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Impact of land use on aboveground carbon storage in a Tropical Montane Forest in Central Andes of Peru

Abstract

Tropical montane forests play a key role in carbon storage, but they face constant threats from land use change. However, the relations between land use change, vegetation structure and carbon stocks remain poorly understood. We aimed to assess aboveground carbon storage in four land use types within a montane forest in the Central Andes of Peru. We quantified carbon stocks from trees, crops, dead biomass, and herbaceous plants across 61 sample plots. We identified a gradient of carbon storage from highest to lowest across land uses: Old-growth Montane Forest ($193.03 \pm 68.2 \text{ t ha}^{-1}$), Montane Forest in Regeneration ($87.52 \pm 50.29 \text{ t ha}^{-1}$), Agroforestry ($48.67 \pm 24.05 \text{ t ha}^{-1}$), and Croplands ($12.46 \pm 9.75 \text{ t ha}^{-1}$). Vegetation structure variables (tree height, DBH, basal area, and tree density, canopy cover) showed a significant positive correlation with aboveground carbon stocks (r^2 ranging from 0.63 to 0.91). In contrast, soil physical properties (textural class (% sand, silt, and clay) and soil bulk density) did not correlate with aboveground carbon stocks. Our estimations indicate that trees are a great carbon pool and the presence of trees with $\text{DBH} \geq 30$ often indicates conservation status. This study proves that there is a loss of carbon storage and vegetation structural characteristics as land use intensifies. Restoration of degraded forests and adoption of an agroforestry approach offer promising alternatives to preserve ecosystem functions and mitigate climate change.

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1 Introduction

Tropical montane forests (TMFs), located between 23.5°N and 23.5°S latitude, represent almost 8% of the world's tropical forests (Spracklen and Righelato, 2014). They are located on the eastern slope of the Peruvian Andes (Young and León, 2000), covering a high portion of the Yunga ecoregion, which represents nearly 14% of the national territory (Tovar et al., 2010). TMFs are unique ecosystems due to their significant altitudinal range (800 to 3500 m a.s.l.), which creates a wide variety of microhabitats and, in turn, a rich diversity of species and high rates of endemism, establishing these forests as global biodiversity hotspots (Young and León, 2000; Myers et al., 2000; Tejedor et al., 2012). In addition, TMFs deliver essential ecosystem services, including carbon sequestration, hydrological cycle regulation, water quality maintenance, and soil erosion control (Martínez et al., 2009; Bruijnzeel, Mulligan, and Scatena, 2011; Spracklen and Righelato, 2014).

Despite their ecological importance, TMFs remain understudied compared to lowland tropical forests. They face strong anthropogenic pressures, including slash-and-burn agriculture, cattle ranching, logging, road construction, and urban expansion (Bush, Hanselman, & Hoogiemstra, 2007; Lucich, Villena, & Quinteros, 2015). Deforestation and landscape fragmentation exacerbate TMFs' vulnerability, which is further intensified by climate change (Fadrique et al., 2018). These changes contribute to increased biodiversity loss, as rising temperatures force species from lower tropical forests to migrate to higher altitudes. This shift results in competition for space and resources with the native TMFs species (Cayuela, Benayas, & Echeverría, 2006; Tejedor et al., 2012).

Land use and land cover change significantly impact both local and regional climate (Denman et al., 2007). Almost one-third of total greenhouse gas emissions are attributed to deforestation and land use change (Jia et al., 2019). In tropical regions, deforestation alone accounts for about one-tenth of total fossil fuel emissions (Denning, 2018). In Peru, up to 2.5 million ha of tropical Peruvian Amazon forests were lost from 2001 to 2019 (Ministerio del Ambiente, 2020), with 250,411 ha lost in Chanchamayo alone (Ministerio del Ambiente, 2020). In our spe-

cific study basin, 124 ha (6.9%) were deforested between 2001 and 2020 (Global Forest Watch, 2021).

While several studies have shown that land use change alters vegetation structure and diversity, which are linked to aboveground carbon stocks (Häger and Avalos, 2017; Solomon et al., 2018; Vizcaíno, Williams, and Ashjornsen, 2019), few studies have quantified how these relationships unfold in tropical montane forests of the Central Peruvian Andes. Moreover, the relative contributions of different aboveground biomass components (e.g., dead wood, herbaceous plants, crops) to total aboveground carbon stocks across land use types are still poorly documented in these ecosystems.

This study aims to fill existing knowledge gaps by examining how different land use types influence aboveground carbon stocks and their allocation among vegetation components in tropical montane forests of central Peru. Specifically, we focus on 1) estimate aboveground biomass carbon stocks across different land uses, 2) identify the distribution of carbon among different aboveground biomass components (dead biomass, trees, herbaceous plants, and crops) in relation to land use, and 3) evaluate the relationship between aboveground carbon stocks, vegetation structure, and soil physical characteristics.

2 Materials and methods

2.1 Description of the study area

The study area is located in the Chanchamayo province of Peru, along the eastern slope of the Andes Mountain range. Two study sites were selected: the Toro River Catchment (11° 2' 32.539" S 75° 22' 7.223" W) and the northwest area of the Pampa Hermosa National Sanctuary (10° 59' 47.094" S 75° 25' 49.076" W), as a reference area (Figure 1).

The Toro River Catchment (TRC; 1854 ha) is located in the Yunga natural region, from 600 to 2500 m a.s.l., and includes Lower Montane Forest and Montane Forest ecosystems (Ministerio del Ambiente, 2019). The average minimum and maximum temperatures are 16.2 ± 0.4 °C and 24.5 ± 0.4 °C, respectively. It has an annual average rainfall of 3142 ± 398.6 mm/

