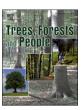
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Soil organic carbon drivers in a high-stock forested region

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ABSTRACT

Forests are pivotal in stocking Soil Organic Carbon (SOC). This study investigated the drivers influencing SOC stock in Chilean Patagonia, a region known for its extensive carbon reserves. We analysed the SOC stock (tons ha^{-1} at 30 cm depth) as the target variable, considering factors such as forest types (Nothofagus pumilio = NP, N. antarctica = NA, N. dombeyi-N. betuloides = ND-NB, evergreen = EV, and mixed broadleaved forests = MI), soil types (Andosols, Entisols, Inceptisols, and Spodosols), and human impacts (unmanaged = U, burned = B, harvesting = H, livestock = L, and harvesting + livestock = H + L). The analysis combined the SOC stock's climatic, topographic, and above- and below-ground drivers. Data were evaluated using analyses of variance (ANOVAs), generalised linear models (GLMs), and principal component analyses (PCA). The results revealed significant differences (p < 0.001) in SOC stocks in forest types, soil types, and human impacts. The SOC stocks were higher in EV, NP, and ND-NB forests (SOC >119 tons ha $^{-1}$) compared to MI and NA forests (SOC \sim 100 tons ha $^{-1}$). The highest SOC stocks were observed in U and H forests (SOC >125 tons ha-1), with Spodosols and Inceptisols showing the highest SOC levels among the soil types. The interaction between NP forests and harvesting presented a high SOC stock. PCAs identified two main groups influencing SOC variation: one related to climatic and topographic factors like seasonal temperatures and altitude and another associated with specific drivers such as pH, canopy cover, decaying wood, vascular plant cover, and lichen cover. We concluded that U and H forests in a region with high SOC stocks maintain equivalent SOC storage. However, special attention is needed for forest management practices involving integrated livestock in harvested forests.

Introduction

Forests are a focal point for global Soil Organic Carbon (SOC) stocks. Forests contribute to the SOC by storing large amounts of carbon in plants and soils (Scharlemann al., 2014; FAO and ITPS, 2018; Sha et al., 2022). This storage is linked to the ability of plants and soils to regulate vital ecosystem processes, including carbon sequestration (Bardgett et al., 2013; Ma et al., 2018; Sha et al., 2022). SOC is derived from decaying plant matter and is a critical component of the carbon cycle (Ontl and Schulte, 2012; Deng et al., 2014; FAO and ITPS, 2018). Calculations reveal that the SOC pool contains over two centuries of current fossil fuel emissions (Mathieu et al., 2015), making it an essential biosphere variable regulating Earth's climate (FAO and ITPS, 2018).

Moreover, soils store approximately 3.2 times more carbon than the atmosphere, and land management can further enhance this potential (Paustian et al., 2016; Zomer et al., 2017).

Previous studies indicate that climate, vegetation types, and soil influence SOC (Carvalhais et al., 2014; Mathieur et al., 2015). Besides this, human activities and the indirect effects of climate change (e.g., warming, drought, or increased rainfall) significantly affect the SOC stocks, reducing its ability to provide essential ecosystem services (Beillouin et al., 2023), compromising its capability to provide essential ecosystem services and hinder global SOC sequestration (Scharlemann et al., 2014; FAO, 2023). International authorities emphasise the need for practical land-use guidelines to achieve climate goals by 2050 (e.g., carbon neutrality), as highlighted by the United Nations Climate Change

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Conference (COP28) and Paris Agreement targets (FAO, 2023; Acen et al., 2024). There was a consented message: Carbon must be regulated on Earth. Despite the recognised importance of forests for SOC storage (FAO, 2023; Peri et al., 2024a,b), there remains a gap in understanding the environmental and human drivers affecting SOC stocks and their variations (Chiti et al., 2023; Pfeiffer et al., 2023; Zhu et al., 2024).

In this context, Patagonia is a forested region that is particularly important worldwide due to its large SOC stocks (FAO, 2023). However, it still needs to be determined how factors such as climate, topography, and above (e.g., forest structure, forest floor)- and below-ground (e.g., soil variables) drivers interacting with human impacts influence high SOC stocks. We hypothesise that these factors should differentially influence SOC stocks in native forests. If so, SOC stock pivotal drivers can provide new insights into forest ecology and management. We aim to investigate these gaps by analysing the interactions between potential drivers of SOC stocks in managed and undamaged native forests. To this end, the following objectives were established: (i) What are the interactions among climate, topography, above- and below-ground drivers, and human impacts in SOC stocks (tons ha⁻¹ at 30 cm depth) in a high-stock forested region? and (ii) How do these factors influence

managed and undamaged native forests SOC stocks?

Material and methods

Study area

The study was conducted in the Chilean Austral Macrozone (43° to 56° SL) in the Patagonia region (Fig. 1), covering the administrative districts of Aysén (108,494 km²) and Magallanes (132,291 km²). It features an altitudinal gradient from sea level to the mountain treeline (~1,500 m a.s.l.) (Veblen et al., 1979; Körner, 2007). The predominant soil orders are Andosols, Inceptisols, Spodosols, and Entisols (FAO-UNESCO 1972-1981). The main climates are predominantly warm temperate (-3°C < Tmin < +18°C) and polar (0 °C \le Tmax < +10°C) (Kottek et al., 2006), with mean precipitations ranging from 500 mm year $^{-1}$ to 4,000 mm year $^{-1}$ (AGRIMED, 2017).

The deciduous and evergreen forests include 18 predominant types comprising several tree species (Huertas Herrera et al., 2023). *Nothofagus* is the most representative genus, with tree species that includes *N. pumilio, N. antarctica, N. dombeyi*, and *N. betuloides*, found in both

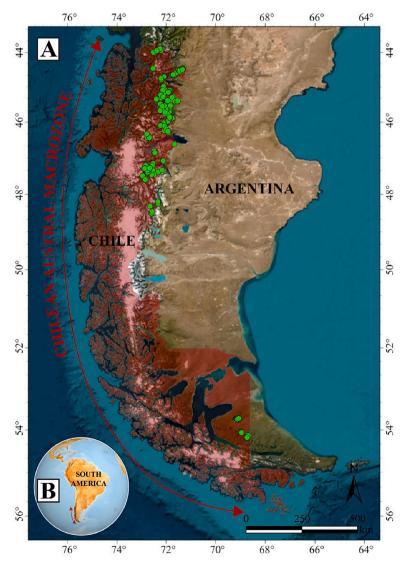


Fig. 1. Study area (A): Patagonia's Chilean Austral Macrozone (highlighted in red). Green dots indicate the studied plots. Basemap source: ESRI ArcGIS software (ArcMap 10.8.3; www.esri.com). Soil Organic Carbon (SOC) stocks in the top 30 cm (B). Orange colours indicate SOC stocks (tons ha⁻¹), ranging from 0 tons ha⁻¹ (light orange) to >200 tons ha⁻¹ (dark orange). Map source: Global Soil Organic Carbon Map v1.5 (GSOC, www.fao.org).

pure stands and mixed broadleaved combinations (e.g., N. pumilio and N. antarctica or N. dombeyi and N. betuloides). Another important forest type is the Evergreen, tree species that include Laurelia sempervirens, Maytenus magellanica, Weinmannia trichosperma, Pilgerodendron uviferum, Laurelia philippiana, Amomyrtus luma, Luma apiculata, Saxegothaea conspicua, Podocarpus nubigenus, Embothrium coccineum, and Drimys winteri.

The study area includes extensive national parks and reserves, covering nearly half of the territory (Tacón et al., 2023). It also includes significant native forested areas within ranches engaged in management activities, where livestock production (*Bos taurus, Equus caballus*, and *Ovis aries*) mainly occurs in *N. antarctica* forests, while timber activities are conducted in *N. pumilio* (Huertas Herrera et al., 2023). Despite the relatively lower impact of human activities in Patagonia than in other regions, forests affected by fires and continuous grazing represent a significant human footprint on the landscape (Huertas Herrera et al., 2021; Brito Rojas, 2022). Several tree species cannot recover naturally, and areas burned in the early to mid-20th century continue to show signs of damage (Quintanilla, 2008; Brito Rojas, 2022).

