

RESEARCH ARTICLE

Restoring soil multifunctionality through forest regeneration in abandoned Amazon pasturelands

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Abandoned pastures with degraded soil quality in the Amazon region often undergo succession to secondary forests. While aboveground responses to natural regeneration have been well investigated, the impacts on soil functioning are still poorly understood. Here we assessed how multiple soil functions respond to the natural regeneration of abandoned pastures in the Amazon, and how many years of forest regeneration are needed to recover soil multifunctionality. We measured key properties of the soil as proxy indicators of six soil functions: (1) support for plant growth, (2) C sequestration, (3) nutrient storage and availability, (4) resistance to degradation, (5) water and air flux regulation, and (6) biological activity along a 45-year chronosequence of natural regeneration in northwestern Colombia, and then we calculated an index of soil multifunctionality. The results revealed significant changes in physical–chemical and biological soil indicators due to the reforestation, increasing soil multifunctionality. The largest effects were found for soil C sequestration, with a sub-index value that was nearly two times higher after 15 years of regeneration, followed by biological activity and resistance to degradation functions that increased 1.4 and 1.3 times, respectively, after 15 years of regeneration. The overall index of soil functioning indicated a clear benefit of restoration, reaching 76% of its soil functioning capacity after 15 years of pasture abandonment. Thus, our findings provide empirical evidence that secondary forest succession can restore soils' capacity to deliver vital ecosystem services in the Amazon region, playing a critical role in ecosystem restoration.

Key words: abandoned pastures, Amazon region, ecosystem services, natural regeneration, soil carbon, soil multifunctionality

Implications for Practice

- Natural revegetation in abandoned pasturelands can serve as an effective nature-based solution to increasing soil carbon stocks in the Amazon region. However, given the time required to reach soil saturation capacity, payment for ecosystem services (PES) certification contracts for regeneration sites should extend beyond 15 years to ensure long-term sustainability.
- In degraded pasturelands, soil multifunctionality is recovered after one and a half decades of secondary forest succession, improving the soil capacity to provide soil ecosystem services.

Introduction

Soils play vital functions that underpin the provisioning of multiple ecosystem services (Smith et al. 2021). Healthy soils support many ecosystem services, including biological productivity (e.g. food, fiber, and energy), sequestering carbon, maintaining nutrient and water cycling, providing habitats for one-quarter of global biodiversity, and preserving natural and cultural heritage (Adhikari & Hartemink 2016; Safaei et al. 2019). Currently, soil functions are under pressure due to accelerated human population growth and rising demand for food, fiber, energy, and human infrastructure (Kopittke et al. 2019). Deforestation followed by

intensive land use and management leads to soil health degradation, negatively affecting its physical, chemical, and biological properties (i.e. Cherubin et al. 2016; Silva-Olaya et al. 2022a). Indeed, it has been estimated that around 20% of global land is degraded to some extent (van der Esch et al. 2022), and

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predictions of further land degradation over the next 25 years highlight potential threats to global food production (ELD Initiative 2015).

In the Amazon region, deforestation is often carried out to establish non-native grass pastures for livestock production. These pastures are largely mismanaged, with extensive grazing, absence of soil management, and low species diversity, which compromise soil health. This accelerates the mining of soil nutrients and degrades soil properties and functions (Olaya-Montes et al. 2021; Polanía-Hincapié et al. 2021; Silva-Olaya et al. 2022b; Chavarro-Bermeo et al. 2022), causing a loss of productivity of grasses over time (de Souza-Braz et al. 2013) that results in land abandonment after a few years of use (de Souza-Braz et al. 2013; Rocha et al. 2016) and the deforestation moves to new areas.

