

RESEARCH

Open Access



Impact of forest degradation on soil properties in the Peruvian Amazon

Geomar Vallejos-Torres^{1*}, Nery Gaona-Jimenez¹, Andi Lozano¹, Harry Saavedra¹, Alberto Alva Arévalo¹, Caleb Ríos Vargas¹, Jorge Saavedra-Ramírez², Juan Tuesta-Hidalgo², Oscar A. Tuesta-Hidalgo², Luis Vilela², Manuel Jesús Valdez-Andía³, Kenneth Reategui⁴, Juan R. Baselly-Villanueva⁵, César Marín^{6,7} and Bárbara Vento⁸

Abstract

Background The Amazonian forests are increasingly threatened due to continuous changes in land use, particularly deforestation. This study aimed to quantify and analyze the vertical distribution of soil glomalin and its relationship with carbon, climate, and soil properties across three forest types of the Peruvian Amazon. A total of 18 plots were selected and sampled in forests with different vegetation cover types: deforested, disturbed, and primary forest. The vertical variation of total glomalin (TG), easily extractable glomalin (EEG), and the number of arbuscular mycorrhizal fungal (AMF) spores was estimated, as it was the relationships of these variables with soil depth, physical-chemical properties, and climate conditions.

Results The mean values for TG, EEG, and AMF showed vertical variations in the three forest cover types, with high values in disturbed forests and degraded soils. Overall, higher mean values were found in the surface soil layers compared to the deep layers. TG, EEG, and AMF were positively correlated with soil organic carbon (SOC) and soil organic matter (SOM). Moreover, the total nitrogen (N), SOC, OM, total phosphorus (P), and soil water content (SWC) presented higher values in the topsoil than the deep layers.

Conclusions The highest production of glomalin in disturbed forests is probably a response to degradation processes. This work is a contribution to expand knowledge about glomalin dynamics in forest soils of the Amazon rainforest and provides essential information for future soil ecosystem restoration practices in tropical forests.

Keywords Deforestation, Disturbed forest, Primary forest, Land-use change, Mycorrhizal fungi

*Correspondence:

Geomar Vallejos-Torres
gvallejos@unsm.edu.pe

¹Universidad Nacional de San Martín, Jr. Maynas N°177, Tarapoto, San Martín, Peru

²Escuela Profesional de Ingeniería en Zootecnia, Universidad Nacional Autónoma de Alto Amazonas (UNAAA), Alto Amazonas, Yurimaguas, Peru

³Universidad Nacional Autónoma de Alto Amazonas (UNAAA), Yurimaguas, Peru

⁴Universidad Nacional Intercultural de la Amazonía, MC26+888, San Jose Km. 0.5, Pucallpa 25004, Peru

⁵Instituto Nacional de Innovación Agraria - INIA, Calle San Roque 209, Maynas 16430, Loreto, Peru

⁶Centro de Investigación e Innovación para el Cambio Climático (CiiCC), Universidad Santo Tomás, Av. Ramón Picarte 1130, Valdivia 5090000, Chile

⁷Amsterdam Institute for Life and Environment, Section Ecology & Evolution, Vrije Universiteit Amsterdam, de Boelelaan 1085, Amsterdam 1018 HV, The Netherlands

⁸Instituto Argentino de Nivología Glaciología y Ciencias Ambientales (IANIGLA), Centro Científico Tecnológico Mendoza - CONICET, Av. Ruiz Leal s/n, Mendoza, Argentina



Introduction

The Amazon rainforest is one of the largest wilderness areas in the world hosting an impressive biodiversity. This tropical forest provides relevant ecosystem benefits such as carbon storage and water retention, which contributes to improving soil conditions [1]. Deforestation involves changes in land use by anthropogenic action in favor of agriculture practices or urbanization, with changes in land cover and loss of many species [2].

Forest soils store significant amounts of organic matter and carbon and play a key role in the balance of the carbon cycle [3]. They are essential carbon sinks that contribute to the global carbon budget and balance [4]. Therefore, fluctuations in soil organic carbon (SOC) strongly influence the atmospheric carbon dioxide concentration [5]. Soil aggregates, are crucial for the stabilization of soil organic carbon (SOC), hosting a wide range of physicochemical properties, which provide the space for the growth and movement of soil microorganisms and communities [6].

Additionally, the quantity and quality of organic matter are relevant parameters enabling soil particle aggregation [7] and stability, based on chemical, physical, and biological parameters, and they play an essential role in carbon sequestration. Arbuscular mycorrhizal fungi (AMF) are among the principal soil aggregators due to the combined effect of extraradical hyphae [8] and the production of glomalin-related soil proteins (GRSP) that promote healthy soil conditions [9]. Recently, Hawkins et al. [10] estimated that -at least temporarily- in a year, the equivalent to ~36% of current annual CO₂ emissions from fossil fuels are stored underground, in the mycelium of mycorrhizal fungi. In addition, it has been shown that the production of GRSP, soil nutrients, and enzyme activities are closely related to soil fertility. At present, one of the biggest challenges is to understand the relationship between soil organic matter (SOM) and glomalin [11]. Under unfavorable environmental conditions, AMF are known to produce more GRSP as a stress-inducible protein to increase the resistance of plants [12].

Quantifying and assessing the adverse effects of deforestation in the Amazon can provide valuable insights for implementing management tasks aimed to preserve this globally and regionally significant ecosystem [2]. As many Amazonian regions in Peru have been seriously affected by deforestation during the last decades [13], particularly by human activities like land-use changes that potentially increase the adverse effects of climate change, decreasing litter decomposition rates and leading to a reduction of soil carbon storage [14]. Recently, a study by Vallejos-Torres et al. [15] provided information on the organic carbon content in soils affected by erosive processes in primary, disturbed, and deforested forests. However, the dynamics of glomalin and arbuscular mycorrhizal fungi

(AMF) in relation to soil organic carbon, soil organic matter, and nitrogen in forest soils of the Amazon rainforest were not explored in depth. Considering this context, it was hypothesized that differences in land use affect the amount of glomalin deposited in Amazonian forest soils. Therefore, the aim of this study was to investigate and analyze the vertical variations of glomalin in forests with differing vegetation cover in the Peruvian Amazon. In addition, the correlations between glomalin and various physical, chemical, and climatic parameters were examined.

Materials and methods

Study sites

This study was conducted in two tropical forests placed in the Central Huallaga, in the Amazon basin of Peru. The study sites correspond to the El Quinillal forest (district of Winge) and to the Ojos de Agua forests (district of Pucacaca), province of Picota, department of San Martin, Peru (Fig. 1). El Quinillal protected forest is placed in the Winge district (07°02'S, 076°17'W, 420 m a.s.l); approximately 85% of the area is located in the Biavo river basin while around 15% is located in the inter-basin of Medio Huallaga River with a total area of 10,557 ha (GRSM, 2017). The Ojos de Agua protected forest is located in the Pucacaca district (6°49'S, 76°26'W, 500 m a.s.l.) with an extension of 2,357 ha. This protected forest is located on the left side of the Huallaga River in a landscape that combines moderate slopes with the forest (Fig. 1). Climate in both studied areas is characterized by a marked seasonality, with a mean temperature of 26 °C, minimum and maximum temperature of 18 °C and 30 °C, respectively, and an accumulated annual precipitation ranging between 1,164 and 1,433 mm [16].

Experimental design

Soil sampling was conducted in the two forest sites ("El Quinillal" and "Ojos de Agua") at three different conservation stages: primary forest, disturbed forest, and a deforested area. On each forest site (deforested, disturbed, and primary), three replicates were established (a subplot of 10 m x 10 m), for a total of 18 subplots sampled following a stratified sampling according to the distribution of the forest type. Soil sampling and analysis were conducted between February and May 2023. Following the methodology of Yu et al. [17], soil samples were taken at five different depths: 0–20 cm, 20–40 cm, 40–60 cm, 60–80 cm, and 80–100 cm, counting a total of 90 soil samples. Moreover, an additional 90 soil samples were collected from the same plots with a cylinder at each selected depth layer to quantify bulk density (BD) and soil water content (SWC).