Sampling design and data-taking

Climatic variables were obtained from the WorldClim version 2.1 database (Fick and Hijmans, 2017) using the monthly bioclimatic variables released in January 2020. We calculated the average temperature (°C) for the warmest month (TEMP-Warm) and coldest month (TEMP-Cold), as well as the mean annual precipitation (PP, mm year -1). Topographic variables, including altitude (ALT, m a.s.l.), slope (SLOPE, %), and aspect (N-S and E-W), were derived from the digital elevation model (DEM) provided by the Shuttle Radar Topography Mission (Farr et al., 2007). The aspect was calculated using sine and cosine functions of magnetic north (Jenness, 2004). All geoprocessing analyses were performed using the ArcToolbox of ArcMap 10.8.3 (ESRI; www.esri.com).

Fieldwork was conducted from January 2022 to February 2024 in 192 plots (1 ha), randomly selected along an extensive latitudinal regional gradient (~2,000 km; Fig. 1) covering the natural distribution of the forests (Gajardo, 1994). Within each plot, we randomly placed a 50 m transect to characterise the forest structure using the point sampling method (BAF 0.5–4 m² ha⁻¹) (Bitterlich 1984) with a Haglöf EC II d-R Digital Clinometer (Haglöf Inc., Sweden). Trees were measured for diameter at breast height (DBH, cm) and dominant height (DH, m). The dominant height was determined by averaging the total height of the two tallest trees, measured with a laser rangefinder (Nikon Forestry Pro, Japan). These measurements allowed the calculation of tree density (DEN, tree ha⁻¹) and basal area (BA, m² ha⁻¹). The canopy cover (CC, %) was characterised using hemispheric photographs taken at the centre of each ground-level transect. This characterisation was done using an 8 mm fisheve lens (Sigma, Japan) mounted on a 35 mm digital camera (NIKON D800, Japan) with a tripod levelling head to ensure the horizontal position of the lens. The Gap Light Analyzer v.2.0 software was used for this purpose (Frazer et al., 2001).

At each plot, we used the point-intercept method (Levy and Madden, 1933), recording data at 50 intercept points spaced 1 meter apart along a 50 m transect to quantify the cover of vascular plants, including tree seedlings (VP, %), and non-vascular plants such as mosses (M, %), liverworts (LIV, %), and lichens (LI, %). Additionally, we measured the cover of fungi (F, %), litter (LIT, %) and categorised debris by size: decaying wood < 5 cm (R3, %), 5-10 cm (R2, %), and > 10 cm (R1, %). Besides this, we estimated the cover of stones (ST, %), bare soil (BS, %), dung (DU, %), and roots (RO, %). We also calculated the dominant height of the understory (UDH, cm) and the soil resistance to penetration

(SR, kgf cm⁻²), an indicator of soil compaction, measured at each sampling point using a Humboldt pocket penetrometer (0–4.5 kgf cm⁻²), as well as the soil pH using a Groline soil pH-meter HI98168 (Hanna Instruments, USA).

We collected soil samples from each plot using a stratified design, with six soil extractions made at a depth of 30 cm along 50 m transects (192 transects \times 6 replicates = 1,152 soil samples). The soil was sampled following the FAO (2020) protocol for measuring, monitoring, reporting, and verifying soil organic carbon. These samples were weighed with a Digital Pocket Scale (g) to determine wet weight in situ. The soil samples were transported to the laboratory, oven-dried at 60 °C, weighed using a precision balance (± 0.0001 g), and sieved through a 2 mm mesh. The soil moisture (SM, %) was determined by measuring the difference between the wet and dry weights of the samples (SM = (wet weight - dry weight) / dry weight \times 100). Soil organic matter content (SOM, %) was calculated using a muffle furnace (Vulcan Model A-1750, USA) at 500 °C. Soil bulk density (SBD, kg m⁻³) was calculated without coarse material >2 mm, using the formula: SBD= (dry weight (g) /soil sample core volume (cm 3)) \times 1,000. Soil organic carbon content (C, %) was calculated with the LECO TruSpec® Micro TRMS CHNS Simultaneous Elemental Determinator (USA), using the Dumas direct combustion method with a sediment calibrator. We conducted these analyses using TruSpec Micro CHN software (LECO Corporation; www.leco.com).

The soil organic carbon (SOC) stocks were calculated by multiplying the carbon content (C, %) by the soil weight for the considered profile depth (tons ha $^{-1}$ at 30 cm), following the methodology described by Martínez Pastur et al. (2021). According to Eggleston et al. (2006), the calculation of SOC stocks involves the following equations: Soil profile volume (m 3 ha $^{-1}$ at 30 cm) =10,000 \times (profile depth (cm)/100); soil weight for the considered profile depth (tons ha $^{-1}$) = volume (m 3 ha $^{-1}$) \times soil bulk density (tons m $^{-3}$) and soil organic carbon (SOC) (tons ha $^{-1}$) = soil weight (tons ha $^{-1}$) \times carbon content (%).

Data analyses

SOC stock (tons ha⁻¹) was the target variable in our analyses. The main factors considered included forest types (N. pumilio = NP, *N. antarctica* = NA, *N. dombeyi-N. betuloides* = ND-NB, evergreen = EV, and mixed broadleaved forests = MI), soil types (Andosols, Entisols, Inceptisols, and Spodosols), and human impacts (unmanaged = U, burned = B, harvesting = H, livestock = L, and harvesting + livestock =H + L). One-way ANOVA analyses were conducted to test the relationship between SOC stocks and these factors, where the SOC values were presented as mean \pm standard error (SE). Besides this, climatic (TEMP-Warm, TEMP-Cold, PP), topographic (ALT, SLOPE, N-S, E-W), and both above- and below-ground drivers such as forest structure (DH, DBH, DEN, CC), soil parameters (SOM, C, SM, pH, SR), and forest floor characteristics (UDH, VP, M, LI, LIV, F, LIT, R3, R2, R1, ST, BS, DU, RO), in forest types, soil types, and human impacts were contrasted using oneway ANOVA analyses (Appendices A-E). Mean comparisons for these analyses were conducted using the Fisher LSD test (p < 0.05), and normality and homogeneity were tested using the Shapiro-Wilk and Levene methods. When assumptions were not met, response variables were log-transformed to normalise distributions. However, untransformed data were presented as mean \pm standard error to facilitate better interpretation of the information.

The significant effects of forest types (NP, NA, ND-NB, EV, MI), soil types (Andisols, Entisols, Inceptisols, Spodosols), and human impacts (U, B, H, L, H + L) as predictor variables on SOC stocks (tons ha^{-1}) were assessed using generalised linear models (GLMs), selecting the best model using the lowest Akaike Information Criterion (AIC). We

Table 1 ANOVAs for the Soil Organic Carbon (SOC) stock (tons ha^{-1}) comparing forest types, soil types, and human impacts. The SOC values are presented as mean \pm standard error (SE).

Forest types	$\text{Mean} \pm \text{SE}$	Soil types	$\text{Mean} \pm \text{SE}$	Human impacts	$Mean \pm SE$
NP	$128.0 \pm 4.8b$	Andisols	$100.7 \pm 5.1a$	U	$126.8 \pm 7.6c$
NA	$91.1 \pm 6.3a$	Entisols	$117.3 \pm 15.5b$	В	$116.3 \pm 8.8b$
ND-NB	$119.7\pm9.8b$	Inceptisols	$117.4\pm4.3b$	Н	$129.3 \pm 5.5 \mathrm{c}$
EV	$128.6\pm8.9b$	Spodosols	$154.9 \pm 9.3c$	L	$89.8 \pm 9.8a$
MI	$108.3 \pm 9.7 ab$			H + L	$102.0 \pm 5.6 ab$
F(p)	12.5 (<0.001)	F(<i>p</i>)	8.5 (<0.001)	F(<i>p</i>)	5.1 (0.001)

Different lowercase letters indicated significant differences according to the Fisher LSD test (p < 0.05). F(p) = Fisher test values and corresponding p-values for each factor. NP = N. pumilio, NA = N. antarctica, ND-NB = N. dombeyi-N. betuloides, EV = evergreen, MI = mixed broadleaved forests, U = unmanaged, B = burned, H = harvesting, L = livestock, and H + L = harvesting + livestock.

employed the Poisson distribution for the GLMs; however, we applied a negative binomial error distribution with a log link function due to significant over-dispersion in the SOC data. Mean comparisons were conducted using Fisher's LSD test (p < 0.05). The ANOVA and GLMs analyses were performed using InfoStat software (Di Rienzo et al., 2018).