Abandoned pastures in the Amazon lead to the regeneration of secondary forests, forming a new forest mass (Müller-Hansen et al. 2019), with different ages and regeneration stages. Changes in vegetation structure along natural forest regeneration have been widely studied (Baer et al. 2002; Rocha et al. 2016; Guo et al. 2018; Hale et al. 2018); however, the impact of the natural regeneration process on soil functioning remains poorly understood (Mendes et al. 2019; Nolan et al. 2021; Bizuti et al. 2022). Assessments of ecosystem restoration have thus tended to be “phytcentric” (Ohsowski et al. 2012), neglecting the role of soil in the reestablishment of ecosystem functions and the provision of ecosystem services (Nolan et al. 2021).

Previous studies suggest that regrowing forests can sequester high amounts of carbon (Gilroy et al. 2014; Finegan et al. 2015), provide suitable habitats for species (Chazdon et al. 2009), and improve soil water quality (de Paula et al. 2018), leading to an overall restoration of soil multifunctionality. However, the regeneration of forest vegetation and recovery of soil functions are influenced by numerous biophysical factors (Cao et al. 2008), and multifunctional recovery may depend on local conditions. Understanding the multifunctional response of soil to forest restoration is critical to support the elaboration and implementation of public and private projects to meet ambitious global commitments in the coming decades, such as the Bonn Challenge (<https://www.bonnchallenge.org/>) and the U.N. Decade on Ecosystem Restoration (2021 to 2030) (<https://www.decadeonrestoration.org/>), as well as commitments in specific regions (e.g. Initiative 20x20 [<https://initiative20x20.org/>], with 17 Latin American countries; EU Biodiversity Strategy for 2030 [<https://www.eea.europa.eu/policy-documents/eu-biodiversity-strategy-for-2030-1>]; AFR100 [<https://afr100.org/>] among others).

Here, we ask how multiple soil functions respond to the natural regeneration of abandoned pastures along a chronosequence in the Amazon region and thus how long it takes for forest regeneration to recover soil multifunctionality. We measured a suite of key physical, chemical, and biological properties of soil, which we used as proxy indicators to calculate an index of soil multifunctionality at each stage of natural regeneration (Silva-Olaya et al. 2022a, 2022b). Based on previous studies indicating high rates of leaf and root turnover of pioneer species and also high litter production early in natural

succession in response to light availability (Martin et al., 2013; Porter et al., 2004, Poorter et al. 2021), we hypothesized that forest regeneration enhances the content of soil organic matter, restoring soil physical and biological functions, and leading to a new steady state in less than two decades (Silver et al. 2000; Poorter et al. 2021).

Since soil functions support the delivery of ecosystem services, this knowledge is invaluable in increasing awareness of the roles of natural regeneration in the tropical region in the achievement of national restoration targets and global initiatives such as sustainable development goals (SDG). Furthermore, this knowledge could assist in science-driven compensation models for ecosystem services schemes, similar to those implemented in various regions of Latin America.

Methods

Study Site

The study was carried out in the northwest portion of the Colombian Amazon region, specifically in the state of Caquetá, along a 42 km transect that extended over three municipalities: Morelia, Belén de Los Andaquíes, and Florencia (Fig. 1), which are representative of the main geomorphological characteristics of the region (*Instituto Geográfico Agustín Codazzi*—IGAC 2014). The climate in this region is tropical rainforest according to the Köppen-Geiger classification, with average temperature of 25.1°C and annual precipitation of 3235 mm (Murad & Pearse 2018).

We used a chronosequence approach to assess how natural regeneration after pasture abandonment affects soil functioning. By analyzing satellite image time series of the northern portion of Caquetá, we identified 18 areas under natural regeneration of abandoned pastures located in the same landscape (hill), which were then classified according to soil type. All areas with the same soil type were visited, and we conducted farmer interviews to confirm the number of years of pasture abandonment, the land use history, and soil textural class. After this, five study areas were selected, all located at elevations ranging from 248 to 251 m above sea level (m.a.s.l.). These areas included one pasture composed of *Brachiaria* sp. established greater than 25 years ago after slash and burn of native forests and four areas with 7, 15, 30, and 45 years of natural regeneration following pasture abandonment. All selected sites shared similar soil types, climate, elevation (250 m.a.s.l), topography, and land use histories. Prior to abandonment, the four regeneration sites were dominated by *Brachiaria* sp., with similar grazing intensity and soil management practices.