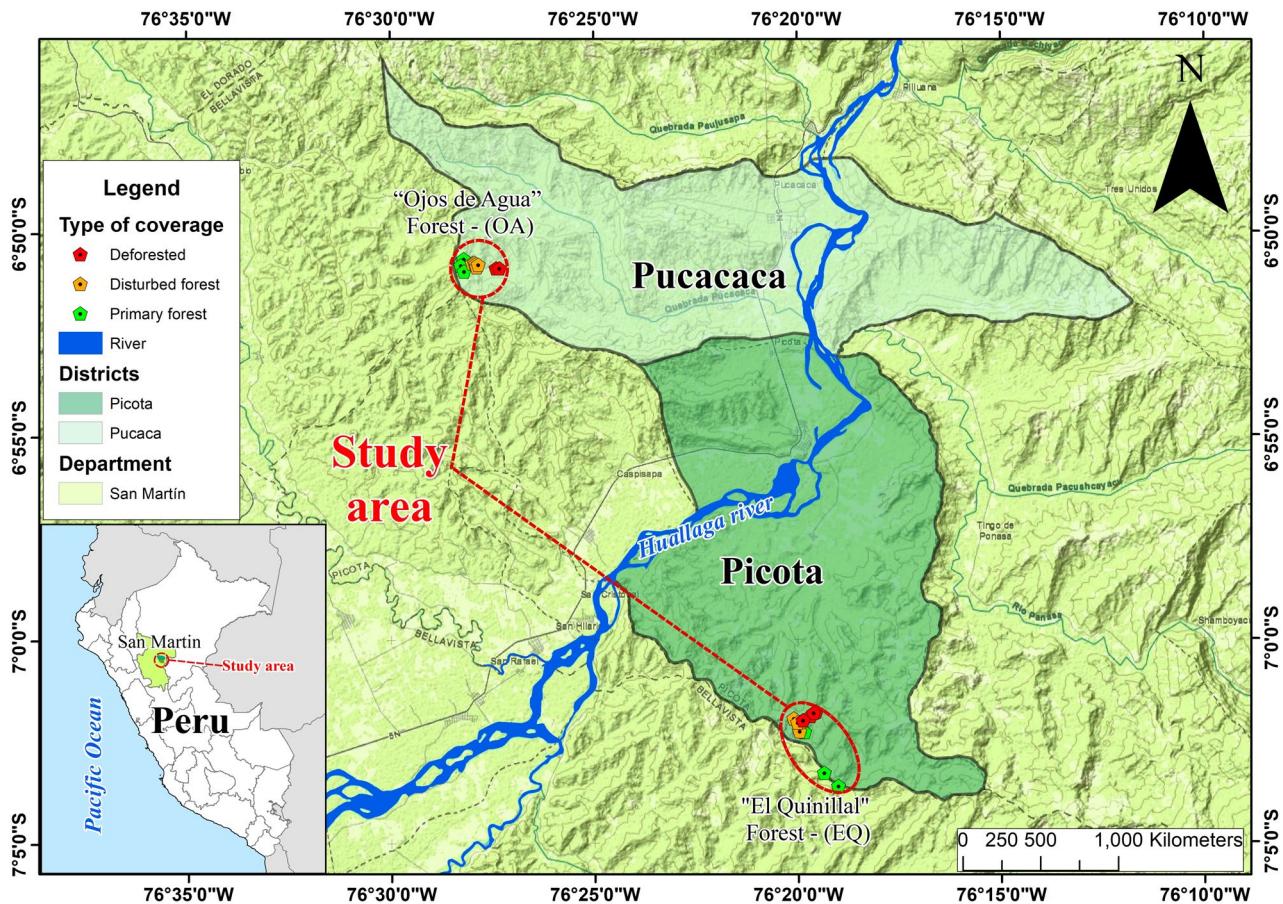


Fig. 1 Map showing the two study areas where soil samples were taken in deforested, disturbed, and primary forests

Extraction of total and easily extractable glomalin and arbuscular mycorrhizal fungal spores

The extraction of glomalin from the 90 soil samples was performed using a standard curve of bovine serum albumin from a 1 g L^{-1} solution, employing six concentrations of this solution between 0.05 and 0.5 g L^{-1} . The detection and measurement of total (TG) and easily extractable glomalin (EEG) was made following the method for proteins firstly suggested by Bradford et al. [18], later modified and improved by Wright et al. [19]. The quantification of arbuscular mycorrhizal fungi (AMF) spores was performed by wet sieving and decantation using the method proposed by Gerdemann and Nicholson [20], Vallejos-Torres et al. [21] and Corazon-Guivin et al. [22].

Soil physical-chemical properties

Soil organic carbon (SOC) was estimated using the method proposed by Walkley and Black [23] and the soil water content (SWC) was measured by the gravimetric method by the sample weight. In this process, the relationship between the liquid and solid weight of the soil was estimated. Soils were dried at 105°C for 48 h, and

then this weight was used to calculate gravimetric water content (GWC). Bulk density at each soil layer depth was measured using metal brass rings of 5.2 cm diameter and 5 cm long [24], and the procedure for measuring the SOC was performed employing the Walkley-Black method [23]. The soil pH was measured in an aqueous extract (1:5; soil: water) using a pH measurement device. Nitrogen (N) was measured by the Kjeldahl method [25], phosphorus (P) by the Olsen method [26], and potassium (K) based on ammonioatomic acetate extraction, according to Novozamsky et al. [27]. The measurement of soil electrical conductivity (EC) was made using a Potentiometric sensor. The data employed in the analysis of soil physico-chemical properties, glomalin content, and organic carbon were obtained from the prior research conducted by Vallejos Torres et al. [15].

Physiographic and climate variables

The elevation of each sampled plot was obtained using the centroid of each plot at a 12.5 m spatial resolution raster layer obtained from the ALOS PALSAR sensor of the NASA database (<https://search.asf.alaska.edu>, accessed September 15, 2023). The digital elevation model (DEM)

was obtained considering the “Hi-Res Terrain Corrected” file type and the “FDB” option. In addition, the climatic variables of the study sites were obtained calculating the centroid of each plot from the database of the World Energy Resource Prediction (POWER) project of the National Aeronautics and Space Administration (NASA) Langley Research Center available at <https://power.larc.nasa.gov/data-access-viewer/> (accessed in September 2023). The period analyzed was from 2001 to 2021 and the climate selected variables for the analysis were annual precipitation (mm), and mean annual, minimum, and maximum temperatures at 2 m (°C). These variables were handled with the ArcGis program, re-scaled to a spatial resolution of 10 m [28].

Data analysis

Given the geographic proximity (~ 27 km) and similar environmental conditions of the study sites, a preliminary statistical evaluation of the variables analyzed was performed using a mixed-effects model with “site” as a random factor. The variance component associated with site was not significant ($p < 0.05$), indicating negligible differences between sites. Therefore, data from both forests were combined for further analysis to improve statistical power and focus on the effects of vegetation cover and soil depth. The analysis focused on three different vegetation covers: primary forest, disturbed forest, and deforested area. The assumptions of normality and homogeneity of variance were verified with the Shapiro Wilk and Bartlett tests, respectively ($p < 0.05$). An analysis of variance (ANOVA) was performed to evaluate the vertical variation of total glomalin (TG), easily extractable glomalin (EEG), and the number of arbuscular mycorrhizal fungi (AMF) spores and its relationship with SOC as a function of the analyzed depths by each cover type; likewise, ANOVA was employed for analyzing variation in soil physical-chemical properties. The comparison of mean values among the depth ranges was carried out using the Tukey test ($p < 0.05$) implemented with the function HSD.test of the R package “*agricolae*” [29]. In addition, the coefficients of variation (CV = standard error/average) were calculated for the different variables according to the different vegetation covers, and linear regressions were performed with the “*lm*” function in the R package “*dplyr*” [30], in order to evaluate the variation rates as a function of depth [37]. All the analysis were performed using the R program [31].

Additionally, the influence of soil and climate variables in the glomalin (TG and EEG) concentrations for two composed depths (topsoil: 0–40 cm and bottom soil: 40–100 cm) was analyzed using Pearson's correlation [36] and structural equation modeling (SEM). The selection of the specific intervals mentioned is based on the results previously proposed by various authors, who highlight

the importance and contrasting differences between them in relation to the variables analyzed. “Wang et al. [32] reported GRSP contents that were 1.8 to 2.0 times higher in the upper 40 cm of soil compared to the 40–100 cm layer. Similarly, Wang et al. [33] identified both direct and indirect effects of soil physicochemical properties, nutrient parameters, and climatic conditions on glomalin and SOC characteristics, analyzing surface (0–40 cm) and deep soils (40–100 cm) separately. Furthermore, Wu et al. [34] emphasized the importance of studying glomalin and SOC dynamics at different soil depths, specifically between 0–40 cm and 40–100 cm.