Principal Component Analyses (PCA) were conducted to explore the interactions among climate, topography, above- and below-ground drivers, and human impacts on SOC stocks. According to FAO-ITPS (2018), the SOC in the top 30 cm in our study area is expected to exceed the world's lowest values, which range from ~ 0 –15 tons ha⁻¹ (e. g., Atacama or Sahara deserts). In this context, we categorised our data into the following thresholds, dividing SOC values into even parts using quantiles: (i) $< 75 \text{ tons ha}^{-1}$, (ii) 76–100 tons ha⁻¹, (iii) 101–120 tons ha^{-1} , (iv) 121–150 tons ha^{-1} , and (v) > 151 tons ha^{-1} . The PCAs were performed using the Cross-Product Matrix and the Variance/Covariance (Centered) coefficients, calculating the scores for columns using the distance-based biplot. The drivers that best explain the principal components were identified by examining the eigenvectors scaled to their standard deviation (called v vectors). Analyses included a randomisation test with a Monte Carlo permutation test (n = 999) to assess the significance of each axis. PCAs were performed using PC-ORD software version 5 (McCune and Mefford, 1999).

Results

We estimated that SOC stocks in the study area ranged from 50 tons ha^{-1} to 361 tons ha^{-1} . We found significant statistical differences (p < 0.05) in SOC stocks (tons ha⁻¹) among forest types, soil types, and human impacts, as presented in Table 1. The ANOVA results showed evergreen (EV), N. pumilio (NP), and N. dombeyi-N. betuloides (ND-NB) forest types had the highest SOC stocks compared to mixed broadleaved forests (MI) and N. antarctica (NA), with NA forming a single group correlated with the lowest SOC stock (on average 91.1 tons ha⁻¹). The SOC stock levels in analysed soil types ranged from 100.7 tons ha^{-1} in the Andosols to 154.9 tons ha⁻¹ in the Spodosols, forming a grouping different from Entisols and Inceptisols, which had SOC levels of ~ 117 tons ha⁻¹. The SOC stocks under human impacts (p = 0.001) showed grouping differences among livestock use treatments (i.e., L and H+L; \sim 100 tons ha⁻¹), along with burned areas (116.3 tons ha⁻¹), in contrast to unmanaged (126.8 tons ha⁻¹) and harvested areas (129.3 tons ha⁻¹), both forming a grouping with similar means of SOC stocks.

The AIC value obtained for the GLMs model (Table 2) indicated that combining forest types, soil types, and human impacts explained the SOC stock better than individual variables alone (lower AIC value = 1,473). Considering the different forest types, the GLM showed that NP forests had lower SOC than EV, the reference forest type. Regarding soil types, Entisols and Spodosols both had a positive and significant effect on SOC compared to the reference soil type, Andisols, which had the lowest SOC stocks. The H and H + L were associated with lower SOC than burned forests for human impacts. The interaction between NP and

H indicated increased SOC stock, similar to the interaction between NP and $\rm H + L$. Most other interactions were not significant, suggesting no notable combined effect on SOC for those specific factor combinations.

PCA analyses showed trends similar to those described previously (Fig. 2). The first two axes explained 65.2 % of the cumulative variance extracted from the first 10 axes, with axis 1 having an eigenvalue of 2.891 and axis 2 an eigenvalue of 2.327. The difference between the eigenvalues of axis 1 and axis 2 was statistically significant (p=0.001). Based on the scaled eigenvectors (i.e., v) vectors), we found two groups of drivers that provide insight into the relationship between the SOC and the analysis factors. The first group, including drivers such as TEMP-Warm (v) vector = 0.8451), TEMP-Cold (v) vector = 0.8867), and ALT (v) vector = -0.8977) that were associated with a broad range of SOC thresholds, from v 75 tons ha⁻¹ to v 151 tons ha⁻¹ across different

Table 2 Generalised linear models (GLMs) predicting soil organic carbon (SOC) stocks in forest types, soil types, and human impacts. Significant effects (p < 0.05) were highlighted in bold.

Predictor	Estimate	Std. Error	z value	p
(Intercept)	5.39	0.40	13.40	< 0.001
MI	-0.76	0.46	-1.68	0.094
ND-NB	-0.21	0.43	-0.49	0.622
NP	-0.82	0.29	-2.82	0.005
Н	-1.20	0.46	-2.59	0.010
H + L	-0.99	0.39	-2.52	0.012
L	-0.62	0.42	-1.48	0.139
U	-0.01	0.17	-0.07	0.947
Entisols	0.52	0.17	2.96	0.003
Inceptisols	0.40	0.35	1.14	0.256
Spodosols	0.53	0.23	2.29	0.022
$MI \times H$	1.21	0.53	2.29	0.022
$ND-NB \times H$	0.78	0.50	1.55	0.121
$NP \times H$	1.28	0.37	3.41	0.001
$MI \times H + L$	0.62	0.44	1.42	0.156
$ND-NB \times H + L$	0.13	0.47	0.27	0.784
$NP \times H + L$	0.94	0.26	3.68	0.000
$ND-NB \times L$	0.08	0.47	0.16	0.869
$NP \times L$	0.50	0.48	1.05	0.294
$MI \times U$	0.01	0.30	0.03	0.980
$ND-NB \times U$	-0.15	0.25	-0.59	0.554
$NP \times Entisols$	-0.42	0.45	-0.92	0.355
MI × Inceptisols	-0.32	0.39	-0.83	0.409
ND-NB × Inceptisols	-0.16	0.28	-0.55	0.581
NP × Inceptisols	-0.27	0.20	-1.32	0.188
$MI \times Spodosols$	-0.07	0.34	-0.21	0.832
$H \times Entisols$	0.07	0.44	0.15	0.877
$H \times Inceptisols$	-0.36	0.47	-0.75	0.453
$H + L \times Inceptisols$	0.07	0.32	0.21	0.835
$U \times Inceptisols$	0.12	0.20	0.59	0.556
$H \times Spodosols$	-0.12	0.26	-0.48	0.630
$NP \times H \times Inceptisols$	0.63	0.38	1.64	0.101

NP = N. pumilio, NA = N. antarctica, ND - NB = N. dombeyi-N. betuloides, EV = evergreen, MI = mixed broadleaved forests, U = unmanaged, B = burned, H = harvesting, L = livestock, and H + L = harvesting + livestock.

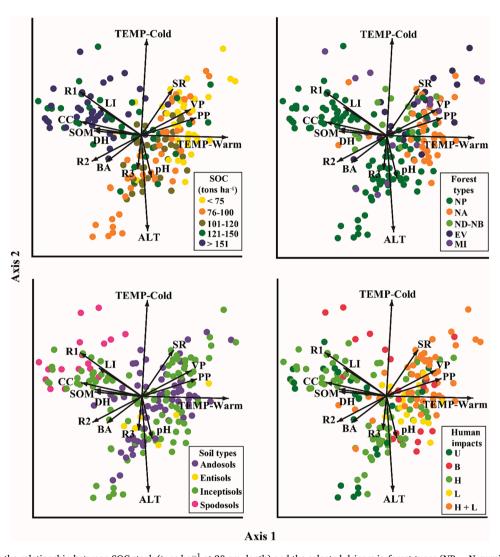


Fig. 2. The PCAs show the relationship between SOC stock (tons ha^{-1} at 30 cm depth) and the selected drivers in forest types (NP = N. pumilio, NA = N. antarctica, ND-NB = N. dombeyi-N. betuloides, EV = evergreen, MI = mixed broadleaved forests), soil types, and human impacts (U = unmanaged, B = burned, H = harvesting, L = livestock, and H + L = harvesting + livestock). Climatic drivers include annual precipitation (PP, mm year⁻¹) and temperature (°C) during the warmest (TEMP-Warm) and coldest month (TEMP-Cold). Topographic drivers include altitude (ALT, m a.s.l.). Above- and below-ground drivers include forest structure parameters such as basal area (BA, $m^2 ha^{-1}$), dominant height (DH, m), and canopy cover (CC, %), as well as soil drivers including soil organic matter concentration (SOM, %), pH, and soil resistance to penetration (SR, kgf cm⁻²), and forest floor characteristics such as cover of vascular plants (VP, %), lichens (LI, %), and debris categorised by size: decaying wood < 5 cm (R3, %), 5–10 cm (R2, %), and > 10 cm (R1, %).

climate and topographic condition. In contrast, PP (v vector =0.5673) was a less climatic influential driver, with higher precipitation values correlated with SOC thresholds between 76 and 100 tons ha^{-1} to $101{-}120$ tons ha^{-1} , while lower precipitation values were linked to SOC thresholds >121 tons ha^{-1} .