The soils in the study sites are classified as Typic Hapludults, which are typically highly weathered and acidic, with elevated Al saturation, low content of basic cations (Ca^{2+} , Mg^{2+} , K^{+} , and Na^{+}), and cation exchange capacity (CEC; IGAC 2014). The distribution of soil particle size to a depth of 40 cm was (1) 465 g/kg of sand, 310 g/kg of clay, and 225 g/kg of silt in pasture area, and 413 g/kg of sand, 341 g/kg of clay, and 246 g/kg of silt in natural regeneration areas.

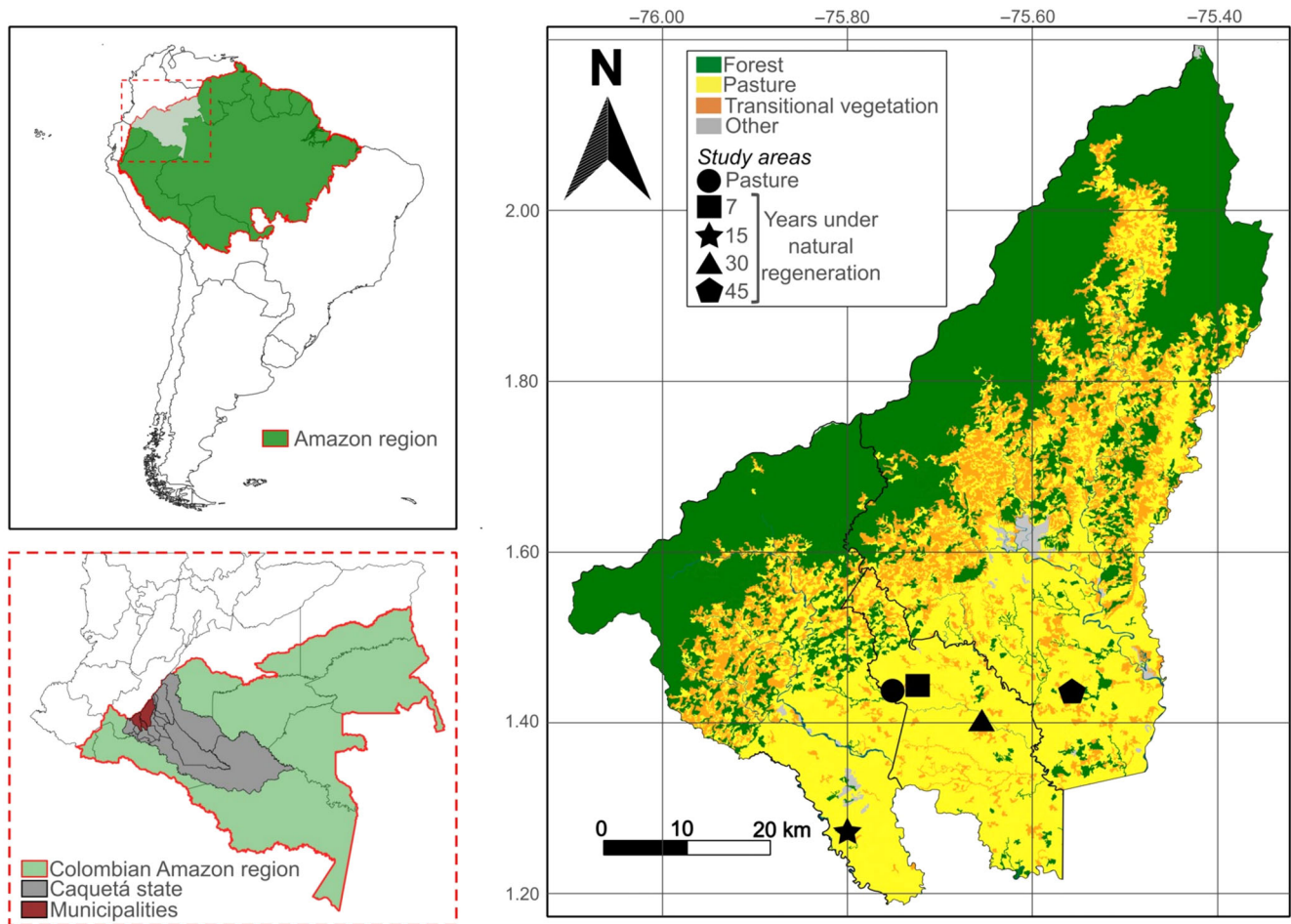


Figure 1. Location of the study sites in the northwest region of the Colombian Amazon.

Soil Sampling and Analysis

A sampling grid composed of six plots of 25 m² spaced 50 m apart was established in each study area, and then four soil samples per plot were collected in 0–10, 10–20, and 20–40 cm soil layers, which, besides reflecting different soil processes, are also highly sensitive to land use change. Soil samples were composited by layer in each plot, totaling 18 samples per study area that were then air-dried and sieved to 2 mm for further chemical analyses.

Additionally, since the 0–10 cm soil layer is particularly rich in organic matter and biological activity, making it the most active zone for enzymes involved in nutrient cycling and decomposition processes, a portion of soil from each 0 to 10 cm sample was refrigerated (4°C) and transported (<24 hours) to the Biogeochemical Process Laboratory at the University of the Amazon for enzymatic analysis.

Furthermore, a small trench (30 × 30 × 40 cm) was opened in each plot to collect undisturbed soil samples by using a metallic cylinder (5 × 5 cm; approximately 98 cm^{−3}) from 0 to 10, 10 to 20, and 20 to 40 cm soil layers, and also soil blocks (5 cm × 5 cm × 10 cm or 20 cm) from the same soil layers, which were analyzed to determine the physical properties of soil.