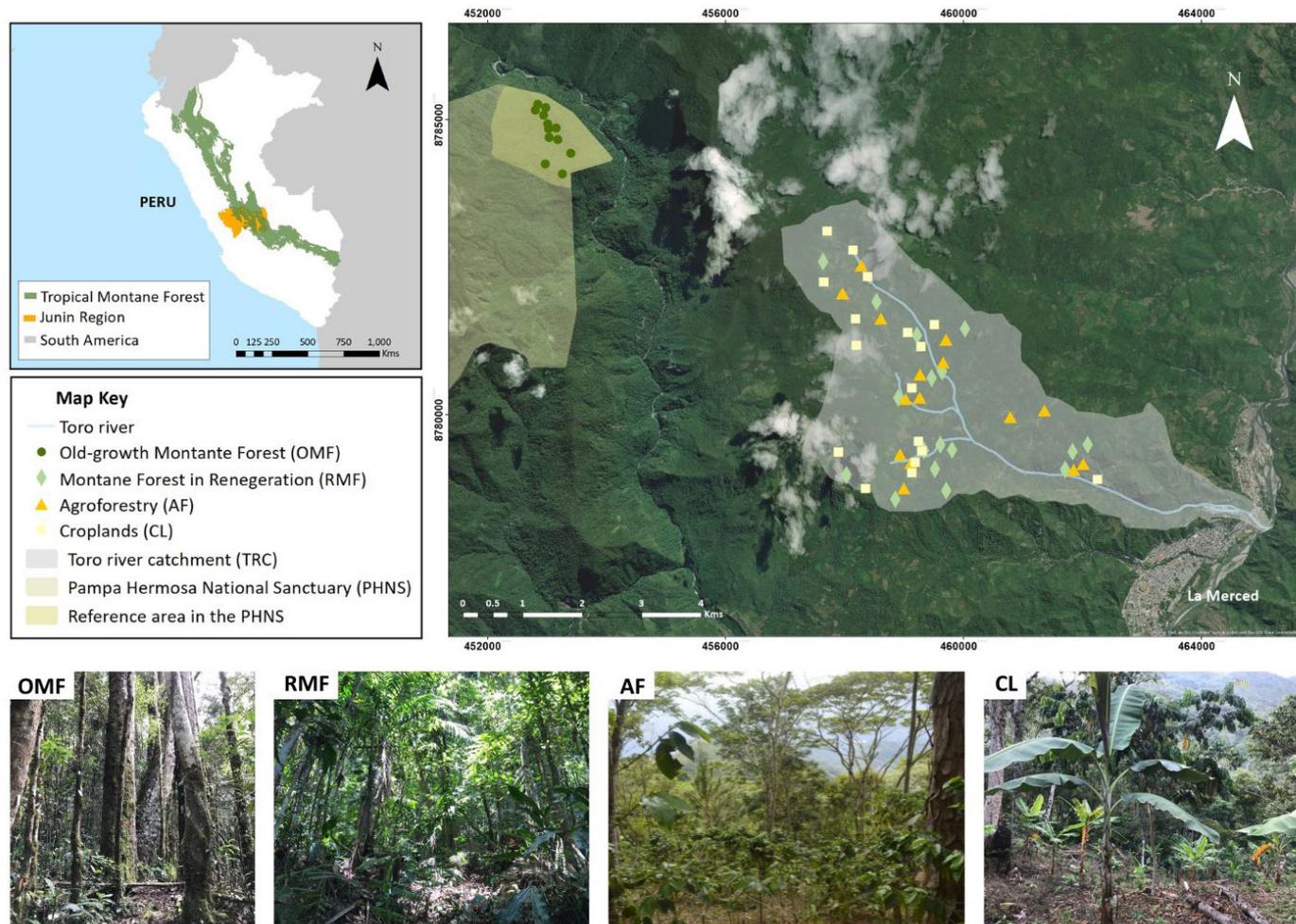


Figure 1. Distribution of sampling plots per land use in the study area: Pampa Hermosa National Sanctuary (reference area) and Toro River catchment.

year and annual potential evapotranspiration (PET) of 1347.6 ± 30.6 mm/year. TRC is the main source of drinking water for the Chanchamayo district and is a key agricultural hub. The area is characterized by three main land uses: Montane Forest in Regeneration (RMF), Agroforestry (AF), and Croplands (CL).

RMF, or secondary forests, includes areas that were deforested and abandoned following agricultural use, allowing for natural regeneration. There is selective logging for species such as “Roble” (*Quercus sp.*), “Nogal” (*Juglans sp.*), “Cedro” (*Cedrela odorata* L.), and “Diablo Fuerte” (*Podocarpus sp.*). Reforestation efforts have introduced “Ulcumano” trees (*Retrophyllum rospigliosii*) in some areas. The floristic composition includes families such as Meliaceae, Moraceae, Sapindaceae, Asteraceae, Araceae, Lauraceae, Piperaceae, Conmelinaceae, and Bombacaceae.

AF includes coffee agroforestry systems associated with a variety of species such as “Nogal” (*Juglans neotropica*), “Pacae” (*Inga sp.*), “Cedro” (*Cedrela odorata*), “Ceiba” (Malvaceae), Fabaceae, “Palo algodón” Bombacaceae, “Ulcumano” (*Retrophyllum rospigliosii*), “palta” (*Persea americana*), “Cecropia” (*Cecropia sp.*).

CL land use is characterized by the dominance of herbaceous plants and the absence of forest cover. It includes sun-grown coffee plantations, “granadilla” (*Passiflora spp.*) and *Capsicum pubescens* association, as well as mixtures of *Passiflora spp.* with vegetables such as “camote” (*Ipomoea batatas*), “calabaza” (*Cucurbita ficifolia*), “maíz” (*Zea mays* L), and “caigua” (*Cyclanthera pedata*). Additionally, CL includes banana plantations, abandoned pastures, sugar cane fields, and citrus crops.

Pampa Hermosa National Sanctuary (PHNS), a natural protected area by Peruvian Government, is located between Chanchamayo and Tarma districts. PHNS ranges between 1,340 and 3,960 m a.s.l. with slopes of up to 70%. The average maximum and minimum temperatures are 19.5 ± 0.5 °C and 10.7 ± 0.4 °C, respectively. It has an average annual precipitation of $2,494.7 \pm 330.5$ mm/year and an annual potential evapotranspiration of $1,068.6 \pm 27.3$ mm/year. PHNS encompasses a transitional complex of Andean-Amazonian ecosystems, including the Humid Puna and Yunga ecoregions. It contains intact areas of Montane forests. However, some areas of the Sanctuary have been disturbed by the selective extraction of timber from the last century until its establishment in 1997, which are currently undergoing natural regeneration processes (Ministerio del Ambiente, 2009; La Torre et al. 2012). An area of 1884.9 ha was taken as a reference zone, called Old-growth Montane Forest (OMF), located in the northwestern part of the Sanctuary within the Ucumayo basin, between 1200 and 1900 m a.s.l. It includes intact Montane forests and ancient *Cedrela spp.* stands dating back over 600 years, as well as “Diablo Fuerte” (*Podocarpus sp.*). Additionally, there are secondary forests that have undergone selective logging but have been conserved for almost 40 years (La Torre et al., 2007).

2.2 Sampling

A total of 61 plots were established under random stratified sampling, following the methodology by RAINFOR (2016). The plots were distributed across land uses: OMF (13 plots), RMF (16 plots), AF (15 plots), and CL (17 plots). Each plot measured 0.1 ha (50 m x 20 m), a size determined by the dimensions and distribution of the land use types, particularly AF and CL, which typically ranged from 0.2 to 0.5 ha. All plots were located at a minimum distance of 15 m

from roads. The inventory was carried out between 2019 and 2020.