The second group included drivers that contributed less to the overall multivariate ordination but contributed to correlations of SOC thresholds, including the forest-type drivers such as CC (υ vector =-0.5666), DH (υ vector =-0.4522), and BA (υ vector =-0.3878), along with LI (υ vector =-0.3685) and SOM (υ vector =-0.4491), which were found together in samples where SOC was >121 tons ha $^{-1}$. Decaying wood (R1, R2, and R3; υ vectors =-0.5241, -0.5277, and -0.3030, respectively) also were associated with higher SOC >101 tons ha $^{-1}$). In contrast, drivers associated with lower SOC <75 tons ha $^{-1}$ included SR (υ vector =0.3883), pH (υ vector =-0.4042), and VP (υ vector =0.5314).

When plots were classified for the forest types, SOC thresholds between 121 and 150 tons ha⁻¹ and > 151 tons ha⁻¹ were associated with NP along with SOC of 101–120 tons ha⁻¹, whereas SOC between 76 and 100 tons ha⁻¹ and 101–120 tons ha⁻¹ were associated with NA, as well as SOC < 75 tons ha^{-1} . The forest types such as ND-NB, EV, and MI showed a wider range of SOC thresholds, from < 75 tons ha⁻¹ to > 151tons ha⁻¹. Regarding the soil types, the multivariate analyses revealed distinct SOC groupings corresponding to specific soil orders. Spodosols were associated with SOC thresholds of 121–150 tons ha⁻¹ and > 151 tons ha⁻¹, while Entisols were correlated with SOC < 76-100 tons ha⁻¹. The Andosols and Inceptisols covered the full range of SOC thresholds. Considering the human impacts, harvested forests exhibited SOC thresholds similar to unharvested forests, with notable similarities in SOC thresholds > 121-150 tons ha $^{-1}$. This was related to environmental drivers, such as forest structure and soil characteristics in Spodosols and Inceptisols. Forests impacted by livestock and those with combined impacts from harvesting and livestock were associated with lower SOC thresholds of 76–100 tons ha⁻¹, with livestock specifically linked to SOC < 75 tons ha⁻¹. Burned forests showed no clear correlation with specific SOC thresholds, appearing across a range of SOC thresholds.

Discussion

Drivers of soil organic carbon stocks in forest types, soil orders, and human impacts

We already know that forests are crucial for SOC storage (FAO and ITPS, 2018; Sha et al., 2022), and Patagonia is a region with high SOC stocks (FAO, 2023; Peri et al., 2024a). Recent advancements in SOC calculations for this region have been published (e.g., Toro Manríquez et al., 2019; Chaves et al., 2023; Pérez-Quezada et al., 2023; Peri et al., 2024a), highlighting the increasing relevance of Patagonia as a natural laboratory for advancing scientific knowledge focused on sustainable development in the world's southernmost region (Martínez-Harms et al., 2022; Huertas Herrera et al., 2023). Our study further contributes to understanding the factors influencing SOC stocks along a broad latitudinal gradient, including deciduous and evergreen forest types growing in different soil orders and SOC stocks in unmanaged, managed, and impacted forests.

We comprehensively exposed that SOC stock analyses should consider multiple factors, including climate, topography, forest structure, understory, and soil physical characteristics (e.g., Fig. 2). The PCA analyses showed the influence of drivers that best explained the variation in SOC were TEMP-Warm, TEMP-Cold, and PP (climatic variables),

ALT (topographic factors), BA, DH, and CC (forest structure), VP, LI, and the three levels of decaying wood (forest floor characteristics), and SOM, pH, and SR (soil parameters), with an inflation factor for biplot scores of 5.47. We consider this level of inflation (moderate multicollinearity) acceptable as it allowed us to identify inconspicuous drivers related to SOC, such as lichens (LI), which had collinearity with decaying wood (R3). These results indicate the complexity of the factors influencing SOC stocks in a high-stock forested region, highlighting the importance of climatic and topographic conditions, soil characteristics, and forest structure (Hepp and Stolpe, 2014). It also shows how human impacts, such as livestock grazing and harvesting, can be involved in SOC reserves. Identifying these key drivers provided a solid foundation for developing policies and management practices aimed at maximizing carbon sequestration capacity in this critical region. This approach was consistent with previous studies that emphasized the importance of these factors in SOC dynamics (Hepp and Stolpe, 2014; Chaves et al., 2023; Aravena Acuña et al., 2024; Peri et al., 2024a,b). Further analysis revealed that pH is inversely related to SOC, as evidenced by the opposite directions of the vectors representing pH and SOC reserves in the PCA (principal axes). Points corresponding to high SOC values (> 151 tons ha⁻¹) were associated with soils and forest types with more acidic pH, such as Spodosols and evergreen forests, reinforcing the idea that lower pH levels contribute to higher SOC stabilization due to reduced microbial activity and chemical mechanisms that favor organic matter accumulation (Yu et al., 2021). In contrast, points with pH closer to neutral were correlated with lower SOC reserves (< 100 tons ha⁻¹), particularly in Entisols and mixed forests, which may be explained by the increased mineralization of organic matter under higher pH conditions. This pattern illustrates that close to neutral pH is related to higher SOC stocks, while higher pH conditions favor processes that limit carbon accumulation in the soil (Yu et al., 2021; Wang and Kuzyakov, 2024).

Our findings also highlight the critical influence of soil bulk density on SOC stocks (Appendix D), as soil bulk density is directly related to soil porosity and the potential for organic matter accumulation (Robinson et al., 2022). Lower soil bulk density values, often found in unmanaged forest soils, promote higher SOC storage by facilitating organic matter incorporation and reducing compaction. In contrast, areas impacted by human activities, such as livestock or harvesting, tend to have increased soil bulk density, which may limit carbon sequestration potential. For example, soils from undisturbed and harvested forests and soils from mixed-use areas (harvesting + livestock) show notable SOC stock differences (Table 1), reflecting how soil bulk density can affect SOC. This reinforces the importance of considering soil bulk density as a key soil physical property in carbon management strategies, particularly in regions with high SOC variability due to human impacts (Peri et al., 2024).

This is in concordance with our hypothesis that these factors significantly (p < 0.05) differentially influence SOC stocks in native forests (see Table 2 and Appendices A-E). We found an evident SOC variability explained by climatic and topographic factors, which were correlated in a wide range of SOC thresholds from < 75 tons ha $^{-1}$ to > 151 tons ha $^{-1}$. Mathieur et al. (2015) also observed that the soil type substantially influences deep soil carbon dynamics more than climate. Here, we found that spodosols are linked to higher SOC thresholds, while Entisols are associated with lower SOC thresholds. Andosols and Inceptisols span a full range of SOC thresholds, suggesting they are more diverse soils regarding carbon accumulation. Therefore, it is unsurprising that factors such as vegetation productivity and organic matter decomposition can influence SOC accumulation, as Carvalhais et al. (2014) reported. Similarly, our statistical analysis suggests that this variability also determines forest location; for example, NP forests

(deciduous species) predominate at higher altitudes, unlike coastal evergreen forests (Appendix A), where precipitation influences SOC, though less markedly. In a study conducted in a more southern Patagonia region, differences in SOC were similarly shaped by geographic location and climatic factors, particularly precipitation (Toro Manríquez et al., 2019).