Following conceptual and empirical studies linking key soil properties to soil ecosystem functions (Silva-Olaya et al. 2022a, 2022b), we measured a suite of soil chemical, physical, and biological properties that were later used as indicators of soil functions. Soil pH was determined in 0.01 M CaCl₂ (Sparks et al. 1996). The exchangeable acidity ($H^+ + Al^{3+}$) was extracted using a 1 M KCl solution, and its concentrations were determined by titration with 0.01 M NaOH using phenolphthalein as indicator and by back-titration with NaF after acidification with 0.01 M HCl (IGAC 2014). The soil phosphorus content was assessed following the Bray II method (Bray & Kurtz 1945). Exchangeable calcium (Ca^{2+}), magnesium (Mg^{2+}), and potassium (K^+) concentrations were quantified using an atomic absorption spectrophotometer in an extract made with 1 M ammonium acetate (Sparks et al. 1996). Soil copper (Cu), iron (Fe), manganese (Mn), and zinc (Zn) content were extracted using a double acid solution (Mehlich I) and then determined by using an atomic absorption spectrophotometer (IGAC 2014). Soil base saturation (BS) and CEC were calculated as described by van Raij et al. (2001).

The concentration of soil organic C (SOC) in the soil was determined by a modified wet oxidation method, without an

external heating procedure, followed by the colorimetric method using a UV–visible spectrophotometer (Heanes 1984). Since this method incompletely oxidizes the organic carbon, a correction factor of 1.3 was used to adjust the easily oxidizable carbon to total organic carbon. SOC stocks were calculated by using Equation (1):

$$\text{Soil C stock} = \text{carbon} \times \text{BD} \times \text{depth} \quad (1)$$

where, the soil C stock corresponds to the SOC stock (Mg C/ha) of each soil layer, BD is the bulk density of the soil (Mg/m³), carbon is the C content (%), and depth is the thickness of the layer (cm). Subsequently, the carbon stock values were corrected using the equivalent mass approach (Ellert & Bettany 1995) with the pasture site as a reference. Coarse fragments were not present in considerable amounts.