2.3 Estimation of carbon stocks from live and dead aboveground biomass

In each plot, we measured both live and dead trees with a diameter at breast height (DBH) ≥ 30 cm. Three subplots (10 x 10 m) were randomly established within each plot to measure alive and dead trees with DBH from 5 to 30 cm. Herbaceous vegetation and leaf litter samples were collected from 0.5 x 0.5 m quadrants (Gibbon et al., 2010), with six repetitions per plot. In the AF and CL subplots, samples included coffee bushes, banana crops, and other types of vegetation. It was assumed that 50% of the dry biomass corresponds to carbon stock (Chave et al., 2005).

2.3.1 Trees

Due to the lack of specific allometric equations for montane forests, four equations for tropical zones with similar climate and precipitation conditions to estimate aboveground biomass were applied (AGB; Table 1). Specific allometric equations were applied for trees in agroforestry and crop areas (Table 2). Only trees with $DBH \geq 5$ cm were considered, as allometric equations often have limitations when applied with smaller DBH values. Some trees were identified with the help of a botanist, mateiro or local people; however, a consistent taxonomic identification of trees through all the plots was not possible for this study. Because of that, the same average wood density value was used (0.614 g/m^3) for all trees and applied to equations as required. This value was suggested by Chave et al. (2006) for the Northwestern Amazon area, in which the study area is located.

Table 1. Allometric equations for the estimation of aboveground biomass. Where AGB: Aboveground biomass in kilograms, DBH: Diameter at breast height in centimeters taken at approximately 1.3 m, ρ : Wood density in g/cm^3 , H: Tree total height in meters.

Equation	Formula	Author
Eq-1	$AGB = 0.0509 \times \rho (DBH)^2 H$	Chave et al., 2005
Eq-2	$AGB = \rho \times \exp \{-1.239 + \ln 1.980 (DBH) + 0.207 ((\ln(DBH))^2 - 0.0281 ((DBH)^3)\}$	Chave et al., 2005
Eq-3	$AGB = \exp \{-2,134 + 2,530 \times \ln(DBH)\}$	Brown, 1997
Eq-4	$AGB = 0.0673 \times (\rho (DBH)^2 H)^{0.967}$	Chave et al., 2014

Table 2. Allometric equations for crops. AGB: Aboveground biomass in kilograms, DBH: Diameter at breast height in centimeters taken at approximately 1.3 m, D: Diameter taken at 15 cm above the ground, H: Tree total height in meters.

Specie	Equation	Author
<i>Inga sp.</i>	$\text{Log}_{10} \text{AGB} = -0.889 + 2.317 \times \text{log}_{10} \text{DBH}$	Segura et al. (2006)
<i>Eucalyptus sp.</i>	$\text{AGBB} = 1.22 \times \text{DBH}^2 \times \text{H} \times 0.01$	Senelwa and Sims (1998)
Multispecies of shade trees	$\text{Log}_{10} \text{AGB} = -0.834 + 2.223 \times \text{log}_{10} \text{DBH}$	Segura et al. (2006)
<i>Bambusa sp.</i>	$\text{AGB} = 0.2223 \times (\text{DBH})^{2.3264}$	Gibbon et al. (2010)
<i>Musa paradisiaca</i>	$\text{AGB} = 0.030 \times \text{DBH}^{2.13}$	Van Noordwijk (2002)
<i>Coffea arabica</i>	$\text{Log}_{10} (\text{AGB}) = -1.113 + 1.578 * \text{Log}_{10} (\text{D}) + 0.581 * \text{Log}_{10} (\text{H})$	Segura et al. (2006)

2.3.2 Crops

Both height and diameter at 15 cm above the soil level were measured in coffee plants, focusing on individuals with a diameter up to 8 cm due to limitations of the equation with greater diameters (Segura et al., 2006; Rugnitz et al. (2009). Diameter and height of bananas pseudo-trunks were recorded, with measurements limited to individuals with a maximum diameter of 28 cm as suggested by Rugnitz et al. (2009; Table 2).

2.3.3 Herbaceous

Herbaceous samples were dried at 70 °C until they reached a constant weight to calculate dry matter weight (Gibbon et al., 2010). The same procedure was applied to crop samples, including bell peppers, corn, passionfruit, aromatic herbs, and tubers.

2.3.4 Dead biomass

We measured diameter (cm) and length (m) of dead trees, fallen trunks and tree stumps and classified their decomposition status (low, medium, or high) following the methodologies by Chao and Phillips (2005) and Cuellar and Salazar (2016). Logs in advanced or high stages of decomposition were excluded from calculations.

For standing dead trees with branches, we used Eq-1 but applied a 3% reduction to account for foliage loss (Goslee et al., 2018). For standing dead trees without branches, tree stumps and fallen dead trees, we used the equation proposed by Rugnitz et al. (2009) and modified by Cuellar and Salazar (2016; formula 1), which incorporated density values based on the trunk's decomposition status (Table 3).

Formula 1:

$$B = (0.7854 \times D^2) \times L \times S$$

Where:

B = Biomass of dead wood in kg

L = trunk length in cm

D = trunk diameter in cm

S = wood density (g/cm^3)

Table 3. Density according to the state of decomposition of the wood.

Decomposition status	Wood density (g/cm^3)	Author
Low	0,38	Wicke et al. 2005
Middle	0,22	Wicke et al. 2005

Dead leaves, fruits, and trunks with a diameter less than 1 cm were considered litter. Samples were dried at 70 °C until reaching a constant weight to calculate the dry matter stock (Gibbon et al., 2010).

2.4 Extrapolation to achieve values per hectare

A direct extrapolation method was applied to scale carbon stock values from 0.1 ha plots (1000 m^2) to a per-hectare basis ($10,000 \text{ m}^2$). The process was done individually for each plot and component. For large trees with $\text{DBH} \geq 30 \text{ cm}$, we summed the carbon values of all individuals within the 0.1 ha plot and then multiplied by 10 to estimate the carbon stock per hectare. For small trees with $\text{DBH} 5\text{--}30 \text{ cm}$, we established three $10 \times 10 \text{ m}$ subplots (each 0.01 ha). We summed the carbon stock within each subplot, then averaged the three totals to represent the carbon stock per 0.01 ha . This value was then multiplied by 100 to scale it to one hectare. For herbaceous vegetation and litter, we used six $0.5 \times 0.5 \text{ m}$ quadrants per plot. We averaged the carbon stock of the six samples and extrapolated to a per-hectare value by scaling up from the total area sampled.