Our results also suggest that other factors detectable at the stand level, such as forest structure and both above- and below-ground drivers, have the potential to influence SOC stocks in this forested region with high carbon storage. Based on our findings, evergreen forests, NP, and ND-NB forests have the highest carbon reserves compared to mixed forests and NA forests. This result may be related to the historical use of NA forests for livestock use (Aravena Acuña et al., 2023), and our results indicate an association with soil resistance-compaction (see Appendix D). In this context, forests impacted by livestock grazing and those with combined impacts of harvesting and grazing are associated with lower SOC thresholds (76–100 tons ha⁻¹), with livestock grazing linked to the lowest SOC thresholds (< 75 tons ha⁻¹). Interestingly, burned forests did not correlate clearly with specific SOC thresholds, indicating that the fire on SOC reserves can vary widely.

Our results reveal that retaining post-harvest residues could increase soil carbon reserves, as observed in other Patagonia studies (Chaves et al., 2023). Specifically, NP forests have the highest timber potential and have been managed for decades, with sustainable forest management practices demonstrating this effect (Martínez Pastur et al., 2019). Consequently, decomposing wood (R1, R2, R3) was associated with high SOC levels, indicating that decomposing material is essential to soil carbon accumulation. Thus, harvested forests showed SOC levels similar to those in unharvested forests (Table 1, Fig 2), suggesting that harvesting does not necessarily reduce SOC reserves. However, quantifying carbon reservoirs directly in roots or other soil-integrated components could provide more detailed information about the effects of management on different forest types (Chaves et al., 2023).

Implications of the SOC results on the forest management

The significant variation in SOC associated with different forest types, soil types, and human impacts emphasises the need for tailored management practices that consider these factors to maintain and enhance SOC stocks. The SOC is vital for many ecological processes in these ecosystems (Billings et al., 2021), as it affects soil fertility, water retention, and nutrient cycling (Jackson et al., 2017), influencing plant growth and habitat stability (Schlesinger and Bernhardt, 2013). Additionally, SOC enhances carbon sequestration in terrestrial ecosystems and supports water quality (Billings et al., 2021), which can also affect marine environments (Zhao et al., 2023) (especially fjord areas that characterise the Patagonian geomorphology), primarily influenced by coastal forests. Managing SOC is essential for ecological balance and sustainability in Patagonia's terrestrial and marine ecosystems. Considering the importance of native forests, it is crucial to estimate the SOC stocks captured by different forest types to measure whether using natural resources affects these extensive carbon reserves. In this context, our study revealed that the best forest management practices for maintaining optimal SOC stocks were harvesting, not livestock use, and the combined pressure of both. Burned areas showed slightly lower but comparable SOC stocks, probably due to the remaining carbon stored in the burned forest, which persisted after human impact. Previous studies (e.g., Mayer et al., 2020; Chaves et al., 2023) suggest that SOC in managed forests enhances carbon capture in natural systems when

residue is not removed, which was reinforced by our results across a large latitudinal gradient of >2,000 km. This suggests that proper forest harvesting practices can be used for climate mitigation and to preserve SOC stocks in one of the world's largest carbon reserve ecosystems. In contrast, livestock use alone did not favor SOC stocks in forest types. However, this may be related to forest overuse, as reported by Huertas Herrera et al. (2023), unlike the proper harvesting practices considered in our study, known as shelterwood cut.

Entisols and Spodosols positively affect carbon reserves without interactions with forest type or human impact. This suggests a natural influence of soil type on carbon stock (FAO, 2020). Consequently, management recommendations for natural environments should consider soil types, such as avoiding overgrazing Entisols to prevent degradation. Furthermore, soil texture influences SOC, as its water retention capacity and aeration directly affect organic matter accumulation (FAO, 2020). Andisols, with predominantly sandy texture and lower water retention capacity, showed lower SOC values, possibly due to faster organic matter mineralization in these volcanic soils (Besoain et al., 2000). In contrast, Spodosols, with a clayey texture, higher water and nutrient retention capacity, and higher organic matter (Thiers et al., 2014), exhibited the highest SOC values, highlighting how soils with higher clay content promote carbon accumulation. Inceptisols and Entisols, with a silty texture, also displayed intermediate SOC values, suggesting that their carbon retention capacity depends on a combination of physical characteristics (young soils with lower organic matter accumulation) (Thiers et al., 2014). The importance of soil texture in carbon management strategies is closely tied to their ability to store and retain carbon over the long term. Soil texture will be further studied in these research plots to establish more specific management criteria according to forest type and human impacts, enabling the implementation of forest management practices tailored to soil characteristics.

Our results highlight the critical role of national parks and reserves in preserving unmanaged forests with high levels of SOC. However, we found that the SOC stocks in these protected areas were similar to those in harvested forests. This principal conclusion was demonstrated through various factors influencing SOC stocks, many of which were related to forest structure and soil variables, in addition to the more well-known factors such as temperature and elevation. While precipitation was also an important factor, its impact on SOC stocks was less significant compared to temperature and elevation. Moreover, these findings align with a SOC mapping study in Patagonian forests (Martínez Pastur et al., 2022), which identified climatic variables, such as temperature and precipitation, as key drivers of carbon stocks. This suggests that beyond climate, forest management and structure play a more complex role in carbon storage, something we also observed when comparing protected areas to harvested forests, where SOC stocks were found to be similar.

This study provides valuable insights into the factors influencing SOC stocks, but there are several limitations to consider for future research. First, soil texture at the plot level was not analysed, despite its significant role in SOC dynamics through water retention, aeration, and aggregate stability. Future studies should include a detailed analysis of soil texture. Second, while forest management practices were evaluated, a more precise distinction among different management types (e.g., silvopastoral systems, selective cutting, thinning) would help better understand their specific impacts on SOC stocks. Additionally, the study's lack of a temporal dimension limits the ability to assess SOC dynamics over time, and future research should incorporate long-term monitoring. Lastly, microbial activity influences were not considered,

though they may significantly affect SOC heterogeneity. Addressing these limitations in future studies will enhance our understanding of SOC dynamics and improve forest management strategies for soil carbon storage in Patagonian forests.

Conclusions

We determined the SOC stocks in the Chilean forests of Patagonia, where the deciduous and evergreen forests had SOC stocks ranging from 50 tons ha⁻¹ to 361 tons ha⁻¹. SOC stock was a central analysis point for understanding the relevance of managed and unmanaged forests in high-stock regions. The SOC in different native forest types was stock-driven in various ways. Therefore, SOC stock changes in managed native forests do not necessarily lead to SOC stock loss; harvesting forests can be compared equally to untouched ones. However, reaching this conclusion requires accurate field-analysed laboratory data to assess potential SOC stock changes and their impacts on forest ecology and the managed landscape. Climate, topography, above- and below-ground drivers, and human impacts influence SOC stocks in native forests. These factors differentially influence SOC stocks in native forests, confirming our hypothesis. Therefore, identifying pivotal SOC drivers can improve our understanding of forest ecology and management.