Finally, the rate of change in SOC stocks (Mg C ha⁻¹ yr⁻¹) for the 0–40 cm soil layer across the chronosequence was calculated using Equation (2), where the previous stage of natural regeneration (or the pasture) was used as baseline:

$$\text{SOC changes rate} = \frac{(\text{SOC stock}_{\text{SNG}} - \text{SOC stock}_{\text{baseline}})}{\text{years}} \quad (2)$$

where SOC changes rate represents the annual rate of increase or loss of SOC (Mg C ha⁻¹ yr⁻¹) due to natural regeneration, SOC stock_{SNG} is the SOC stock in 0–40 cm layer in the stage of natural regeneration being assessed (e.g. 7, 15, 30, and 45 years of regeneration), SOC stock_{baseline} is the SOC stock in 0–40 cm layer at the baseline stage (e.g. pasture for the 7-year regeneration stage, or 7 years for the 15-year regeneration area). The years represent the time elapsed since the previous stage of natural regeneration (e.g. 7 years were used to calculate the C changes rate from pasture to 7 years old natural regeneration, 8 years for the change from 7 to 15 years old area, and 15 years for the change from 15 to 30 and 45 years of natural regeneration).

Soil macroporosity, microporosity, and total porosity were determined following the analytical methods described by Peters et al. (2014). For that aim, we used undisturbed soil samples collected by a cylinder (98 cm³), which were saturated by capillarity rise and then weighed and transferred to a tension table at –6 kPa water potentials until reaching hydraulic equilibrium, after which the soil water content was determined. The weight of those dried soil samples was also used for the determination of the soil bulk density (g/cm³) (Dane & Topp 2002).

Wet aggregate stability was assessed using the Yoder wet sieving procedure (Yoder, 1936). Briefly, the soil blocks collected at each soil depth were gently broken apart along natural breakpoints and sieved (8 mm). Subsamples of 40 g were then placed on the topmost of a nest of five sieves arranged by mesh size (4–0.053 mm) and shaken in water at 30 oscillations per minute for 30 minutes. The aggregates remaining on each sieve were oven-dried at 105°C for 48 hours and then weighed for the determination of the mean weight diameter (MWD) according to van Bavel (1950).

Other soil physical properties, such as resistance to soil penetration and visual evaluation of soil structure method (VSS), were assessed in situ. For resistance to soil penetration, a hand penetrometer (Eijkelkamp) with angle and surface area of a cone of 60 and 2 cm², respectively, was used. The VSS was performed following the methodological approach described by Guimarães et al. (2011) and used by Cherubin et al. (2019) in the Amazon region. Briefly, an undisturbed soil block of approximately 20 × 10 × 25 cm deep was removed and gently manipulated to analyze the characteristics of the main structural units, presence of layers of contrasting aggregate size and shape, root distribution, and signs of biological activity. A soil quality score (Sq) ranging from 1 (good soil quality) to 5 (poor soil quality) was assigned to each layer identified as having a distinct soil structure using the visual interpretation chart proposed by Guimarães et al. (2011).

The absolute activities of two extracellular hydrolytic enzymes—acid phosphatase and β-1,4-glucosidase—reflecting soil P and C mineralization processes were assessed as previously described by Tabatabai (1994). For acid phosphatase, 1 g of soil was incubated with *p*-nitrophenyl-phosphate substrate at 37°C for 1 hour and the released *p*-nitrophenol determined via spectrophotometry using a VarioScan Lux multimode microplate reader (405 nm). Activity of β-1,4-glucosidase enzyme was assessed by incubating the same amount of soil (1 g) with a substrate of *p*-nitrophenyl-β-D-glucopyranoside at 37°C for 1 hour and measuring the released *p*-nitrophenol via spectrophotometry (400 nm) at a varioScan Lux multimode microplate reader.