The structural equation model (SEM) was developed to evaluate the direct and indirect factors influencing soil organic carbon (SOC). The model structure was based on the ecological theory of indirect site influence (specifically climate and elevation) and soil properties on SOC through the activity of arbuscular mycorrhizal fungi and glomalin accumulation [35].

The SEM analysis was performed using SPSS AMOS version 2.1 [39], and model fit was assessed using the Chi-square (χ^2) statistic, Goodness-of-Fit Index (GFI), Tucker-Lewis Index (TLI), and Root Mean Square Error of Approximation (RMSEA).

Results

Vertical glomalin variation in three cover types

The analysis of variance (ANOVA) showed significant differences ($p < 0.05$) in TG, EEG, and AMF concentrations across soil depths (Table 1). The highest concentrations were recorded in the surface layer (0–20 cm) and the lowest in the deeper layers (80–100 cm), regardless of vegetation cover type.

In the deforested forest, TG reached its highest value in the 0–20 cm layer (63.91 ± 13.32 mg/g) and decreased to 1.23 ± 0.87 mg/g at 80–100 cm (~98.1%, Fig. 2A). In the disturbed forest, TG decreased by 87.1% (from 49.57 ± 5.37 to 6.41 ± 3.42 mg/g, Fig. 2B), and in the primary forest, by 87.8% (from 45.33 ± 18.83 to 5.51 ± 2.78 mg/g, Fig. 2C). The EEG followed the same decreasing pattern, with reductions of 92.6%, 92.3%, and 96.5% in the deforested, disturbed, and primary forests, respectively (Figs. 2D–F).

The AMF abundance also decreased with depth. In the deforested forest, spore numbers declined from 1739.67 ± 941.72 to 80.5 ± 19.72 spores/100 g (~95.4%, Fig. 2G); in the disturbed forest, from 1469.33 ± 887.77 to 45.33 ± 34.49 (~96.9%, Fig. 2H); and in the primary forest, from 1064.33 ± 335.36 to 65.17 ± 28 (~93.9%, Fig. 2I).

Regarding SOC, TG/SOC showed significant differences ($p < 0.05$) between the 0–40 cm and 60–100 cm layers in the deforested and disturbed forests, with the highest values in the surface layers (1.54 ± 0.10 and 0.88 ± 0.21 , respectively; Figs. 2J–L). In the primary

Table 1 Pearson correlation coefficients between total glomalin (TG), easily extractable glomalin (EEG), arbuscular mycorrhizal fungi (AMF), and soil and climate properties for surface and deep soil layers

Variables	0–40 cm			40–100 cm		
	TG	EEG	AMF	TG	EEG	AMF
Soil chemical properties						
SOC	0.436**	0.429**	0.072	0.558**	0.677**	0.673**
OM	0.287	0.358*	0.130	0.585**	0.548**	0.521**
N	0.287	0.358*	0.130	0.567**	0.534**	0.515**
P	0.290	0.320	0.012	0.341*	0.161	0.076
K	0.613**	0.086	0.534**	0.485**	-0.143	0.147
pH	-0.168 ^{ns}	-0.039 ^{ns}	-0.184 ^{ns}	-0.147 ^{ns}	0.057 ^{ns}	-0.071 ^{ns}
EC	0.240 ^{ns}	0.259 ^{ns}	0.556**	-0.147 ^{ns}	0.084 ^{ns}	-0.214 ^{ns}
Soil physical properties						
BD	-0.592**	-0.024 ^{ns}	-0.289 ^{ns}	-0.522**	-0.073 ^{ns}	-0.469**
SWC	0.418*	0.039 ^{ns}	0.388	0.546**	0.198 ^{ns}	0.475**
Climate and environmental conditions						
Mean minimum temperature	0.550**	-0.125	0.253	0.219	-0.352**	-0.067
Mean annual temperature	0.546**	-0.113	0.186	0.219	-0.359**	-0.113
Mean maximum temperature	0.506**	-0.053	0.085	0.184	-0.321*	-0.171
Annual precipitation	-0.007	-0.008	-0.895**	0.002	-0.050	-0.496**
Elevation	-0.210	0.085	-0.821**	-0.144	0.132	-0.388**

*correlation is significant at $p < 0.05$ (two-tailed), ** $p < 0.05$ (two-tailed). SOC=soil organic carbon; OM=organic matter; N=nitrogen; P=phosphorous; K=potassium; EC=electric conductivity; BD=bulk density; SWC=soil water content

forest, no significant differences were observed ($p > 0.05$). However, the EEG/SOC ratio varied significantly in the disturbed and primary forests (Figs. 2M–O), while the AMF/SOC ratio showed the highest values in the 0–40 cm layer, with reductions of 65.5% and 77.5% toward deeper layers (Figs. 2P–R).

The coefficient of variation (CV) increased with depth, indicating more heterogeneity in the conditions for the lower horizons. In the disturbed forest, CV values for TG and TG/SOC were highest in the 80–100 cm layer, while EEG showed lower variability between 20 and 60 cm.

In summary, TG, EEG, and AMF decreased significantly with depth, showing reductions exceeding 85% between the 0–20 cm and 80–100 cm layers. The surface layers (0–40 cm) were the most biologically active layers, playing a key role in SOC storage and soil structural stability.

Vertical variations of physical and chemical soil properties

The ANOVA revealed significant differences ($p < 0.05$) in SOC, OM, N, and P concentrations across soil depths (Fig. 3). The highest concentrations were found in the surface layer (0–20 cm) and the lowest in the deepest layer (80–100 cm), regardless of vegetation cover type (Figs. 3A–L).

In the deforested forest, SOC decreased from 41.74 ± 10.14 t/ha to 7.45 ± 5.33 t/ha (-82.1% , Fig. 3A). In the disturbed forest, it declined from 58.31 ± 11.64 to 12.84 ± 2.29 t/ha (-78% , Fig. 3B), and in the primary forest, from 79.60 ± 20.83 to 11.12 ± 3.48 t/ha (-86% , Fig. 3C). OM followed a similar pattern, with reductions

of 96.5%, 87.4%, and 87.2% in the deforested, disturbed, and primary forests, respectively (Figs. 3D–F).

N showed a significant decrease ($p < 0.05$) with depth, dropping by an average of 90% across the three forest types (Figs. 3G–I). P also declined significantly ($p < 0.05$), with reductions of 85.2%, 73.9%, and 66.3% in the deforested, disturbed, and primary forests, respectively (Figs. 3J–L).

K did not show significant differences ($p < 0.05$) with depth in the deforested and primary forests, although it decreased by 63.9% in the disturbed forest (Figs. 3M–O). pH slightly increased with depth across all forest types, ranging between 7.9 and 8.4 (Figs. 3P–R). Electrical conductivity (EC) remained stable in the deforested and disturbed forests but decreased significantly ($p < 0.05$) in the primary forest (-31.5% , Fig. 3U).

BD increased significantly ($p < 0.05$) with depth in the deforested and disturbed forests, with increments of 26.8% and 19.4%, respectively (Figs. 3V–W). Soil water content (SWC) decreased significantly ($p < 0.05$) with depth in the deforested (-47.4%) and primary (-44.4%) forests (Figs. 3Y–AB).

Overall, soil chemical and physical properties decreased significantly with depth, while BD increased due to compaction and reduced organic matter inputs. The surface layers (0–40 cm) represent the most fertile and biologically active zone, playing a key role in carbon storage, nutrient cycling, and soil structural stability (Fig. 3).