CRediT authorship contribution statement

Mónica Toro-Manríquez: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Alejandro Huertas**

Herrera: Writing – review & editing, Validation, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. Soraya Villagrán Chacón: Investigation. Anaïs Pourtoy: Investigation. Samuel Planté: Investigation. Sabina Miguel Maluenda: Investigation. Guillermo Martínez Pastur: Writing – review & editing, Supervision, Conceptualization. Giovanni Daneri: Writing – review & editing, Resources, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. The statistical significance of climatic variables, including annual precipitation (PP, mm year⁻¹), temperature (°C) during the warmest (TEMP-Warm) and coldest month (TEMP-Cold), in forest types, soil types, and human impacts using one-way ANOVAs. The table shows each category's mean \pm standard error values. Different lowercase letters indicated significant differences according to the Fisher LSD test (p < 0.05). F(p) = Fisher test values and corresponding p-values for each factor. NP = N. pumilio, NA = N. antarctica, ND-NB = N. dombeyi-N. betuloides, EV = evergreen, EV

Forest types	PP	TEMP- Warm	TEMP-Cold	Soil types	PP	TEMP- Warm	TEMP-Cold	Human impacts	PP	TEMP- Warm	TEMP- Cold
NP	420.2 ± 14.3a	$15.5 \pm 0.2a$	−1.7 ± 0.2a	Andisols	741.4 ± 25.0c	17.1 ± 0.2b	−1.4 ± 0.2a	U	522.0 ± 45.3a	$15.2 \pm 0.3 a$	−1.8 ± 0.4a
NA	$\begin{array}{c} 568.1 \pm \\ 19.6 \mathrm{b} \end{array}$	$\begin{array}{c} 18.1 \pm \\ 0.2 b \end{array}$	-0.9 ± 0.2 ab	Entisols	471±41.7b	$18.2 \pm 0.4 \text{c}$	$-1.0~\pm$ 0.1a	В	$500.4 \pm 43.5a$	$\begin{array}{c} 16.4 \pm \\ 0.4 b \end{array}$	$-1.4 \pm 0.4a$
ND-NB	$883.3 \pm \\28.7c$	$17.4 \pm 0.2b$	$-0.2 \pm 0.2 bc$	Inceptisols	$487.1 \pm \\21.4b$	$\begin{array}{c} 16.6 \pm \\ 0.2 \mathrm{b} \end{array}$	$-1.1~\pm$ 0.2a	Н	476.6 \pm 24.6a	$15.8 \pm 0.2 \text{a}$	$-1.3\pm 0.2 \mathrm{bc}$
EV	967.7 \pm 67.5c	17.9 \pm 0.3b	$\textbf{0.5} \pm \textbf{0.4c}$	Spodosols	$290.9 \pm \\14.8a$	$13.5 \pm 0.1 \text{a}$	$0.2 \pm 0.2 b$	L	636.3 \pm 65.1ab	$17.8 \pm 0.3 bc$	$-1.2\pm 0.2\mathrm{b}$
MI	$609.6 \pm 45.2b$	$16.4 \pm 0.4 \text{a}$	$-0.6~\pm$ 0.4ab					H + L	$703.7 \pm \\34.7b$	$18.1 \pm 0.1c$	$\begin{array}{l} -0.2 \pm \\ 0.2c \end{array}$
F (p)	99.5 (<0.001)	46.4 (<0.001)	14.8 (<0.001)	F (p)	35.6 (<0.001)	22.9 (<0.001)	18.7 (<0.001)	F (p)	0.7 (0.028)	14.0 (<0.001)	3.0 (0.019)

Appendix B. The statistical significance of topographic variables, including altitude (ALT, m a.s.l.), slope (SLOPE, %), and aspect (N-S and E-W), in forest types, soil types, and human impacts using one-way ANOVAs. The table shows each category's mean \pm standard error values. Different lowercase letters indicated significant differences according to the Fisher LSD test (p < 0.05). F(p) = Fisher test values and corresponding p-values for each factor. NP = N. pumilio, NA = N. antarctica, ND-NB = N. dombeyi-N. betuloides, EV = evergreen, MI = mixed broadleaved forests, U = unmanaged, B = burned, H = harvesting, L = livestock, and H + L = harvesting + livestock

Forest types	ALT	SLOPE	N-S	E-W	Soil types	ALT	SLOPE	N-S	E-W	Human impacts	ALT	SLOPE	N-S	E-W
NP	591.5 \pm	4.1 ±	$-0.2~\pm$	$0.1~\pm$	Andisols	592.7 \pm	6.6 ±	$-0.2~\pm$	$-0.3~\pm$	U	554.1	6.3 ±	$-0.3~\pm$	0.0 ±
	34.2b	0.3b	0.1ba	0.1b		29.9b	0.6b	0.1a	0.1a		± 74.0bc	0.9ab	0.1ab	0.1a
NA	465.6 \pm	3.3 \pm	0.1 \pm	0.1 \pm	Entisols	519.8 \pm	5.0 \pm	0.1 \pm	$-0.2~\pm$	В	550.1	4.4 \pm	$-0.2~\pm$	$0.2 \pm$
	34.3ab	0.4a	0.1b	0.1b		79.6b	1.1b	0.4ab	0.2ab		± 83.4bc	0.9a	0.2ab	0.1b
ND-	338.5 \pm	8.6 \pm	$-0.6 \pm$	$-0.5~\pm$	Inceptisols	487.9 \pm	3.8 \pm	$-0.3~\pm$	$0.0 \pm$	H	536.4	4.1 \pm	$-0.1~\pm$	$-0.1~\pm$
NB	39.4a	1.4c	0.1a	0.1a		33.8b	0.4ab	0.1a	0.1ab		\pm 35.2b	0.4a	0.1b	0.1a
EV	322.1 \pm	6.3 \pm	$-0.5~\pm$	$-0.4~\pm$	Spodosols	177.2 \pm	2.1 \pm	$0.3 \pm$	$0.3 \pm$	L	619.6	$6.7~\pm$	$-0.4~\pm$	$-0.1~\pm$
	51.6a	1.4bc	0.1ab	0.1a		11.8a	0.2a	0.1b	0.2b		± 42.3c	1.3b	0.2a	0.1a
MI	348.7 \pm	$6.3 \pm$	$-0.1~\pm$	$-0.6~\pm$						H + L	347.2	4.2 \pm	$-0.3~\pm$	$-0.2\ \pm$
	66.1ab	1.4bc	0.2ab	0.1a							$^{\pm}$ 29.4a	0.6a	0.1ab	0.1a
F (p)	9.7	8.4	3.9	9.9	F (p)	26.5	9.5	5.3	3.7	F (p)	4.0	3.4	2.1	4.4
	(<0.001)	(<0.001)	(0.004)	(<0.001)		(<0.001)	(<0.001)	(0.002)	(0.012)		(0.036)	(0.011)	(0.046)	(0.002)

Appendix C. The statistical significance of forest structure, including basal area (BA, m^2 ha⁻¹), dominant height (DH, m), diameter at breast height (DBH, cm), tree density (DEN, trees ha⁻¹), and canopy cover (CC, %), in forest types, soil types, and human impacts using one-way ANOVAs. The table shows each category's mean \pm standard error values. Different lowercase letters indicated significant differences according to the Fisher LSD test (p < 0.05). F(p) = Fisher test values and corresponding p-values for each factor. NP = N. pumilio, NA = N. antarctica, ND-NB = N. dombeyi-N. betuloides, EV = evergreen, MI = mixed broadleaved forests, U = unmanaged, B = burned, H = harvesting, L = livestock, and H + L = harvesting + livestock