Assessment of Soil Functions

In this study, we used a robust and flexible three-step framework developed and applied by Silva-Olaya et al. (2022a, 2022b) to assess changes in soil multifunctionality due to the natural regeneration process in the Colombian Amazon region. Through this framework, we evaluated the potential for soil to provide six key functions: (1) plant growth, (2) C sequestration, (3) nutrient storage and availability, (4) resistance to degradation, (5) water and air flux regulation, and (6) biological activity, along a chronosequence of abandoned pastures.

In step I (selection), we selected appropriate soil properties to use as proxy indicators of the six soil functions assessed based on previous studies (Table 1) (e.g. Cherubin et al. 2016; Olaya-Montes et al. 2021; Polanía-Hincapié et al. 2021; Lustosa Carvalho et al. 2022; Silva-Olaya et al. 2022a, 2022b). Then, the soil data from the 0 to 10, 10 to 20, and 20 to 40 cm layers were averaged to create a 0 to 40 cm layer. These indicators are sensitive to shifts in land use and are therefore critical for assessing potential impacts of a changing environment on soil functions.

For the soil functions “Support for plant growth” and “Nutrient storage and availability,” where three or more soil properties (i.e. proxy indicators) were measured, we performed a principal component analysis (PCA) to select the indicators that best represent variation in the study areas. The principal components with eigenvalues ≥1 (Kaiser’s criteria) were examined, and the indicators receiving weight loading values within 50% of the maximum weight loading under every Principal component (PC) were retained (Velasquez et al. 2007; Lavelle et al. 2014;

Table 1. Ecosystem services linked to the soil functions and the properties used as proxy indicators of each function. Underlined indicators in soil functions support for plant growth and nutrient storage and availability were selected based on the PCA analysis for the further scoring process.

<i>Ecosystem services</i>	<i>Soil functions</i>	<i>Indicators</i>	<i>Justification</i>
Provisioning (provision of food, wood, and fiber)	Support for plant growth	Bulk density (BD); soil penetration resistance (SPR); visual evaluation of the soil structure (VESS)	The indicators reflect the soil's physical conditions, shaping root growth, nutrient uptake, and water availability.
Regulating (climate regulation)	Carbon sequestration	Soil C stock (see Eq. 1)	Soil C stock quantifies the amount of carbon stored in soil, providing insight into the soil's role in climate regulation. This indicator is also sensitive to land use changes.
Regulating (nutrient cycling)	Nutrient storage and availability	CEC Active soil acidity (pH); base saturation (BS); potential soil acidity (Al + H concentration); phosphorus concentration (Bray II P); potassium (K) concentration; calcium (Ca) concentration; magnesium (Mg) concentration; copper (Cu) concentration; iron (Fe) concentration; zinc (Zn) concentration; manganese (Mn) concentration	Indicators such as CEC, pH, base saturation, and potential acidity reflect the soil's capacity to hold and exchange nutrients, as well as their availability to plants. Concentrations of phosphorus, K, Ca, Mg, and essential indicate the soil's ability to supply critical nutrients required for plant growth and development.
Regulating (erosion control)	Resistance to degradation	Aggregate mean weight diameter (MWD); soil organic C content (SOC)	Indicators reflect the soil structure stability, which provides a robust measure of soil's ability to resist physical degradation and maintain long-term sustainability.
Regulating (water purification)	Water and air flux regulation	Soil macroporosity (MaP); soil microporosity (MiP)	Indicators represent the soil's porous characteristics, which determine the soil's ability to retain and transmit water and air. While macropores facilitate the rapid movement of air and water through the soil, micropores hold water and regulate its availability to plants.
Supporting and regulating (biodiversity and nutrient cycling, respectively)	Biological activity	Acid phosphatase β -Glucosidase	Both indicators are involved in crucial biochemical processes. Together, these enzyme activities offer a reliable measure of microbial activity.