The extrapolation was done per plot, not from the sum of all plots. Each component's per-hectare estimate was calculated for each plot, and then the mean and standard deviation (SD) were calculated across all plots within each land use type.

2.5 Physical variables of soil and vegetation structure

At the midpoint of each established sampling plot, one soil sample per plot was taken by sweeping the vertical profile of a 1-meter-deep soil pit, ensuring representation across the depth gradient, following the methodology proposed by Cuellar and Salazar (2016). The samples were analyzed by the Soil Laboratory of the National Agrarian University of La Molina, and the following variables were determined (percentage of sand, silt, and clay), bulk density (g/cm^3), organic matter content (%), and hydraulic conductivity (mm/day). Additionally, for each sampling plot, vegetation structure variables were recorded, such as tree density (individuals/ha), basal area (m^2/ha), forest canopy cover (%), and land cover (%), the latter two being recorded with a densitometer along two measuring diagonals established within the plot from its ends, according to the methodology proposed by Food and Agriculture Organization (2015).

2.6 Statistical analysis

We applied the Shapiro-Wilk test to assess the normality of data distribution, which was non-normal, and Kruskal-Wallis nonparametric test to evaluate carbon stocks across different land uses and vegetation components. Dunn's post hoc test was performed, applying the Benjamini-Hochberg correction for multiple comparisons, with a significance of $p < 0.05$ (Benjamini and Hochberg, 1995; Quinn and Keough, 2002). To identify the correlation of total carbon stock of AGB with the physical soil variables and vegetation structure, the Spearman test was used, as it is more appropriate for nonparametric samples.

A Principal Components Analysis (PCA) was also performed using a correlation matrix because the variables were at different scales (Quinn and Keough, 2002). The PCA was done for data reduction and visualization, considering the first two main Principal Components (PC). Correlation was among the vari-

ables to understand how they relate to each other and contribute to each PC. Additionally, a multiple comparison test of Principal Components 1 and 2 between land-use was performed using the Tukey test, as the data presented a parametric distribution. Finally, a PERMANOVA test with Bray-Curtis's index was applied to identify the significance of the grouping and statistical differences. Tests were performed with the statistical programs PAST (PAleontological Statistics) version 3.6 and R Studio (2021).

3 Results

3.1 Carbon Stocks

3.1.1 Comparison between equations

A total of 1,138 trees with $\text{DBH} \geq 5$ cm from OMF and RMF were measured to compare equations performance. There were significant differences between the estimates of Eq-1 (0.49 ± 1.20 Mg/tree), Eq-2 (0.57 ± 1.42 Mg/tree), Eq-3 (0.68 ± 1.79 Mg/tree) and Eq-4 (0.50 ± 1.20 Mg/tree). While all four equations show minimal variation with small DBH values, these become more evident with higher DBH values (Figure 2). Eq-2 and Eq-3 generally provide higher estimates, as they rely on DBH to estimate total tree height. In contrast, Eq-1 and Eq-4, which do not have significant differences between their estimates ($p < 0.05$), incorporate field-measured height values and avoid overestimation (Spracklen and Righelato, 2016).

3.1.2 Carbon estimates at each land use

Total aboveground carbon storage varied significantly across different land uses, from 1.42 Mg C ha^{-1} in CL to 289.9 Mg C ha^{-1} in OMF (Figure 3). Aboveground carbon stocks in OMF ranged from 107 Mg C ha^{-1} to 290 Mg C ha^{-1} , with an average (193.03 ± 68.20 Mg C ha^{-1}) significantly higher ($p < 0.05$) than RMF, AF and CL.

Carbon stocks in RMF (87.52 ± 50.29 Mg C ha^{-1}) were not significantly different ($p < 0.05$) to AF (48.67 ± 24.05 Mg C ha^{-1}). RMF had greater variability in total aboveground carbon values per plot due to the presence of forests at different stages of regeneration (6 to 50 years old). High outliers were observed in plots