Forest types	BA	DH	DBH	DEN	CC	Soil types	BA	DH	DBH	DEN	CC	Human impacts	BA	DH	DBH	DEN	CC
NP	35.6 \pm	18.3 \pm	45.0 ±	638	71.7 \pm	Andisols	29.8 \pm	16.2 \pm	39.8 \pm	970.1 \pm	68.4 ±	U	50.8 ±	19.8 ±	43.0 ±	975.3 \pm	79.6 ±
	2.2b	0.6b	2.6b	$\pm 81.8ab$	2.0b		2.4	0.9	3.0	161.8b	2.5		4.3c	1.1b	3.0	180.6ab	2.3c
NA	23.4 \pm	$9.2 \pm$	24.2 \pm	957.6 \pm	58.7 \pm	Entisols	40.6 \pm	14.1 \pm	33.4 \pm	599.5 \pm	71.9 \pm	В	9.3 \pm	8.7 \pm	41.9 \pm	136.0 \pm	35.9 \pm
	2.9a	0.9a	2.3a	234.3b	3.1a		9.4	2.8	3.1	148.0a	9.1		2.0a	1.7a	11.2	60.4a	5.2a
ND-NB	31.5 \pm	21.7 \pm	43.2 \pm	684.5 \pm	73.2 \pm	Inceptisols	31.3 \pm	16.6 \pm	42.3 \pm	508.2 \pm	68.1 \pm	H	34.2 \pm	$18.9 \; \pm$	40.9 \pm	731.7 \pm	74.6 \pm
	4.8b	1.7b	4.4ab	151.6ab	4.1b		2.2	0.7	2.8	73.3a	2.1		2.2bc	0.6b	2.2	114.8ab	1.6bc
EV	30.3 \pm	17.2 \pm	53.4 \pm	600.1 \pm	67.9 \pm	Spodosols	30.4 \pm	16.7 \pm	35.3 \pm	755.7 \pm	61.0 \pm	L	24.6 \pm	13.8 \pm	39.6 \pm	1063.9 \pm	69.4 \pm
	5.0ab	2.1b	8.0b	239.3ab	5.9b		6.1	1.8	4.5	241.0ab	6.6		4.0b	2.4b	6.6	441.6b	4.3bc
MI	21.9 \pm	17.2 \pm	36.3 \pm	494.1 \pm	60.5 \pm							H + L	$26.0\ \pm$	$14.5~\pm$	38.4 \pm	588	62.6 \pm
	4.9a	2.3b	6.2ab	207.7a	7.0a								2.7b	1.1b	3.8	$\pm 115.8 ab$	3.2b
F	4.3	23.1	6.7	1.0	5.1	F	0.7	1.7	1.5	2.9	0.4	F	14.7	16.0	0.3	2.7	22.6
<i>(p)</i>	(0.003)	(<0.001)	(<0.001)	(0.034)	(0.001)	(p)	(0.585)	(0.176)	(0.212)	(0.037)	(0.732)	(p)	(< 0.001)	(<0.001)	(0.876)	(0.034)	(<0.001)

Appendix D. The statistical significance of soil parameters, including soil organic matter concentration (SOM, %), soil organic carbon content (C, %), soil moisture (SM, %), pH, soil resistance to penetration (SR, kgf cm $^{-2}$), and soil bulk density (SBD, kg m $^{-3}$), in forest types, soil types, and human impacts using one-way ANOVAs. The table shows each category's mean \pm standard error values. Different lowercase letters indicated significant differences according to the Fisher LSD test (p < 0.05). F(p) = Fisher test values and corresponding p-values for each factor. NP = N. pumilio, NA = N. antarctica, ND-NB = N. dombeyi-N. betuloides, EV = evergreen, MI = mixed broadleaved forests, U = unmanaged, B = burned, H = harvesting, L = livestock, and H + L = harvesting + livestock

Forest types	SOM	C	SM	hф	SR	SBD	Soil types	SOM	C	SM	Нd	SR	SBD	Human impacts	SOM	C	$_{ m SM}$	Нd	SR	SBD
NP	± 6.9 ∓	$12.8 \pm$	43.6 ±	5.0 ±	$\textbf{2.4} \pm$	459.8 ±	Andisols	$26.5\pm$	$12.0 \pm$	76.4 ±	4.9 ±	$2.5 \; \pm$	$361.4 \pm$	U	28.0 ±	$13.6 \; \pm$	47.6 ±	4.8 ±	$1.8 \pm$	$390.5 \; \pm$
	1.3ab	0.6b	2.7a	0.0b	0.1a	20.2b		1.7b	0.9a	9.1	0.1a	0.2	17.6a		2.3	1.1	7.5	0.1a	0.2a	35.3a
NA	$22.0 \pm$	$10.1~\pm$	$63.6 \; \pm$	± 0.5	$3.0 \pm$	404.3 ±	Entisols	$21.7 \pm$	$12.0 \pm$	$67.1 \pm$	$5.7 \pm$	$\textbf{2.5} \; \pm$	$\textbf{458.2} \pm$	В	$24.9 \; \pm$	$10.3 \; \pm$	$38.5 \; \pm$	4.8 +	$3.3 \pm$	564.4 ±
	2.6a	1.3ab	12.8a	0.1b	0.2b	33.3ab		4.7a	2.3a	16.1	0.4b	0.7	84.1ab		3.0	1.2	8.9	0.1a	0.3b	54.8b
ND-NB	$28.9 \; \pm$	$13.5 \; \pm$	76.6 ±	4.5 +	$\textbf{2.5} \pm$	$393.9 \; \pm$	Inceptisols		$10.9~\pm$	48.9 ±	4.9 ±	2.6 ±	$\textbf{502.8} \pm$	Н	$\textbf{27.4} \pm$	$13.1~\pm$	$51.3 \pm$	5.0 ±	2.4 ±	443.7 ±
	3.5b	1.7b	9.5ab	0.1a	0.3a	51.5ab			0.6a	3.9	0.1a	0.1	23.4b		1.6	8.0	3.8	0.1b	0.1ba	21.8a
EV	$29.7 \; \pm$	$14.5 \; \pm$	$119.7 \pm$	4.8 ⊞	$\textbf{2.5} \pm$	$331.1 ~\pm$	Spodosols	$39.1 \pm$	$18.9 \pm 2b$	43.9 ±	4.5 ±	$\textbf{2.5} \; \pm$	$\textbf{371.5} \pm$	Г	$\textbf{23.5} \; \pm$	$10.2 \; \pm$	$64.2 \pm$	$\textbf{5.0} \pm$	$2.5 \; \pm$	$357.3 \; \pm$
	2.5b	1.5b	16.8b	0.2b	0.3a	36.2a		3.8c		7.1	0.1a	0.2	48.8a		2.5	1.0	10.7	0.1b	0.3ba	41.6a
MI	$16.4~\pm$	7.5 ±	$\textbf{51.5} \pm$	± 6.4	$3.0 \pm$	$\textbf{584.2} \; \pm$								H + L	$21.7 \pm$	$10.8 \; \pm$	$82.5 \; \pm$	4.9 ±	$3.0 \pm$	439.3 \pm
	2.7a	1.2a	8.2a	0.1b	0.4b	69.0c									2.2	1.2	12.1	0.1ab	0.2b	34.7a
щ	3.9	4.2	6.6	3.4	2.5	3.9	H		8.3		3.9	0.2	7.1	H	1.7	1.7	6.0	3.9	4.9	2.7
(<i>d</i>)	(0.005)	(0.003)	(< 0.001)	(0.012)	(0.043)	(0.004)	(<i>a</i>)	(<0.001)	(<0.001)	(0.201)	(0.005)	(0.879)	(<0.001)	(<i>d</i>)	(0.156)	(0.155)	(0.473)	(0.002)	(0.001)	(0.030)

Appendix E. The statistical significance of forest floor characteristics, including the understory dominant height (UDH, cm), the cover of vascular plants (VP, %), non-vascular plants such as mosses (M, %), liverworts (LIV, %), and lichens (LI, %), the cover of fungi (F, %), litter (LIT, %), debris categorised by size: decaying wood < 5 cm (R3, %), 5-10 cm (R2, %), and > 10 cm (R1, %), cover of stones (ST, %), bare soil (BS, %), dung (DU, %), and roots (RO, %), in forest types, soil types, and human impacts using one-way ANOVAs. The table shows each category's mean \pm standard error values. Different lowercase letters indicated significant differences according to the Fisher LSD test (p < 0.05). F(p) = Fisher test values and corresponding p-values for each factor. NP = N. pumilio, NA = N. antarctica, ND-NB = N. dombeyi-N. betuloides, EV = evergreen, EV = ever