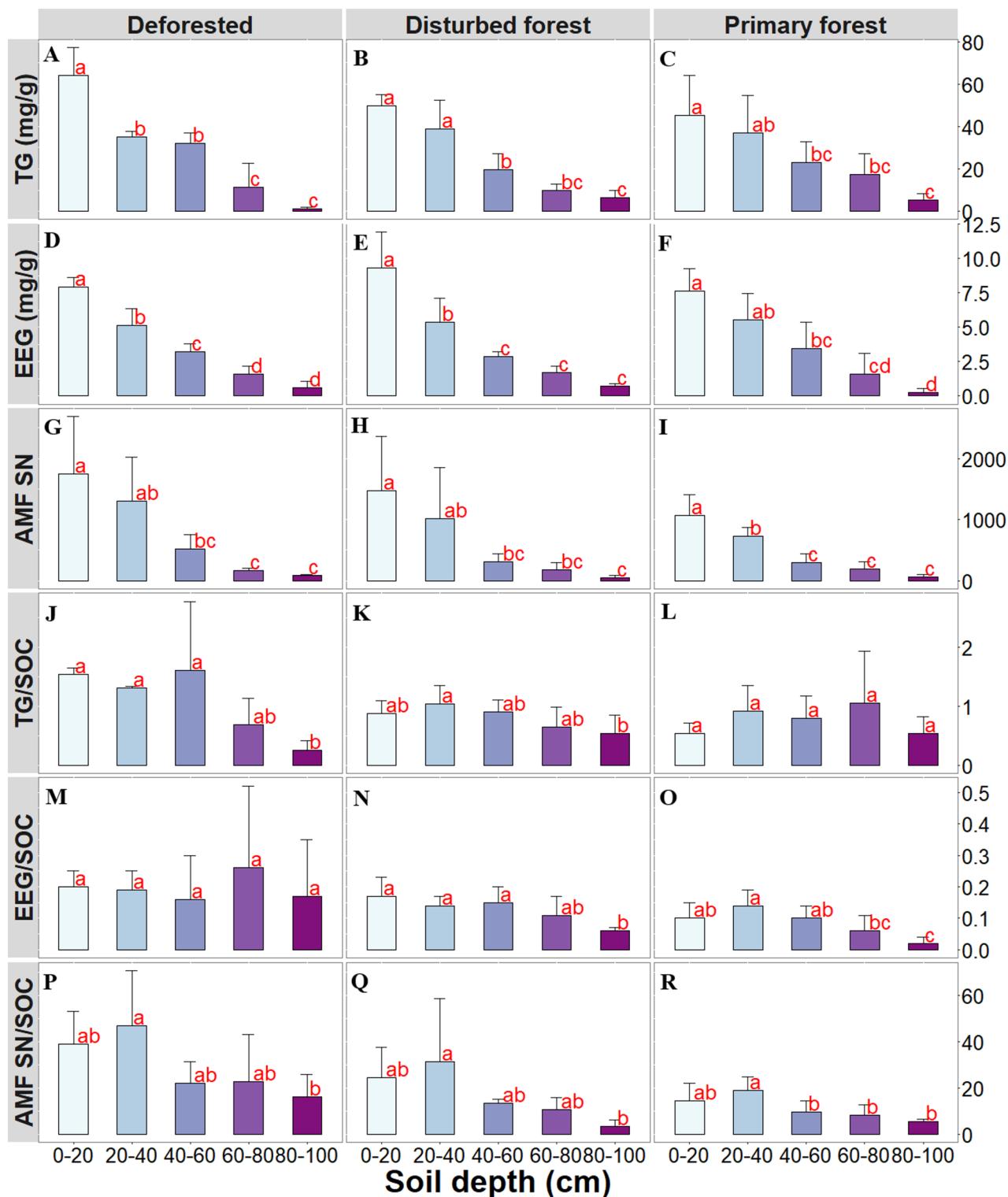


Fig. 2 Mean values comparison of total (TG) and easily extractable glomalin (EEG), and number of arbuscular mycorrhizal fungi (AMF) spores at different soil depths in the three forest types. SOC = soil organic carbon. Different letters indicate significant mean differences

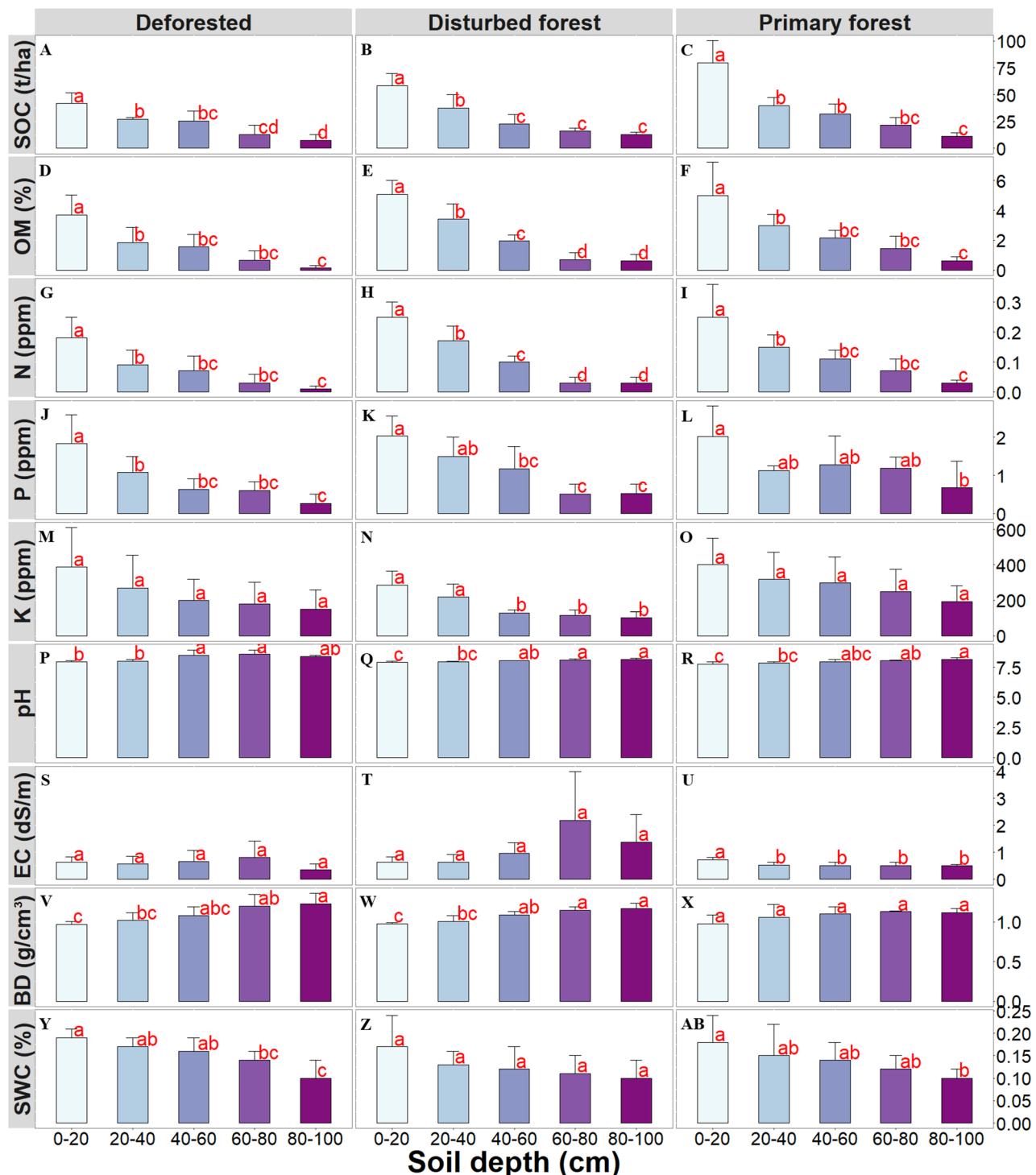


Fig. 3 Mean values comparison at different soil depth for chemical and physical variables according to the analyzed forest cover types. SOC = soil organic carbon; OM = organic matter; N = nitrogen; P = phosphorus; K = potassium; EC = electric conductivity; BD = bulk density; SWC = soil water content. Different letters indicate significant mean differences

Relationship of glomalin and soil physical-chemical properties

There were significant correlations between glomalin and soil nutrients ($p < 0.05$). In the surface layers, TG

presented correlations with SOC and K; EEG was significantly correlated with SOC, OM, and N. The number of AMF spores was correlated with K. In deep layers, the TG was correlated with all the analyzed soil nutrients.

The EEG and the AMF spores were correlated with SOC, OM, and N with a great degree of correlation with SOC, showing a R^2 of 0.68 and 0.67, respectively (Table 1).

The correlation between glomalin and soil physical properties was significant ($p < 0.05$). At surface layers, TG presented negative correlation with BD, while the number of AMF spores was positively correlated with EC and SWC. At deep layers, significant correlations were obtained for TG and AMF spores with BD (negative) and SWC (positive), respectively. EEG showed no significant correlations with physical properties for both shallow and deep soil layers (Table 1).