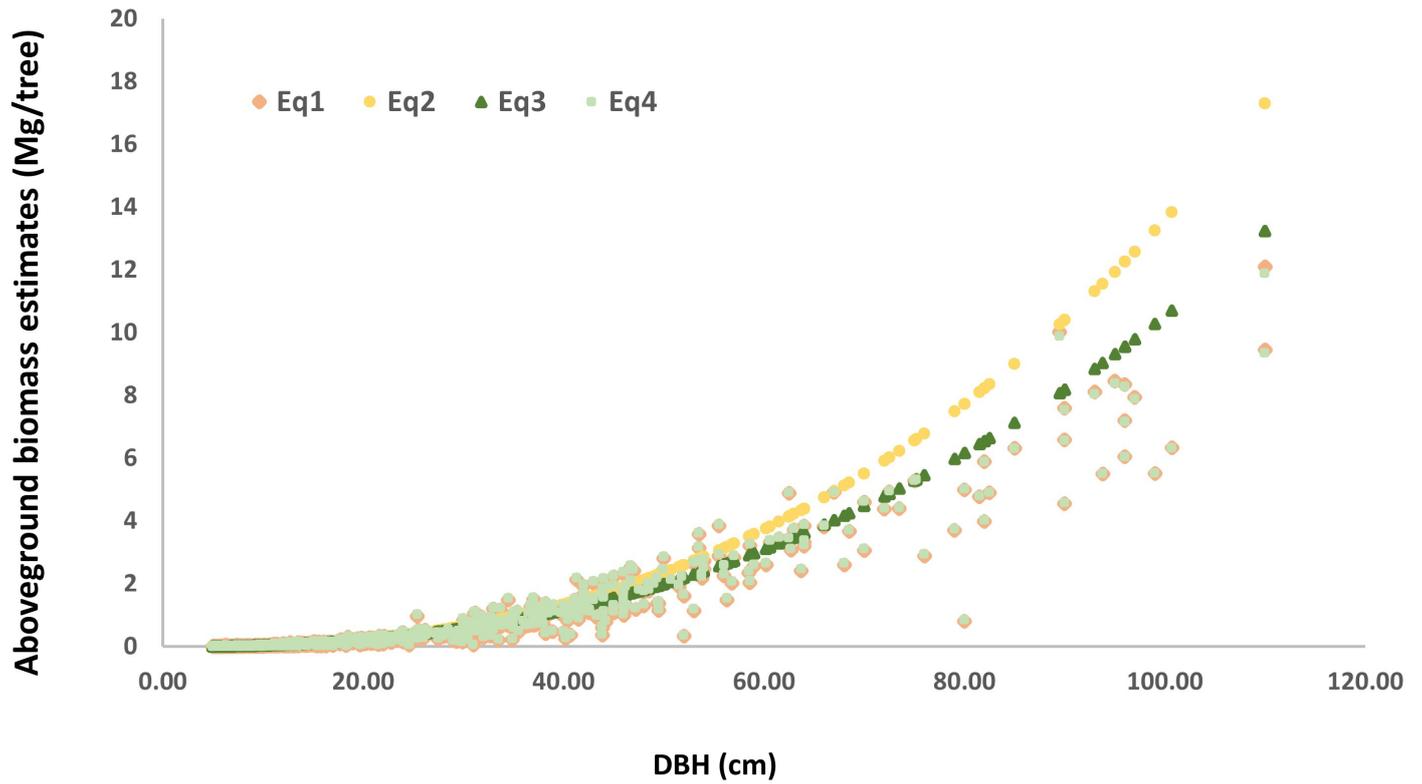


Figure 2. Comparison between biomass estimates (Mg/tree) for each measured tree in OMF and RMF applying equations Eq1, Eq2, Eq3 and Eq4.

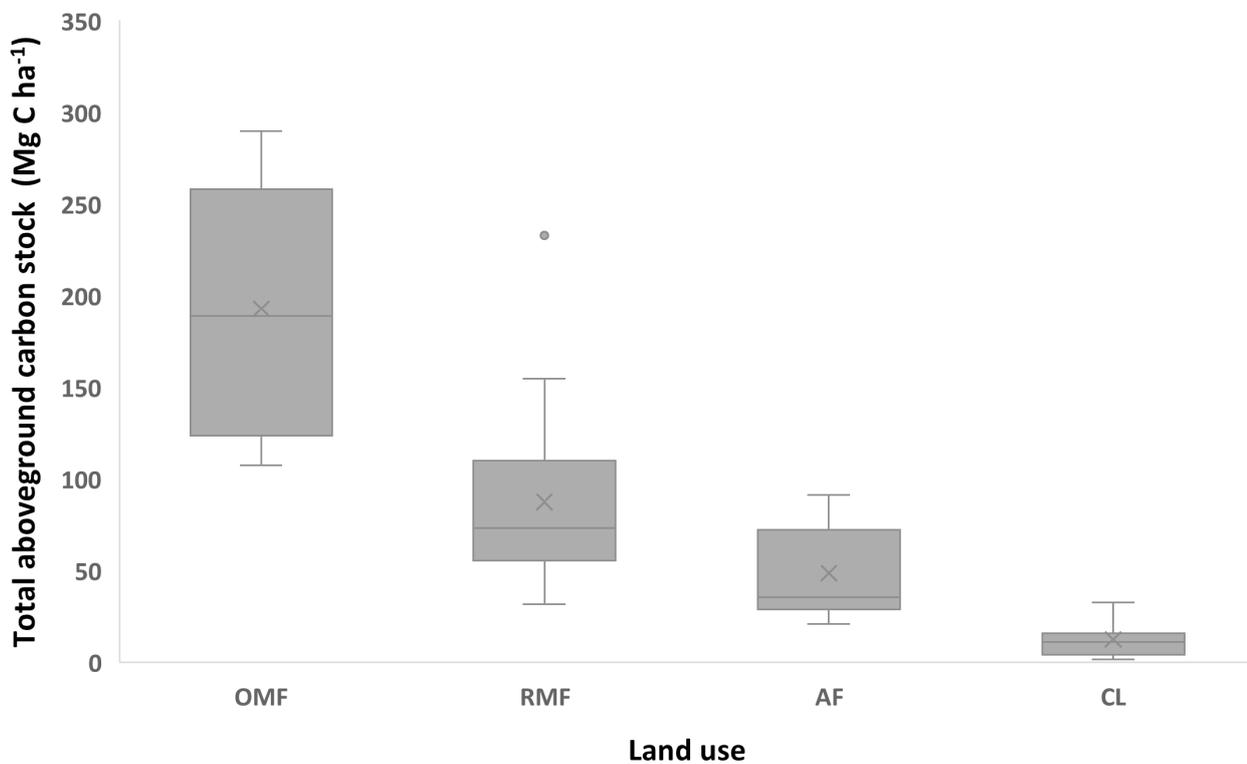


Figure 3. Carbon stocks (Mg C ha⁻¹) for each land use (OMF: Old-growth Montane Forest, RMF: Montane Forest in Regeneration, AF: Agroforestry, CL: Croplands)..

Table 4. Carbon stocks in Mg C ha⁻¹ for aboveground biomass components in each land use (average ± standard deviation). OMF: Old-growth Montane Forest, RMF: Montane Forest in Regeneration, AF: Agroforestry, and CL: Croplands. Similar letters in the average values of each component indicate no significant differences between them across land uses, considering a p-value of 0.05.

Components of the Aboveground biomass	Average carbon stock (Mg C ha ⁻¹)			
	OMF n = 13	RMF n = 16	AF n = 15	CL n = 17
Large trees (DBH ≥ 30 cm)	145.98 ± 61.94 a	34.87 ± 25.80 b	17.02 ± 20.12 b	0.75 ± 1.95 c
Small trees (5 cm ≤ DBH < 30 cm)	29.83 ± 9.92 a	40.66 ± 28.46 a	10.79 ± 8.38 b	2.28 ± 4.16 c
Herbaceous	0.83 ± 0.59 a	1.27 ± 0.95 a	0.49 ± 0.34 b	1.39 ± 1.86 a
Dead biomass	16.39 ± 8.49 a	10.64 ± 7.19 ab	6.97 ± 4.23 bc	4.81 ± 5.49 c
Crops	0 ± 0 c	0.08 ± 0.32 b	13.39 ± 6.04 a	3.22 ± 4.64 b

either reforested only with *Ulcumano* trees (*Retrophyllum rospigliosii*), which represent 18.7% of RMF plots (3 out of 16) but just one plot was an outlier, or in forests undergoing regeneration for more than 20 years. In contrast, AF showed a more homogeneous distribution, higher values are associated with agroforestry systems up to 40 years old and banana-coffee associations.

The lowest carbon stocks of all land uses were found in CL (12.46 ± 9.79 Mg C ha⁻¹). The highest carbon values in CL were found in aged coffee crops (40 years old), while the lowest values were observed in fallow land and areas with *Passiflora spp.* and crops.