Factors	UDH	VP	M	LIV	LI	F	LIT	R1	R2	R3	ST	BS	DU	RO
Forest														
types														
NP	30.0 \pm	$51.3\pm3.6a$		0.1 ± 0.1	$\textbf{0.7} \pm \textbf{0.2}$	0.1 ± 0.0		8.3 ± 1.0 ab	3.1 ± 0.4 b		$\textbf{0.7} \pm \textbf{0.3}$		0.4 ± 0.1	$\textbf{0.4} \pm \textbf{0.1a}$
	1.8a		0.6a				1.9			1.0ab		1.6bc		
NA	33.3 \pm	85.0 \pm	$1.8 \pm$	0.0 ± 0.0	0.2 ± 0.1	0.0 ± 0.0		1.4 ± 0.3 a	$0.4\pm0.1a$	3.1 \pm	0.3 ± 0.3		0.4 ± 0.1	$0.0 \pm 0.0 a$
	3.8ab	7.6ab	0.5a				2.9			0.8a		1.2ab		
ND-NB	28.7 \pm	$46.5\pm9.8a$		0.0 ± 0.0	0.5 ± 0.3	0.1 ± 0.1		$3.8 \pm 1.2a$	$2.1~\pm$	12.5 \pm	0.3 ± 0.2	$1.5\pm0.8a$	0.8 ± 0.6	0.0 ± 0.0 a
	6.6a		0.8ab				4.3		0.9ab	5.5b				
EV	$51.3 \pm$	101.4 \pm	6.8 \pm	0.2 ± 0.1	0.2 ± 0.1	0.0 ± 0.0		$2.2 \pm 0.7a$	$0.7 \pm 0.2a$	12.7 \pm	0.4 ± 0.3		1.1 ± 0.8	$0.8 \pm 0.3b$
	5.0c	13.3b	1.9b				3.7			4.5b		4.2c		
MI	44.9 \pm	82.6 \pm	4.7 \pm	0.0 ± 0.0	0.1 ± 0.1	$\textbf{0.0} \pm \textbf{0.0}$	27.7 \pm	$11.1 \pm 4.4b$		9.4 \pm	0.0 ± 0.0		0.5 ± 0.3	$0.2\pm0.1a$
	5.5bc	16.1ab	1.7ab				4.4		1.0ab	2.0ab		3.8bc		
F (p)	6.0	9.4	3.8	0.9	1.8	1.3	1.9	10.8	7.5	3.6	0.4	4.6	1.1 (0.374)	
Cail tumos	(<0.001)	(<0.001)	(0.005)	(0.444)	(0.137)	(0.289)	(0.111)	(<0.001)	(<0.001)	(0.008)	(0.815)	(0.001)		(<0.001)
Soil types Andisols	240 22	63.1 ± 5.3b	21 05	00 + 00	02 01	00 + 00	22.0	$2.9 \pm 0.4a$	1.3 ± 0.3 a	72	02 02	E 1 1 0o	$0.7\pm0.2a$	01 010
Alidisois	34.9 ± 3.2	03.1 ± 3.30	3.1 ± 0.3	0.0 ± 0.0	0.2 ± 0.1	0.0 ± 0.0	23.6 ± 2.1	2.9 ± 0.4a	1.3 ± 0.3a	7.2 ± 1.1a	0.3 ± 0.2	3.1 ± 1.0a	$0.7 \pm 0.2a$	0.1 ± 0.1a
Entisols	33.5 ± 6.1	70 F J	02 + 02	0.0 ± 0.0	00 + 00	00 + 00		1.3 ± 0.6 a	$4.3\pm1.8b$	1.1a 19.5 ±	0.0 ± 0.0	1E 2	$3.0 \pm 2.3b$	0.2 0.20
EHUSOIS	33.3 ± 0.1	79.5 ± 23.5b	0.2 ± 0.2	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	8.5	1.3 ± 0.0a	4.3 ± 1.60	7.2b	0.0 ± 0.0	13.3 ± 9.2b	3.0 ± 2.30	0.2 ± 0.2a
Inceptisols	22 5 1 2 1	$71.1 \pm 5.1b$	22 07	01 + 00	07 02	01 + 00		$5.6 \pm 0.7a$	$2.4~\pm$	8.0 ±	0.7 ± 0.3		0.3 ± 0.1 a	0 = 1 0 1 h
inceptisois	33.5 ± 2.1	/1.1 ± 5.10	3.2 ± 0.7	0.1 ± 0.0	0.7 ± 0.2	0.1 ± 0.0	22.4 ± 1.9	5.0 ± 0.7a	2.4 ± 0.3ba	8.0 ± 1.3a	0.7 ± 0.3	12.5 ± 1.6b	$0.3 \pm 0.1a$	0.5 ± 0.1D
Spodosols	22.2 2.2	$38.2 \pm 7.3a$	26 00	02 02	04 04	00100		23.5 ± 4.2b		1.3a 1.2 ±	0.2 ± 0.2		0.0 ± 0.0 a	0.0 0.00
Spodosois	33.2 ± 3.3	38.2 ± 7.3a	2.0 ± 0.8	0.3 ± 0.3	0.4 ± 0.4	0.0 ± 0.0	20.2 ± 4.9	23.5 ± 4.20	2.9 ± 1.4ba	1.2 ± 0.9a	0.2 ± 0.2	10.4 ± 3.7b	$0.0 \pm 0.0a$	$0.0 \pm 0.0a$
F (p)	0.1 (0.990)	2.4 (0.011)	1 4	1.0	1.6	0.7	0.9	27.5	2.4 (0.071)		1.3	3.3	5.9	5.4 (0.002)
Ι (μ)	0.1 (0.550)	2.4 (0.011)	(0.248)	(0.392)	(0.189)	(0.562)	(0.465)	(<0.001)	2.7 (0.0/1)	(0.009)	(0.287)	(0.023)	(<0.001)	3.4 (0.002)
Appendix E	. (cont.).													
Human	UDH	VP	M	LIV	LI	F	LIT	R1	R2	R3	ST	BS	DU	RO
impacts	0511	**		22.		•	22.2		112	110	01	20	20	110
U	38.5 ±	47.7 ±	7.1 ± 2.0 b	0.3 ± 0.2	$2.0.5 \pm 0.3$	3 0.0 ± 0.0	33.7 ±	7.8 ±	4.6 ± 1.10	: 10.1 ±	$2.7 \pm 1.$	2b 4.9 ± 1	.9a 0.0 ± 0.0	0.2 ± 0.1
	4.1b	6.2a					3.2c	1.6bc		2.0b				
В	28.2 \pm	53.7 ±	$2.0 \pm 0.7a$	0.0 ± 0.0	0.4 ± 0.2	0.1 ± 0.1	8.8 ± 2.7	a 12.4 \pm	0.0 ± 0.0	a 0.5 ±	$0.0 \pm 0.$	0a 19.5 ±	0.7 ± 0.3	0.1 ± 0.1
	5.7ab	12.2ab						4.5c		0.2a		3.6b		
Н	36.6 ±	59.9 ±	$1.9 \pm 0.3a$	0.1 ± 0.0	0.8 ± 0.2	0.1 ± 0.0	25.8 ±	7.8 ±	$2.7 \pm$	8.7 ±	$0.3 \pm 0.$	2a 9.3 ±	0.5 ± 0.3	0.5 ± 0.1
	2.3b	4.7ab		010	, 0.2	, 0.0	2.1bc	0.8bc	0.3bc	1.5b	0.	1.7ab	011	
L	22.5 ±	58.2 ±	$3.1 \pm 1.9a$	0.0 ± 0.0	0.1 ± 0.1	0.0 ± 0.0			a 1.2 ± 0.61		$0.1\pm0.$.6a 0.3 ± 0.3	0.1 ± 0.1
	3.9a	7.8ab					4.1b			0.6ab				
H + L	33.3 ±	91.6 ±	$3.2 \pm 0.8a$	0.0 ± 0.0	0.1 ± 0.0	0.0 ± 0.0		1.8 ± 0.4	a 1.0 ±	8.7 ±	$0.0 \pm 0.$	0a 11.2 ±	0.9 ± 0.3	0.3 ± 0.1
. –	3.3ab	8.0b		010	, 010	0.0	2.6b	0	0.3ab	1.9b	0.	2.2ab	0	
F (p)	6.8	2.8 (0.027)	5.0	2.4	1.3	1.0	7.2	5.7	7.2	3.6	6.6	4.1	1.4	1.3
· 4)	(<0.001)	2.0 (0.027)	(<0.001)	(0.053)	(0.289)	(0.386)	(<0.001)	(<0.001)	(<0.001)	(0.007)	(<0.001			(0.279)
	(<0.001)		(<0.001)	(0.053)	(0.209)	(0.360)	(<0.001)	(<0.001)	(<0.001)	(0.007)	(<0.001	, (0.004)	(0.231)	(0.2/9)

Data availability

Data will be made available on request.

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