The correlation between TG, EEG and number of AMF spores and climatic variables showed different degrees of strength. However, higher correlations were observed when compared to the edaphic factors (e.g., AMF - annual precipitation correlation) (Table 1). TG and EEG only presented positive and negative correlations with mean annual temperature in surface and deep soils, respectively. The number of AMF spores was negatively correlated with precipitation and altitude in both the surface and deep soil layers (Table 1).

The concentration of TG and EEG in each soil layer depended on their interaction with the soil's physico-chemical properties and the site conditions (Figs. 4A–B). In the surface layers, the number of AMF spores was primarily influenced by precipitation (coefficient = -0.90), suggesting that excessive surface moisture may negatively affect fungal reproduction; likewise, bulk density also showed a moderate restrictive effect (Fig. 4A). At deeper soil layers, spore abundance was more strongly limited by bulk density (coefficient = -0.48) than by precipitation (Fig. 4B). In terms of SOC accumulation, the deep soil model showed a stronger dependence on the EEG fraction, reinforcing its value as a functional indicator of SOC stabilization processes.

Discussion

Vertical glomalin variation in three cover types

The Amazon rainforest is facing one of the most critical moments due to severe changes in vegetation. In the Peruvian Amazon, the regions with high percentage of deforestation involve the districts of Ucayali, Madre de Dios, Loreto, and San Martín, with 36,306, 36,306, 19,829, and 13,080 ha, respectively [40]. Although glomalin it is considered a highly relevant protein, a recent molecular study has suggested that, based on its composition, it may actually be a carbohydrate (glomalose). If glomalin is indeed a carbohydrate this reclassification has important implications as proteins and carbohydrates differ significantly in their biochemical properties, ecological roles, and origins [41]. The production of GRSP has been closely linked to both carbon accumulation and soil aggregate stability [42]. The observed patterns

in glomalin concentrations across soil depths and cover types are consistent with previous research highlighting the role of GRSP in soil function (Fig. 2). For instance, in forest ecosystems in China, GRSP contributed significantly to soil organic carbon (SOC) storage, supporting healthier regional vegetation [43]. Furthermore, soil aggregate stability has been shown to be greater in mycorrhized soils compared to non-inoculated treatments under stress conditions, reinforcing the ecological importance of AMF spores in maintaining soil structure [44]. According to our analysis, the variation of TG, EEG, and the number of AMF spores indicates a clear pattern: glomalin concentrations decrease from the top to the bottom soil layers across the three cover types. This vertical distribution helps explain why surface soils consistently exhibit higher glomalin levels, which are crucial for maintaining soil structure and stability. In this context, these components showed high concentrations in surface layers (0–40 cm) (Fig. 2A–I), consistent with patterns observed in other studies. Similar results regarding glomalin distribution across soil depth layers were reported in cultivated soils of China, highlighting the general tendency for glomalin to accumulate near the surface [34]. The EEG/SOC ratio was higher in the 60–80 cm soil layer in the deforested forest, indicating a stronger contribution of glomalin-related soil protein (GRSP) to soil organic carbon (SOC) in these systems (Fig. 2M). This aligns with previous findings postulating that GRSP plays a crucial role in SOC accumulation when the early carbon sink function is limited [44, 45]. The abundance of AMF and the AMF/SOC ratio progressively decreased with soil depth, showing higher concentrations in the 0–20 cm and 20–40 cm layers, particularly in deforested and disturbed forest sites. This pattern suggests more active mycorrhizal colonization and a greater contribution to soil organic carbon in the upper horizons of impacted ecosystems (Fig. 2). The AMF spores have contributed positively to soil health through the production of organic acids and glomalin, protecting against soils erosion and promoting the stabilization of soil macro-aggregates [42].

The concentration of TG and AMF spores as well as their relationships with available SOC are strongly influenced by vegetation cover type (Figs. 2). In a study of soil profiles soil in Brazilian forest, it was reported that more than 50% of the total fungal biomass is concentrated within 30 cm with fungal presence extending to depths of up to 8 m depth [46]. However, contrasting findings were reported by Egboka et al. [47], who observed that the abundance of AMF decreased with soil depth in forest soils of Nigeria.

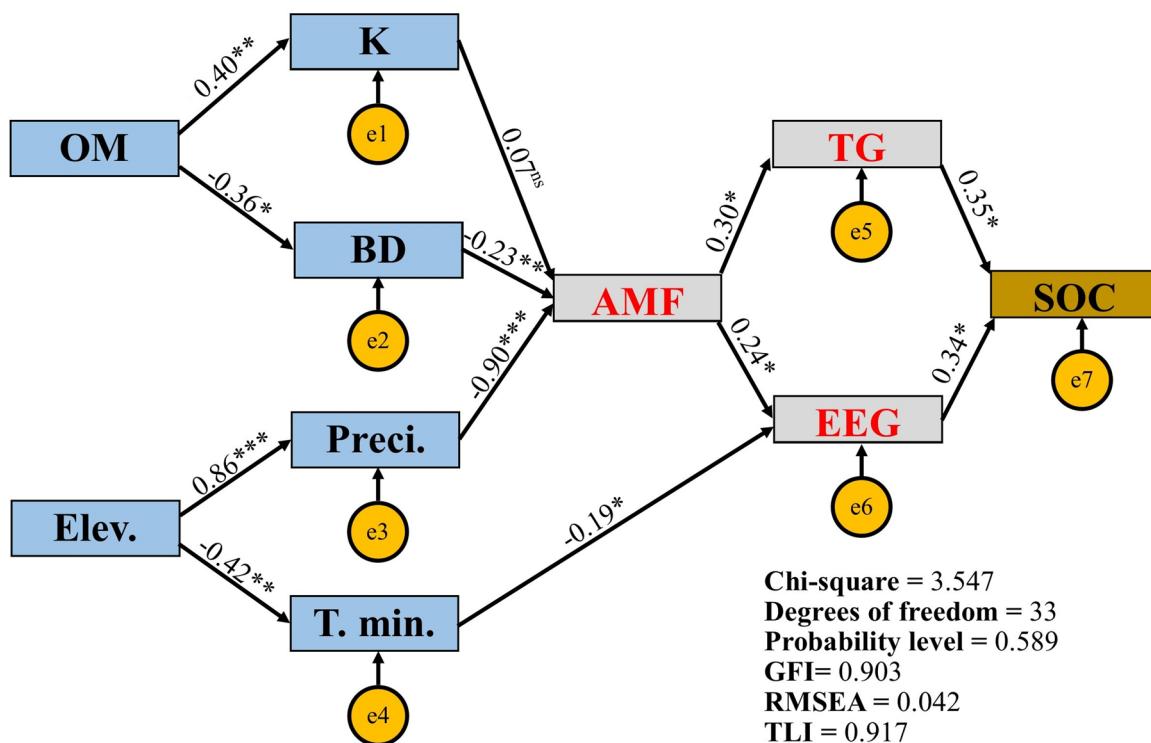
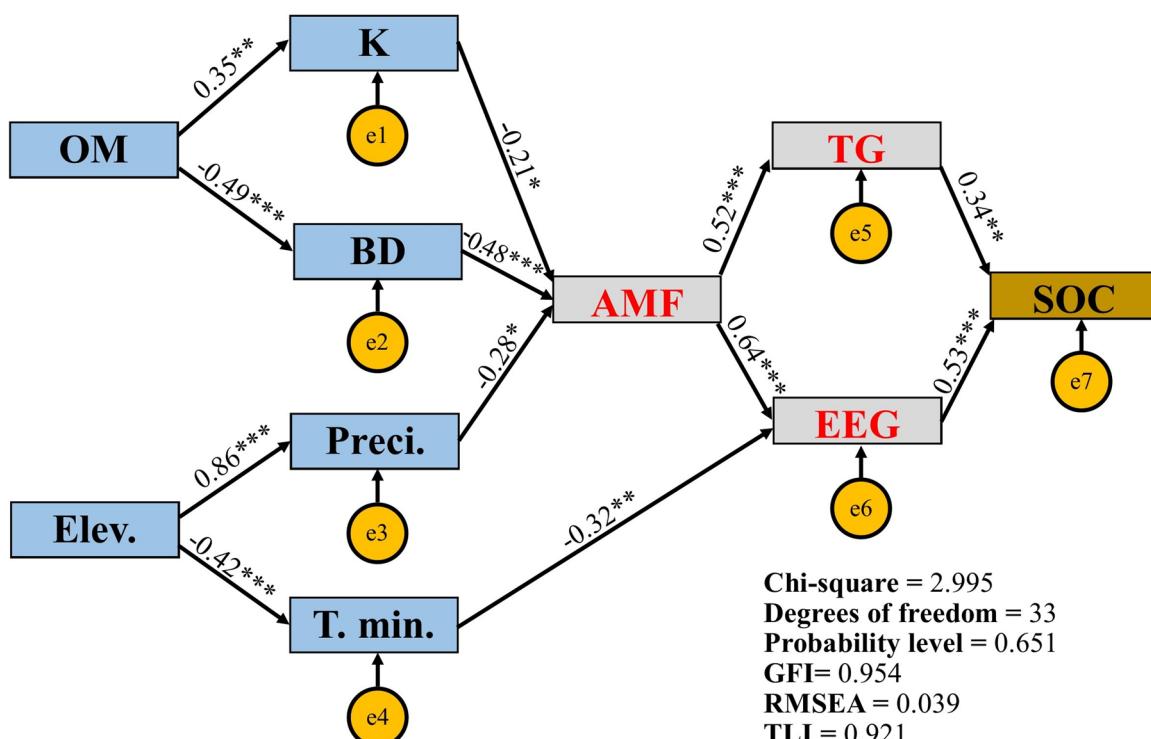
A**B**