3.2 Carbon distribution in aboveground biomass components

In both OMF and RMF, the carbon stored in all trees with a DBH ≥ 5 cm accounted for 91% and 86% of the total carbon. In OMF, 75.6% of the total aboveground carbon was stored in old-growth trees (DBH ≥ 30 cm), a significantly higher stock (p < 0.05) than other land uses. In contrast, RMF and AF did not show significant differences between each other (Table 4).

Trees with DBH ≥ 5 cm were the primary contributors to carbon storage in RMF comprising up to 46.4% of the total carbon stock. In AF, the distribution of aboveground carbon stocks was more balanced, with contributions from large trees with DBH ≥ 30 cm (35%), small trees with DBH between 5 and 30 cm (22%), crops (27.5%), and aboveground dead biomass (14.3%).

The highest carbon stocks in CL are from dead biomass (38.6%) and crops (26%), with herbaceous plants contributing 11% of the total AGC, higher than other land uses.

3.3 Relationships between aboveground carbon stocks, soil physical characteristics and vegetation structure

Soil carbon stock has a moderate negative relationship with soil bulk density (r² = -0.38) and a moderate positive relationship with soil organic matter (r² = 0.31). There was no significant correlation with other variables such as hydraulic conductivity (r² = 0.07), sand % (r² = -0.14), silt % (r² = -0.09), or clay % (r² = 0.21).

A strong positive relationship was found between total aboveground carbon (AGC) and endogenous vegetation structure variables, such as forest canopy cover (r² = 0.84). Among all sampling plots, structur-

Table 5. Correlation between vegetation structure, soil variables, and AGC (Mg C ha⁻¹). Values marked with (*) show statistically significant correlations, with significance levels at p < 0.05 (*), p < 0.01 (**), and p < 0.001 (***).

Correlation values of the total carbon stock Mg C ha ⁻¹ with different variables		
Variables	R ²	p value
Sand (%)	-0.14	-
Silt (%)	-0.09	-
Clay (%)	0.21	-
Soil bulk density (g/cm ³)	-0.38	*
Soil hydraulic conductivity (mm/day)	0.07	-
Soil organic matter (%)	0.31	**
Land cover (%)	-0.45	
Canopy cover (%)	0.84	
Large trees DBH (≥ 30 cm)	0.25	*
Large trees total height (m)	0.63	
Large tree basal Area (m ² /ha)	0.74	
Large tree density (ind/ha)	0.77	
Small trees (5 cm ≤ DBH < 30 cm)	0.86	
Small trees total height (m)	0.79	
Small tree basal area (m ² /ha)	0.91	
Small tree density (ind/ha)	0.87	

al variables of small trees with DBH between 5 and 30 cm (including DBH, total height, basal area, tree density) had higher correlation values (r^2 from 0.79 to 0.91) compared to the structural variables of large trees with DBH ≥ 30 cm (r^2 from 0.25 to 0.77; Table 5).

3.4 Differences between land uses

The PCA accounted for 66.3% of the data variance. Principal Component 1 (PC1) explained 50.4% of the variance while Principal Component 2 (PC2) explained 15.9 % (Supplementary Table 1).

PC1 was significantly different across land uses (Supplementary table 4) and was primarily influenced by vegetation structure and biomass-related variables, which had highest positive loadings such as canopy cover (0.343), total AGC (0.344), and small tree DBH (0.322; Table 6). This suggests that sites with greater canopy cover also tend to have higher aboveground carbon stocks, reflecting environments with more biomass and greater carbon storage.

PC2 showed no significant differences between OMF and CL, nor between RMF and AF (Supplementary table 4) and was notably influenced by soil bulk den-

sity (0.444) and large trees DBH ≥ 30 cm (0.519), while soil organic matter (-0.422) showed a stronger negative correlation (Table 6). This suggests that PC2 captures a soil condition and forest maturity gradient, where more compacted soils are associated with less organic matter and potentially degraded conditions.

Table 6. Loadings of PC1 and PC2. Higher values of each PC are highlighted.

Variables	Loadings	
	PC 1	PC 2
Canopy cover (%)	0.343	0.078
Land cover (%)	-0.190	-0.103
Soil organic matter (%)	0.176	-0.422
Soil bulk density (g/cm ³)	-0.139	0.444
Large trees DBH (≥ 30 cm)	0.166	0.519
Large trees total height (m)	0.240	0.421
Large trees basal area (m ² /ha)	0.294	0.205
Large trees density (ind/ha)	0.312	-0.097
Small trees DBH (5 cm \leq DBH < 30 cm)	0.322	0.080
Small trees total height (m)	0.321	0.074
Small trees basal area (m ² /ha)	0.313	-0.193
Small trees density (ind/ha)	0.324	-0.182
Total AGC (Mg C ha ⁻¹)	0.344	-0.167

