of soil organic carbon and its relation to climate and vegetation. *Ecol Appl* 322
10(2):423-436. [https://doi.org/10.1890/1051-0761\(2000\)010\[0423:TVDOSO\]2.0.CO;2](https://doi.org/10.1890/1051-0761(2000)010[0423:TVDOSO]2.0.CO;2) 323
- Lal R (2005) Forest soils and carbon sequestration. *For Ecol Manag* 220(1-3):242-258. <https://doi.org/10.1016/j.foreco.2005.08.015> 324
- Lan X, Du H, Song TQ et al (2019) Vegetation carbon storage in the main forest types in Guangxi and the related influencing factors. 325
Acta Ecol Sin 39(6):2043-2053. <https://doi.org/10.5846/stxb201803210557> 326
- Li K, Peng M, Zhao CD et al (2019) Vicennial implementation of geochemical survey of land quality in China. *Earth Sci Front* 327
26(6):128-158. 328

- Liu RT, Ma SJ, Zhang XW et al (2024) Research progress on the estimation model of carbon storage in five major carbon pools for forest ecosystems and their influencing factors. *Forestry Construction* 42(6):11-25.
- Lyu XZ, Jia WW (2025) Distribution and modelling of carbon stocks in understorey vegetation and young trees in the Lesser Khingan Mountains forests. *J Southwest For Univ* 45(5):130-138.
- Mei XS, Dong LB, Chen GM (2024) Driving factors of carbon sink in natural *Larix gmelinii* forests based on structural equation models. *J Beijing For Univ* 46(9):1-10.
- Pan Y, Birdsey RA, Fang J et al (2011) A large and persistent carbon sink in the world's forests. *Science* 333(6045):988-993. <https://doi.org/10.1126/science.1201609>
- Sanaei A, Ali A, Yuan Z et al (2021) Context-dependency of tree species diversity, trait composition and stand structural attributes regulate temperate forest multifunctionality. *Sci Total Environ* 757:143724. <https://doi.org/10.1016/j.scitotenv.2020.143724>
- Sha GL, Chen YY, Wei TX et al (2022) Distribution of soil carbon and its driving factors under typical restored vegetation in hilly areas of Loess Plateau. *Soil* 54(6):1265-1272.
- Su LC, Chen XS, Luo ZZ et al (2024) Effects of nitrogen addition on the sequestration and CO₂ emissions in forest soils: a review. *Acta Ecol Sin* 44(7):2717-2733.
- Su YQ, Zhang Y, Jia XR et al (2017) Application of several diversity indexes in forest community analysis. *Ecol Sci* 36(1):132-138.
- Terrer C, Phillips RP, Hungate BA et al (2021) A trade-off between plant and soil carbon storage under elevated CO₂. *Nature* 591(7851):599-603. <https://doi.org/10.1038/s41586-021-03306-8>
- Wang JQ, Xing YQ, Chang XQ et al (2024) Assessment of the effectiveness of the Northeast Natural Forest Protection Project and identification of hot spot areas. *Acta Ecol Sin* 44(3):1231-1241.
- Wang WJ, Wang K, Wang YY et al (2022) Comparative study on tree, shrub and herb composition and carbon sink function between coniferous and broadleaved forests in Northeast China. *J Beijing For Univ* 44(10):52-67.

- Wang Y, Deng L, Wu G et al (2018) Estimates of carbon storage in grassland ecosystems on the Loess Plateau. *Catena* 164:23-31. 351
<https://doi.org/10.1016/j.catena.2018.01.007> 352
- Wei YW, Zhou WM, Yu DP et al (2014) Carbon storage of forest vegetation under the Natural Forest Protection Program in North-east China. *Acta Ecol Sin* 34(20):5696-5705. <https://doi.org/10.5846/stxb201301240142> 353
 354
- Wu BG, Cheng M, Quan SX et al (2024) Assessment and analysis of forest ecosystem carbon reserves in ecological green core area of Greater Changsha Metropolitan Region. *J Northwest For Univ* 39(6):135-144. 355
 356
- Xie HS, Xu DY, He YT et al (2024) Analysis and optimization on China's natural forest protection policy system. *Acta Ecol Sin* 44(24):11347-11358. 357
 358
- Xu W, Zhang B, Xu Q et al (2024a) Enhanced carbon storage in mixed coniferous and broadleaf forest compared to pure forest in the north subtropical-warm temperate transition zone of China. *Forests* 15(9):1520. <https://doi.org/10.3390/f15091520> 359
 360
- Xu Z, Tsang DCW (2024b) Mineral-mediated stability of organic carbon in soil and relevant interaction mechanisms. *Eco-Environ Health* 3(1):59-76. <https://doi.org/10.1016/j.eehl.2023.12.003> 361
 362
- Yang F, Wei XP, LingHu RM et al (2026) Spatial patterns and drivers of carbon density in terrestrial ecosystems in Southwest China. *Environmental Science* 1-29. 363
 364
- Ye XM, Wei TX, Yu H et al (2025) Carbon storage and influencing factors of typical forest ecosystems in loess hilly region. *Chin J Ecol* 44(5):1409-1416. 365
 366
- You HZ, Bi J, Wang C et al (2018) Altitudinal distribution rule of *Betula platyphylla* forest's soil organic carbon density and its influencing factors in Xiaowutai Mountain in Hebei. *Ecol Environ Sci* 27(3):432-437. 367
 368
- Zhang L, Zhang DL, Mao ZJ (2017) Characteristics of soil organic carbon and its components in different successional series of broadleaved Korean pine forest in Xiaoxing'an Mountains. *Sci Silvae Sin* 53(9):11-17. 369
 370
- Zhang SL, Zhang HJ, Zhang W et al (2015) Comparison of water-holding characteristics and biomass of litter under different forest types in Xiaoxing'an Mountains. *Bull Soil Water Conserv* 35(4):85-90. 371
 372

Zhao ZB, Li HZ, Wang HM et al (2025) Forest carbon storage, carbon density and increasing carbon sink pathways at Heilongshan forest farm. Bull Soil Water Conserv 45(5):144-154. 373 374

Zi YY, Xi M, Kong FL et al (2016) Temporal and spatial distribution of soil organic carbon and its storage in the coastal wetlands of Jiaozhou Bay, China. Chin J Appl Ecol 27(7):2075-2083. 375 376