Fig. 4 Structural equation models (SEM) for glomalin **A**, in the surface (0–40 cm) and **B**, deep soil layers (40–100 cm). The squares represent the measured variables and the circles the error associated with the measured variable. *, ** and ***significance at $p < 0.05$, 0.01, and 0.001, respectively

Vertical variations of physical and chemical soil properties

In the studied forests, both physical and chemical variables, along with climatic parameters such temperature and precipitation, exert a direct influence on soil conditions, with notable differences observed between surface and deeper soil layers. Soil physicochemical properties accounted for more than 60% of the variation in glomalin levels along an urban–forest gradient in China, highlighting the dominant role of local soil conditions over land-use type. This suggests that, although changes in land use as urbanization and vegetation characteristics influence glomalin production, the underlying soil environment remains the primary driver of its spatial distribution [48]. Regardless of forest cover type, at deeper soil layers, variables such as SOC, OM, and N showed a stronger positive effect on the concentration of TG, EEG, and AMF while variables like pH, BD, and EC were generally less influential (Table 1).

According to Wang et al. [49] the relationship between glomalin and soil physical properties showed a negative correlation with pH and EC and a positive correlation with SOC, N, and P [50]. Singh et al. [51] reported a strong association between GRSP and SOC, pH, N, and P, but found no relationship with EC. In addition, Cissé et al. [52] observed a positive relationship between GRSP, SOC, and N in the topsoil layers. This pattern can be explained by the fact that nutrient availability, particularly N, can stimulate glomalin production, while higher P concentrations may inhibit mycorrhizal colonization [53].

Differences between surface and deep soil layers have been reported in previous studies [54, 55]. In surface soils, glomalin concentrations were primarily influenced by nutritional components, particularly SOC and N, as they showed linear decreases with the soil depth, while in deeper layers, physical and chemical properties, such as pH and BD, showed linear increases [34]. Our SEM revealed that soil depth and climatic factors indirectly influenced TG, AMF, and EEG through their effects on soil properties (Fig. 4). The growth of vegetation in forest ecosystems can promote SOC accumulation, leading to its increased content and in consequence, the accumulation of large quantities of carbon throughout the entire soil profile [49].

Finally, climatic variables such as temperature and precipitation parameters played a significant role in glomalin concentration with effects observed at soil depths of up to 100 cm. This pattern is probably related to the availability of SOC and OM, which stimulate mycorrhizal interactions (Table 1). Soil degradation in deforested areas is recognized to reduce AMF abundance, leading to declines in organic matter and overall soil fertility [33]. Previous studies have demonstrated that climate variability directly impacts soil processes as GRSP respond

to elevated CO₂ and nitrogen levels in subtropical forests, contributing to greater carbon accumulation in deforested soils. Variation in climatic parameters has been demonstrated as an impact on soils, while GRSP responded to elevated CO₂ and N concentration in a subtropical forest, which increased the C accumulation in deforested soils [56]. Furthermore, temperature is recognized as an influential driver of soil structure [57]. In surface soil layers from the studied forests, increases in temperature are likely associated with higher TG (total glomalin) levels, whereas a decrease in precipitation would negatively affect the concentration of AMF spores (Table 1). The observed positive effects on AMF communities may be attributed to the varying sensitivities of AMF spores to nutrient availability and soil moisture, both of which are shaped by precipitation dynamics [57].

Conclusions

This study highlights the critical role of AMF spores and glomalin/glamalase in maintaining soil health and resilience in tropical forest ecosystems of the Peruvian Amazon. The results demonstrate that vegetation cover and land-use change significantly influence AMF abundance and glomalin production, which are closely linked to SOC dynamics and fertility. Deforestation and forest disturbance lead to reductions in AMF activity, particularly in surface soil layers, affecting carbon storage and soil structure. Topsoil (0–40 cm) is a key zone for glomalin production and nutrient retention, with the highest concentrations of GRSP and AMF spores observed in disturbed and recently deforested areas. This suggests a potential compensatory response of soil microbial communities to environmental stress and land-use change. Soil properties such as organic matter, nitrogen, pH, moisture content, and vegetation type strongly regulate glomalin distribution, indicating that both biotic and abiotic factors are critical in governing soil microbial processes. Surface soils in disturbed and recently deforested forests exhibited greater nutrient storage capacity (e.g., carbon, nitrogen) than those in primary forests, reinforcing the role of glomalin and AMF in early soil recovery processes following disturbance.

Effective management and restoration strategies should prioritize the upper 40 cm of soil, focusing on maintaining vegetation cover, enhancing organic matter inputs, and preserving mycorrhizal communities to improve soil fertility and carbon sequestration in degraded tropical ecosystems.

Overall, these findings underscore the importance of AMF and glomalin in soil restoration frameworks and offer key insights for mitigating the impacts of deforestation on soil function and climate resilience in the Peruvian Amazon.

Acknowledgements

GV-T. Kindly thanks to the National University of San Martin, Tarapoto for financing this research work.

Author contributions

Conceptualization: G.V-T. Methodology: A.L; C.M.. Software: H.S. Validation: A.A.A. Formal analysis: N.G-J., J.S. Investigation: J.T-H., O.A.T-H. Resources: M.J.V-A. Data curation: K.R. Writing-original draft: W.M-C. Writing-review & editing: J.R.B-V; C.M. Visualization: G.V-T. Supervision: C.M. Project administration: B.V. Funding acquisition: C.M; G.V-T.. All co-authors reviewed the final version and approved the manuscript before submission.

Funding

National University of San Martin, Tarapoto.

Data availability

No datasets were generated or analysed during the current study.

Declarations

Ethics and consent to participate

Not applicable.

Consent to publish

Not applicable.

Competing interests

The authors declare no competing interests.