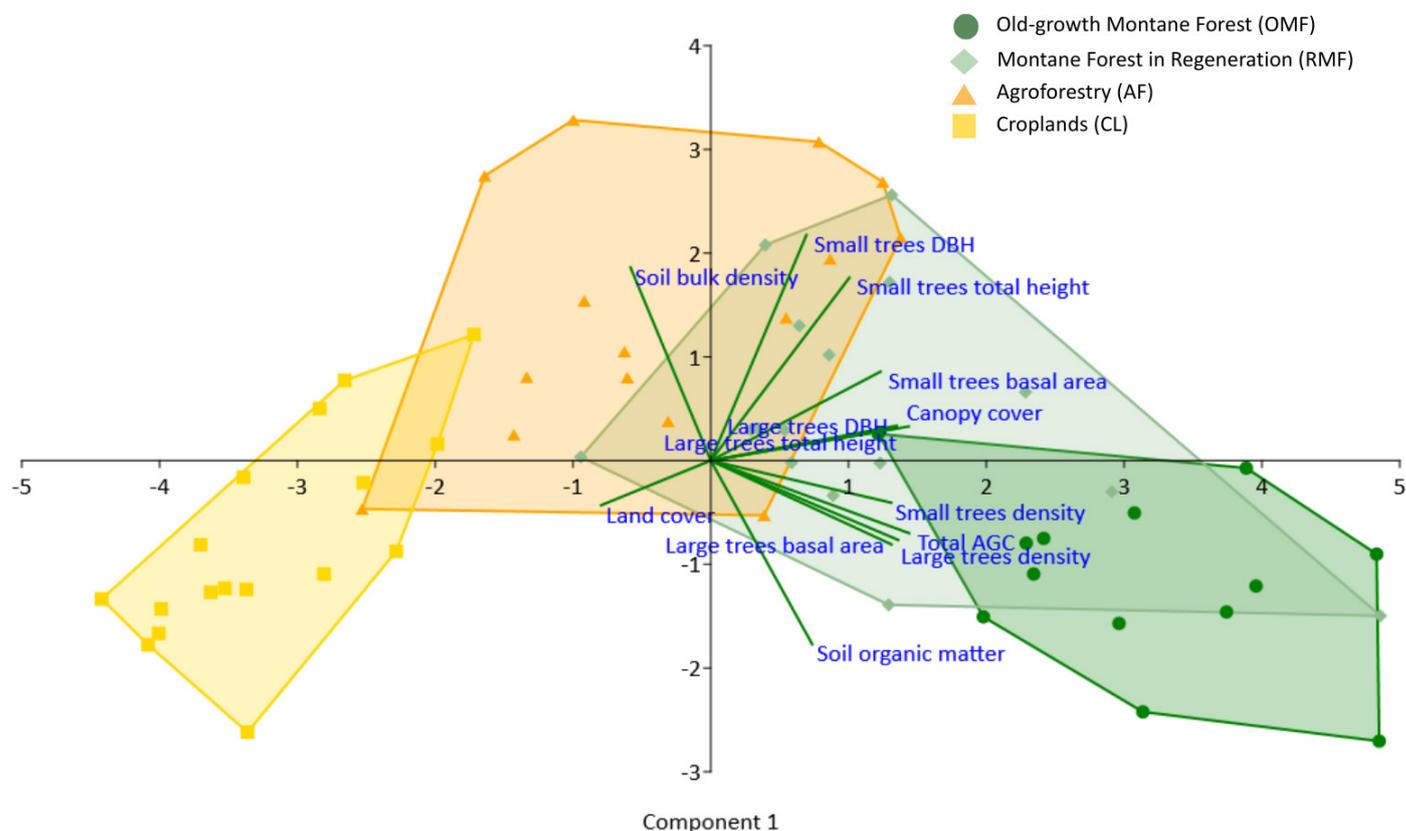


Figure 4. Principal component analysis (PCA) considering the four land uses, vegetation structure and soil variables.

The PCA biplot showed that plots within the same land use show greater similarity to each other compared to plots in different land uses (Figure 4). A conservation gradient is evident, with OMF plots clustered at the far right of the graph and CL plots at the far left. Vegetation structure variables most effectively characterize OMF and RMF. Tree density and total AGC are the best indicators for the OMF plots, while canopy cover and basal area are significant for both OMF and RMF. Additionally, variables such as small tree DBH and small tree height are key for explaining certain RMF and AF plots, while soil bulk density is a key variable for explaining AF.

The PCA results are supported by PERMANOVA ($F = 21.31$, $p < 0.0001$), confirming the presence of significant differences between land use types, despite some overlap between land uses as indicated by the biplot. All pairwise comparisons are statistically significant ($p < 0.001$).

4 Discussion

4.1 Differences among the allometric equations

Some equations, such as those from Chave et al. (2014), are pan-tropical and developed using large datasets covering a wide range of forest types, including tropical montane forests. Others, such as the equations by Álvarez et al. (2012), are specific to Andean Forest species and structural characteristics. Local equations tend to perform better in capturing biomass variation in specific forest types due to better alignment with wood density and tree architecture. Allometric models are also influenced by the size range of trees used during model development. Equations calibrated with data from larger or taller trees may over- or under-estimate biomass when applied to plots dominated by smaller trees, such as regenerating forests or agroforestry systems.

In our study, we selected allometric equations based on the availability of input variables, ecological representativeness, and previous validation in similar Andean settings. Nevertheless, we acknowledge that applying multiple equations introduces variability in biomass estimates. To address this, we conducted a sensitivity check and found that while absolute values varied slightly, the relative differences among

land uses remained consistent. Equations that incorporate multiple variables (such as height and wood density) provided better sensitivity to this structural heterogeneity, as previously documented in similar studies in the tropical Andes. As a result, using equations based only on DBH can lead to substantial inaccuracies in carbon estimations, particularly if they are not adjusted to the specific characteristics of the ecosystem being analyzed.

4.2 Total aboveground carbon stocks by land use

Our results show that land use change has a direct influence on AGC by affecting the size of carbon-storing components within the ecosystem. Increased ecosystem disturbance leads to alterations in the carbon cycle dynamics (Noormets et al., 2015). AGC stocks estimated in the study area, particularly in OMF and RMF (193.03 and 87.52 Mg C ha⁻¹ respectively), are within the lower end of the carbon stocks range reported by Spracklen and Righelato (2014) in a synthesis inventory from tropical montane forests worldwide (77 Mg C ha⁻¹ to 785 Mg C ha⁻¹, average of 271 Mg C ha⁻¹) and they are also within the range reported by Tito et al. (2022) in a synthesis of Peruvian TMFs (52.5 to 485 Mg C ha⁻¹). RMF carbon stock values are also similar to the ones reported by Huacra Huasco et al. (2014) for Montane Forests in the Kosñipata Valley between 72.05 and 98.82 Mg C ha⁻¹.

In contrast, AF and CL showed substantial declines in carbon stocks, with 75% and 90% reductions compared to OMF, respectively. Similar reduction patterns have been documented in coffee and monoculture agricultural systems compared to conserved forests. Lapeyre, Alegre, and Arevalo (2004) observed a reduction of almost 99% in AGB when montane forests were converted to croplands. Similarly, Diaz et al. (2016) found an 82% decrease in carbon stocks in croplands compared to conserved forests, while Vizcaino et al. (2020) reported a reduction of about 75% in intensive agricultural areas compared to conserved forests.

4.3 Carbon stocks by aboveground biomass component

In undisturbed forests, the presence of large trees is a feature that significantly contributes to car-

bon stocks (Slik et al., 2013; Berenguer et al., 2014; Spracklen and Righelato, 2016). Although their density per unit area is low compared to small trees (DBH between 5 and 30 cm), they store a high amount of carbon per individual. We found that trees with DBH ranging from 90 to 120 cm store between 8 and 12 Mg C /tree. However, as land use transitions into intensive agricultural practices, large trees and their contribution to carbon storage disappear. Large trees carbon stocks in RMF, AF, CL decline by nearly 76%, 88%, and 99%, respectively, compared to large trees in conserved forests.

Small trees (DBH between 5 and 30 cm) are a feature of secondary forests. RMF plots have higher carbon stocks in this component compared to OMF, which is attributed to areas where reforestation with *Retrophyllum rospigliosii* has led to high carbon stocks similar to old-growth forests. Although RMF and AF land uses shows similarities in carbon stocks from large trees (DBH \geq 30 cm), this diameter class differentiates regenerating forests from intervened land uses (AF and CL) in their path towards forest regeneration.