Received: 26 November 2024 / Accepted: 23 December 2025

Published online: 16 January 2026

References

1. Gatti L-V, Basso LS, Miller JB, Gloor M, Gatti L, Cassol HL, Neves RA. Amazonia as a carbon source linked to deforestation and climate change. *Nature*. 2021;595(7867):388–93. <https://doi.org/10.1038/s41586-021-03629-6>.
2. Lapola DM, Pinho P, Barlow J, Aragao LEO et al. The drivers and impacts of Amazon forest degradation. *Science*. 2023;379, Issue 6630. <https://doi.org/10.1126/science.abp8622>
3. Soucémarianadin L, Cécillon L, Chenu C, Baudin F, Nicolas M, Girardin C, Barré P. Is Rock-Eval 6 thermal analysis a good indicator of soil organic carbon stability? – A method-comparison study in forest soils. *Soil Biol Biochem*. 2018;117:108–16. <https://doi.org/10.1016/j.soilbio.2017.10.025>.
4. Guo J, Wang B, Wang G, Wu Y, Cao F. Vertical and seasonal variations of soil carbon pools in Ginkgo agroforestry systems in Eastern China. *CATENA*. 2018;171:450–9. <https://doi.org/10.1016/j.catena.2018.07.032>. ISSN 0341-8162.
5. Sun T, Wang Y, Hui D, Jing X, Feng W. Soil properties rather than climate and ecosystem type control the vertical variations of soil organic carbon, microbial carbon, and microbial quotient. *Soil Biol Biochem*. 2020;148(107905):0038–717. <https://doi.org/10.1016/j.soilbio.2020.107905>.
6. Cai WX, He NP, Li MX, Xu L, Wang LZ, Zhu JH, et al. Carbon sequestration of Chinese forests from 2010 to 2060: Spatiotemporal dynamics and its regulatory strategies. *Sci Bull*. 2022;67(8):836–43. <https://doi.org/10.1016/j.scib.2021.12.012>.
7. Holtz EWF, Gonzalez MG, Giuffré L, Esteban A, Ciarlo EA. Glomalin and their relationship with soil carbon. *Int J Appl Sci Technol*. 2016;6 (2): 70–73 https://jast.thebrpi.org/journals/Vol_6_No_2_June_2016/10.pdf
8. Vallejos-Torres G, Torres SC, Gaona-Jimenez N, et al. The combined effect of arbuscular mycorrhizal fungi and compost improves growth and soil parameters and decreases cadmium absorption in Cacao (*Theobroma Cacao* L.) plants. *J Soil Sci Plant Nutr*. 2022;22:5174–82. <https://doi.org/10.1007/s42729-022-00992-9>.
9. Yang Y, Luo W, Xu J, Guan P, Chang L, Wu X, Wu D. Fallow land enhances carbon sequestration in glomalin and soil aggregates through regulating diversity and network complexity of arbuscular mycorrhizal fungi under climate change in relatively High-Latitude regions. *Front Microbiol*. 2022;13:930622. <https://doi.org/10.3389/fmicb.2022.930622>.
10. Hawkins HJ, Cargill RI, Van Nuland ME, Hagen SC, Field KJ, Sheldrake M, Kiers ET. Mycorrhizal mycelium as a global carbon pool. *Curr Biol*. 2023;33(11):R560–73. <https://doi.org/10.1016/j.cub.2023.02.027>.
11. Haddad MJ, Sarkar D. Glomalin, a newly discovered component of soil organic matter: part II: relationship with soil properties. *Environ Geosci*. 2003;10(3):99–106. <https://doi.org/10.1306/eg.05020303005>.
12. Moura JB, Souza RF, Vieira WG, Lucas LS, Santos JM, Dutra S, Marín C. Effects of a Megafire in the arbicular mycorrhizal fungal community and parameters in the Brazilian Cerrado ecosystem. *For Syst*. 2022;31(1):e001. <https://doi.org/10.5424/fs/2022311-18557>.
13. Centro Nacional de Planeamiento Estratégico, CEPLAN. análisis de la deforestación y pérdida de vegetación a nivel nacional y el impacto a nivel regionales. 2023; https://geo.ceplan.gob.pe/uploads/Analisis_deforestacion.pdf
14. Vallejos-Torres G, Gaona-Jimenez N, Pichis-García R, Ordoñez L, García-González P, Quinteros A, Lozano A, Saavedra-Ramírez J, Tuesta-Hidalgo JC, Reategui K, Macedo-Córdova W, Baselly-Villanueva JR, Marín C. Carbon reserves in coffee agroforestry in the Peruvian Amazon. *Front Plant Sci*. 2024a;15:1410418. <https://doi.org/10.3389/fpls.2024.1410418>.
15. Vallejos-Torres G, Lozano-Chung A, Ordoñez-Sánchez L, García-González P, Quinteros A, Gaona-Jimenez N, Mendoza-Caballero W, Macedo-Córdova W, Saavedra-Ramírez J, Baselly-Villanueva JR, & Marín C. Forest land-use change affects soil organic carbon in tropical dry forests of the Peruvian Amazon. *Forest Systems*, 2024b;(3), 20896. <https://doi.org/10.5424/fs/202433-20896>.
16. Vecco GCD. Estudios Biológicos participativos En El territorio integral Kichwa (TIK). Sitio prioritario Bosque Seco Del Huallaga Central, provincias de Bellavista y Picota, San Martín. Servicio Nacional de Áreas Naturales Protegidas por el Estado y Gobierno Regional de San Martín.) Roosevelt García-Villacorta (ed.). 2014. 172 p.
17. Yu H, Zha T, Zhang X, Ma L. Vertical distribution and influencing factors of soil organic carbon in the loess Plateau, China. *Sci Total Environ*. 2019;693:133632. <https://doi.org/10.1016/j.scitotenv.2019.133632>.
18. Bradford MM. A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-Dye binding. *Anal Biochem*. 1976;72:248–54. [https://doi.org/10.1016/0003-2697\(76\)90527-3](https://doi.org/10.1016/0003-2697(76)90527-3).
19. Wright SF, Upadhyaya A, Buyer JS. Comparison of N-linked oligosaccharides of glomalin from arbicular mycorrhizal fungi and soils by capillary electrophoresis. *Soil Biol Biochem*. 1998;30:1853–7.
20. Gerdemann JW, Nicolson TH. Spores of mycorrhizal endogone species extracted from soil by wet Sieving and decanting. *Trans Br Mycol Soc*. 1963;46:235–44. [https://doi.org/10.1016/S0007-1536\(63\)80079-0](https://doi.org/10.1016/S0007-1536(63)80079-0).
21. Vallejos-Torres G, Arévalo L, Iliquin I, Solis R. Respuesta En Campo de clones de Café a La Inoculación Con consorcios de Hongos Micorrízicos arbucleares En La Región Amazónas, Perú. Información tecnológica. 2019;30(6):73–84. <https://doi.org/10.4067/S0718-07642019000600073>.
22. Corazon-Guivin MA, Vallejos-Torres G, Vallejos-Tapullima A, Tenorio-Cercado MÁ, Caballero WM, Marín C, Santos VM, et al. *Rhizoglonus Cacao*, a new species of the glomeraceae from the rhizosphere of *Theobroma Cacao* in Peru, with an updated identification key for all species attributed to rhizoglonus. *Nova Hedwigia*. 2022;115(1–2):99–115. https://doi.org/10.1127/nova_hedwigia/2022/0698.
23. Walkley A, Black IA. An examination of the Degtjareff method for determining soil organic matter and a proposed modification of the chromic acid Titration method. *Soil Sci*. 1934;37:29–38. <https://doi.org/10.1097/00010694-193401000-00003>.
24. Blake GR, Hartge K. Bulk density. In: Klute A, editor. Methods of soil analysis: part 1 physical and mineralogical methods. Madison, Wisconsin, USA: American Society of Agronomy; 1986. pp. 363–75. [https://www.scirp.org/\(S\(i43dyn45teexjx455ql13d2q\)\)/reference/ReferencesPapers.aspx?ReferenceID=498675](https://www.scirp.org/(S(i43dyn45teexjx455ql13d2q))/reference/ReferencesPapers.aspx?ReferenceID=498675).
25. Kjeldahl J. Neue methode Zur bestimmung des stickstoffs in organischen Körpern. *Fresenius Z F Anal Chemie*. 1883;22:366–82. <https://doi.org/10.1007/BF01338151>.
26. Olsen SR, Sommers LE, Phosphorus et al. pp. 403–430. In Page AL, editors. Methods of soil analysis: Part 2. Chemical and microbiological properties. *Agronomy Monographs* 9. 2nd ed. ASA and SSSA, Madison, Wisconsin, USA. 1982, <https://doi.org/10.2134/agronmonogr9.2.2ed.c24>.
27. Novozamsky I, Houba V. Critical evaluation of soil testing methods for K Proc. 20th Coll. Int. Potash Inst., Baden bei Wien, Austria. IPI, Bern. 1998;7:165–185. <https://research.wur.nl/en/publications/critical-evaluation-of-soil-testing-methods-for-k>.
28. Casas GG, Baselly-Villanueva JR, Limeira MMC, Torres CMME, Leite HG. Clasifying the risk of forest loss in the Peruvian Amazon rainforest: an alternative

approach for sustainable forest management using artificial intelligence. *Trees Forests People*. 2023;14:100440. <https://doi.org/10.1016/j.tfp.2023.100440>.

29. Mendiburu F, Agricolae R. versión 1.0–9. Universidad Nacional Agraria La Molina. Lima Perú. 2010, <https://coesincelejo.files.wordpress.com/2011/01/manualpracticoagricolae.pdf>
30. Wickham H, François R, Henry L, Müller K, Vaughan D. dplyr: A Grammar of Data Manipulation. R package version, 2023; 1.1.4. <https://dplyr.tidyverse.org>
31. R Core Team. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2024, <http://www.R-project.org>
32. Wang Q, Wang W, Zhong Z, et al. Variation in glomalin in soil profiles and its association with Climatic conditions, shelterbelt characteristics, and soil properties in Poplar shelterbelts of Northeast China. *J Res*. 2020;31:279–90. <https://doi.org/10.1007/s11676-019-00909-w>.
33. Wang W, Zhong Z, Wang Q, et al. Glomalin contributed more to carbon, nutrients in deeper soils, and differently associated with climates and soil properties in vertical profiles. *Sci Rep*. 2017;7:13003. <https://doi.org/10.1038/s41598-017-12731-7>.
34. Wu M, Zhang S, Gu X, He Z, Liu Y, Mo Q. Accumulation of Glomalin-Related soil protein regulated by plantation types and vertical distribution of soil characteristics in Southern China. *Forests*. 2024;15(8):1479. <https://doi.org/10.3390/f15081479>.
35. Zhao Y, Xiao Y, Chen W, Wang B, Qian Z. Land-Use change impacts on Glomalin-Related soil protein and soil organic carbon in Huangshan mountain region. *Forests*. 2025;16(9):1362. <https://doi.org/10.3390/f16091362>.
36. Hernández-Lalinde JDH, Espinosa-Castro J, Tarzona M, Rodríguez J, Chacón J, Tolosa C, Arenas M, Carrillo S, Bermúdez V. Sobre el uso adecuado del coeficiente de correlación de Pearson: definición, propiedades y suposiciones. 2018, <https://bonga.unisimon.edu.co/server/api/core/bitstreams/13d3c100-2643-4d4-9084-7ffb5402fb31/content>
37. Chambers JM. Chapter 4 of statistical models. In: Chambers JM, Hastie TJ, editors. *Linear models*. Wadsworth & Brooks/Cole; 1992. <https://doi.org/10.1177/09622802900100>.
38. Arbuskle JL. Amos 26.0 User's Guide. Chicago: IBM SPSS, Antoninka A, Reich PB, Johnson NC. Seven years of carbon dioxide enrichment, nitrogen fertilization and plant diversity influence arbuscular mycorrhizal fungi in a grassland ecosystem. *Nuevo Phytol*. 2019;192:200–214. <https://doi.org/10.1111/nph.14699> 137.2011.03776x
39. Sierra Y. Perú alcanza cifra de deforestación más alta en los últimos 20 años. 2022, <https://es.mongabay.com/2021/10/peru-aumenta-deforestacion-cifra-s-bosques/>
40. Alptekin B, Hirsch H, Kleven B, King L, McLimans C, Daniels D, Irving T, Floss D and Ané JM. From glomalin to glomalose: unraveling the molecular identity of the MAb32B11 antigen. *New Phytologist*. 2025.
41. Rivas Y, Canseco M, Knicker H, Etcheverría P, Godoy R, Matus F, Gallardo R. Variación En El Contenido de glomalina relacionada a Las proteínas Del suelo, después de Un incendio forestal En Un Andisol En bosques de araucaria Araucana Del centro-sur de Chile. Bosque (Valdivia). 2016;37(2):409–17. <https://doi.org/10.4067/S0717-92002016000200019>.
42. Gao WQ, Wang P, Wu QS. Functions and application of glomalin-related soil proteins: a review. *Sains Malaysiana*. 2019;48(1):111–9. <https://doi.org/10.17576/jsm-2019-4801-13>.
43. Ji LL, Tan WF, Chen XH. Arbuscular mycorrhizal mycelial networks and glomalin-related soil protein increase soil aggregation in calcareous regosol under well-watered and drought stress conditions. *Soil Tillage Res*. 2019;185:1–8. <https://doi.org/10.1016/j.still.2018.08.010>.
44. Fall AF, Nakabonge G, Ssekandi J, Founoune-Mboup H, Apori SO, Ndiaye A, Badji A, Ngom K. Roles of arbuscular mycorrhizal fungi on soil fertility: contribution in the improvement of Physical, Chemical, and biological properties of the soil. *Front Fungal Biol*. 2022;3:723892. <https://doi.org/10.3389/ffnb.2022.723892>.
45. de Araujo AP, Santana MC, Bonfim JA, de Lourdes D, Cardoso EJBN. Digging deeper to study the distribution of mycorrhizal arbuscular fungi along the soil profile in pure and mixed Eucalyptus grandis and acacia mangium plantations. *Appl Soil Ecol*. 2018;128:1–11. <https://doi.org/10.1016/j.apsoil.2018.03.015>.
46. Egboka NT, Fagbola O, Nkwopara UN, Okoli NH, Afangide AI, Nwosu TV. Density of arbuscular mycorrhizal fungi and nutrient status of soils in selected land use types and soil depths. *Sarhad J Agric*. 2022;38(2):633–47. <https://doi.org/10.17582/journal.sja/2022/38.2.633.647>.
47. Wang WJ, Wang Q, Zhou W, Xiao L, Wang HM, He XY. Glomalin changes in urban-rural gradients and their possible associations with forest characteristics and soil properties in Harbin City, Northeastern China. *J Environ Manag*. 2018;224:225–34. <https://doi.org/10.1016/j.jenvman.2018.07.047>.
48. Wang Q, Wu Y, Wang WJ, Zhong ZL, Pei ZX, Ren J, Wang HM, Zu YG. Spatial variations in concentration, compositions of glomalin related soil protein in Poplar plantations in Northeastern China, and possible relations with soil physicochemical properties. *Sci World J*. 2014;13. <https://doi.org/10.1155/2014/160403>.
49. Wang Q, Wang WJ, He XY, Zhang WT, Song KS, Han SJ. Role and variation of the amount and composition of glomalin in soil properties in farmland and adjacent plantations with reference to a primary forest in North-Eastern China. *PLoS ONE*. 2015;10:e0139623. <https://doi.org/10.1371/journal.pone.0139623>.
50. Singh AK, Rai A, Singh N. Effect of long term land use systems on fractions of glomalin and soil organic carbon in the Indo-Gangetic plain. *Geoderma*. 2016;277:41–50. <https://doi.org/10.1016/j.geoderma.2016.05.004>.
51. Cissé G, Essi M, Kedi B, Nicolas M, Staunton S. Accumulation and vertical distribution of glomalin-related soil protein in French temperate forest soils as a function of tree type, climate and soil properties. *CATENA*. 2023;220:106635. <https://doi.org/10.1016/j.catena.2022.106635>.
52. Aliasgharzad N, Malekzadeh E. Glomalin and Carbon Sequestration in Terrestrial Ecosystems. In: Ahammed, GJ., Hajiboland, R, editors *Arbuscular Mycorrhizal Fungi and Higher Plants*. Springer. 2024, Singapore. https://doi.org/10.1007/978-981-99-8220-2_11
53. Wang Q, Mei D, Chen J, Lin Y, Liu J, Lu H, Yan C. Sequestration of heavy metal by glomalin-related soil protein: implication for water quality improvement in Mangrove wetlands. *Water Res*. 2019;1:148:142–52. <https://doi.org/10.1016/j.watres.2018.10.043>.
54. Wang WJ, Qiu L, Zu YG, Su DX, et al. Changes in soil organic carbon, nitrogen, pH and bulk density with the development of larch (*Larix gmelinii*) plantations in China. *Glob Change Biol*. 2011;17:2657–76. <https://doi.org/10.1111/j.1365-2486.2011.02447.x>.
55. Zhang J, Tang X, He X, Liu J. Glomalin-related soil protein responses to elevated CO₂ and nitrogen addition in a subtropical forest: potential consequences for soil carbon accumulation. 2015;83: 142–9. <https://doi.org/10.1016/j.soilbio.2015.01.023>.
56. Wang J, Zhang J, Wang C, Ren G, Yang Y, Wang D. Precipitation exerts a strong influence on arbuscular mycorrhizal fungi community and network complexity in a semiarid steppe ecosystem. *Eur J Soil Biol*. 2021;102:103268. <https://doi.org/10.1016/j.ejsobi.2020.103268>.

Publisher's note

Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.