AF showed a reduction of up to 70% in total tree carbon stocks compared to RMF. These carbon stocks are within the range reported by Ehrenbergerová et al. (2015) for shade trees in coffee agroforestry systems in Central Peru (27.5 ± 3.2 to 57.5 ± 4.5 Mg C ha⁻¹).

Herbaceous plants are the most ephemeral component of the ecosystem, especially in agricultural systems where they are frequently cleared. They store the lowest carbon stocks among all components across the four land uses. There was a slightly higher carbon stock in CL herbaceous plants due to the presence of herbaceous crops and the proliferation of pastures and plants in fallow land following intensive farming practices, including burning and clearing.

Dead biomass carbon stocks across four land uses align with reported values for TMFs in Ecuador (from 0.4 to 23 Mg C ha⁻¹, average of 9.1 Mg C ha⁻¹, as reported by Wilcke et al., 2005). OMF has the highest carbon stock value in dead biomass (16.39 ± 8.49 Mg C ha⁻¹). However, dead biomass in CL represents the highest percentage (38.6%) of the total AGC, which

is mainly due to the presence of tree trunk remnants in plots converted to agricultural areas. In natural forests, dead biomass, particularly fallen logs, does not have a specific relationship with the number of living trees and follows a random pattern (Wilcke et al., 2005; Berenguer et al., 2014). Dead biomass is a temporary reservoir of aboveground carbon, and its nutrients eventually integrate into the soil's organic layer upon decomposition (Clark et al., 2002). It plays a critical role in promoting tree growth and maintaining soil properties, thereby contributing to the long-term maintenance of carbon stocks within the ecosystem (Noormets et al., 2015).

Crops' carbon stock values were significantly higher in AF compared to CL. This finding is consistent with results reported by Ehrenbergerová et al. (2015), where shade-grown coffee plants stored more carbon than shade-free coffee plants.

4.4 Aboveground carbon, vegetation structure and physical characteristics of the soil

Dynamics between soil characteristics and aboveground carbon stocks are influenced by diverse factors such as ecosystem type and study scale. Previous research conducted at landscape scale in Amazonian forests (approximately 10 km²) has shown a significant association between aboveground carbon and soil variables such as texture and fertility (Berenguer et al., 2014). In our study scale (20 km²), we found a moderate positive correlation between aboveground carbon and soil organic matter (0.31), as well as a negative correlation with soil bulk density ($r^2 = -0.38$). Lower bulk density typically reflects healthier and less compacted soils that allow for water infiltration, soil aeration and root penetration. Soil organic matter improves soil structure and soil water-holding capacity, soils with thick organic horizons are characteristic of TMFs, especially at higher elevations (Girardin et al., 2013). Both variables are essential to set conditions for vegetation development and aboveground carbon accumulation.

Vegetation structural attributes, such as tree density and basal area, have a consistently positive correlation with carbon stocks in 78% of cases in tropical forests (Van der Sande et al., 2017). In our study area, vegetation structure variables (height, DBH, basal area, tree density, and canopy cover) have

strong correlations with AGC (r^2 from 0.63 to 0.87) and show variations across different land uses. This correlation is particularly strong in old-growth and secondary forest areas. In contrast, the correlation in croplands is weak, but there is a strong correlation with soil cover percentage. Similar patterns were observed by Gonzales, Kroll, and Vargas (2014) in Central Rainforest forests, Slik et al. (2010) in Borneo's TMFs, Vizcaino et al. (2020) in Mexico's TMFs.

The decline in tree individuals and canopy cover are closely linked to reduced aboveground carbon storage. Beyond that, the loss of tree structure, mainly trees with DBH ≥ 30 cm, has broader ecological implications. It alters forest microclimatic conditions, including high humidity, reduced radiation, and buffering of extreme temperatures, leading to biodiversity loss and potentially causing negative cascading effects on other ecosystem functions (De Beenhouwer et al., 2013; Gilroy et al., 2014; Berenguer et al., 2014).

4.5 Differences between land uses

Land use trajectory in our study area closely resembles other TMFs in Peru and globally, particularly the conversion of forest into coffee plantations, which is a common trend in TMFs (De Beenhouwer et al., 2013; Tito et al., 2022). Currently, conserved forests are often located in remote areas, but factors such as road development and environmental factors facilitate deforestation. Soil type and average annual precipitation were identified as the most important predictors of deforestation, reflecting the extensive agricultural-based livelihood systems across TMFs (Bax & Francesconi, 2018). In addition, roads and urban development significantly elevate the risk of deforestation, fragmentation and land use change, potentially tripling the likelihood of such events (Gonzales, Kroll, and Vargas, 2014). The regeneration of these remnant TMF patches, mostly secondary forests, is at risk of going back to active land use due to the agricultural demands of local stakeholders. Conservation of the remaining TMF areas depends largely on the local population and farmers' knowledge of effective ecosystem management and economic opportunities. In addition, prioritizing secondary forest conservation is strategic because their trees are already growing, sequestering and storing

carbon at higher rates than plantations (Tito et al., 2022). On the other hand, agroforestry systems offer a promising agricultural alternative that can preserve vegetation structure and prevent substantial losses in ecosystem services, particularly carbon storage, while selection of shade trees excludes exotic species. Additionally, there is great potential to convert abandoned and monoculture areas into agroforestry systems and, ideally, into regenerating forests, which would facilitate the reaccumulation of carbon in the ecosystem (Gilroy et al., 2014; Berenguer et al., 2014).

5 Conclusions

This study demonstrates that land use and management practices significantly influence AGC, vegetation structure and soil characteristics in TMFs. Among the four land uses evaluated, Old-growth montane forests (OMF) store the highest carbon stocks, reflecting their ecological integrity and undisturbed structure. In contrast, croplands (CL) showed the lowest carbon storage, with values reduced by over 90% compared to OMF.

These findings suggest a gradient of ecosystem service loss in terms of carbon storage and vegetation structural characteristics as land use intensifies. Restoring degraded forest areas and implementing alternative agricultural approaches, like agroforestry, emerge as promising alternatives to mitigate further loss of ecosystem functions and services, as well as opportunities for climate change mitigation.

Effective management and conservation of TMFs is crucial to maintaining their role as carbon sinks and preventing their transition to carbon emitters. This involves not only protecting existing forest patches but also actively promoting sustainable land use practices and restoration efforts that consider local tree species. By enhancing agroforestry systems and focusing on the restoration of degraded lands, we can support the recovery of carbon stocks and sustain the ecological integrity of these vital forest ecosystems that are crucial to addressing climate change-related challenges.

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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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