Rodriguez et al. 2021). When more than one indicator was retained, a correlation analysis was used to determine whether any of them were redundant (Andrews et al. 2002). Based on the results, all three indicators were retained for plant growth soil function, and five indicators: CEC, phosphorus, Ca, Mg, and Fe concentration were retained for "Nutrient storage and availability."

In step II (indicator interpretation), the values of all indicators were normalized to an ordinal score from 0 to 1 using linear scoring functions. The normalization was performed by classifying the indicators into "more is better" and "less is better" categories based on their relationship with soil functioning. For "more is better" and "less is better" indicators, Equations (3) and (4) were used, respectively:

$$S = \frac{X}{X_{\max}} \quad (3)$$

$$S = \frac{X - X_{\min}}{X_{\max} - X_{\min}} \quad (4)$$

where S is the score varying from 0 to 1, X is the soil indicator value, and $X_{\max}$ and $X_{\min}$ are the maximum and minimum value of each soil indicator observed between the study areas.

Lastly, since six key soil functions were assessed, in step III (integration), we integrated the indicator scores related to each soil function to create a soil function sub-index (SF_{si}) (Oliveira et al. 2019; Silva-Olaya et al. 2021). For the calculation of SF_{si} for resistance to degradation, water and air flux regulation, and biological activity, which were each composed of two indicators, the weight of each indicator was equal (0.5).

For the plant growth and nutrient storage and availability functions, represented by three and five indicators, respectively, the weight of each indicator was 0.33 and 0.2, respectively.

For C sequestration, the SF_{si} was not weighted because it was composed of only one indicator.

Finally, after the SF_{si} were determined, we used a simple additive approach to integrate those scores into an overall index of soil multifunctionality. Therefore, the scores of SF_{si} were summed, and then the product was divided by the number of functions assessed.

Statistical Analysis

Differences in measured soil physical, chemical, and biological properties (0–40 cm), and indicator values for each soil function, were tested with a linear simple model (lm) using the “lme4” package (Bates et al., 2015), that considered the regeneration stage as a fixed factor. The assumption of normality was checked using the Shapiro test ($p < 0.05$) and $Q-Q$ plot, while homogeneity of variance was checked using Bartlett test ($p < 0.05$) and residual versus fitted plot. For the soil properties showing non-normal distribution and heterogeneity, unequal variance was adjusted in the model. Differences in mean values between study areas were assessed using Tukey’s Honestly Significant Difference (HSD) test ($p < 0.05$) by using the “multcomp” package (Hothorn et al., 2008).

PCA was performed in order to (1) select the indicators that best represent variation in the study area, (2) determine the

weight of each indicator to the SF_{si} for plant growth and nutrient storage and availability, and (3) correlate SF_{si} to identify synergies and trade-offs between soil functions. For that aim, the “FactoMineR” package was used.

All statistical analyses were performed with the R software version 4.2.0 (R Core Team 2020), using the RStudio version 1.3.1 integrated development environment RStudio version 1.3.1. (RStudio Team 2021).

Results

Changes in Soil Physical, Chemical, and Biological Indicators Along the Natural Regeneration Chronosequence of Abandoned Pastures

Most of the soil physical properties we measured improved at the forest succession sites compared to the pasture sites (Fig. 2). A 16 and 24% decrease in soil bulk density and soil resistance to penetration, respectively, were observed in areas with more than 30 years of regeneration ($p < 0.05$). Similarly, higher aggregate MWD was observed in forest systems compared to pastures. Soil microporosity increased by $0.05 \text{ cm}^3/\text{cm}^3$ after 15 years of forest restoration (Fig. 2). The VESS assessment also indicated trends in soil structure that followed the traditional laboratory methods for assessing soil physical

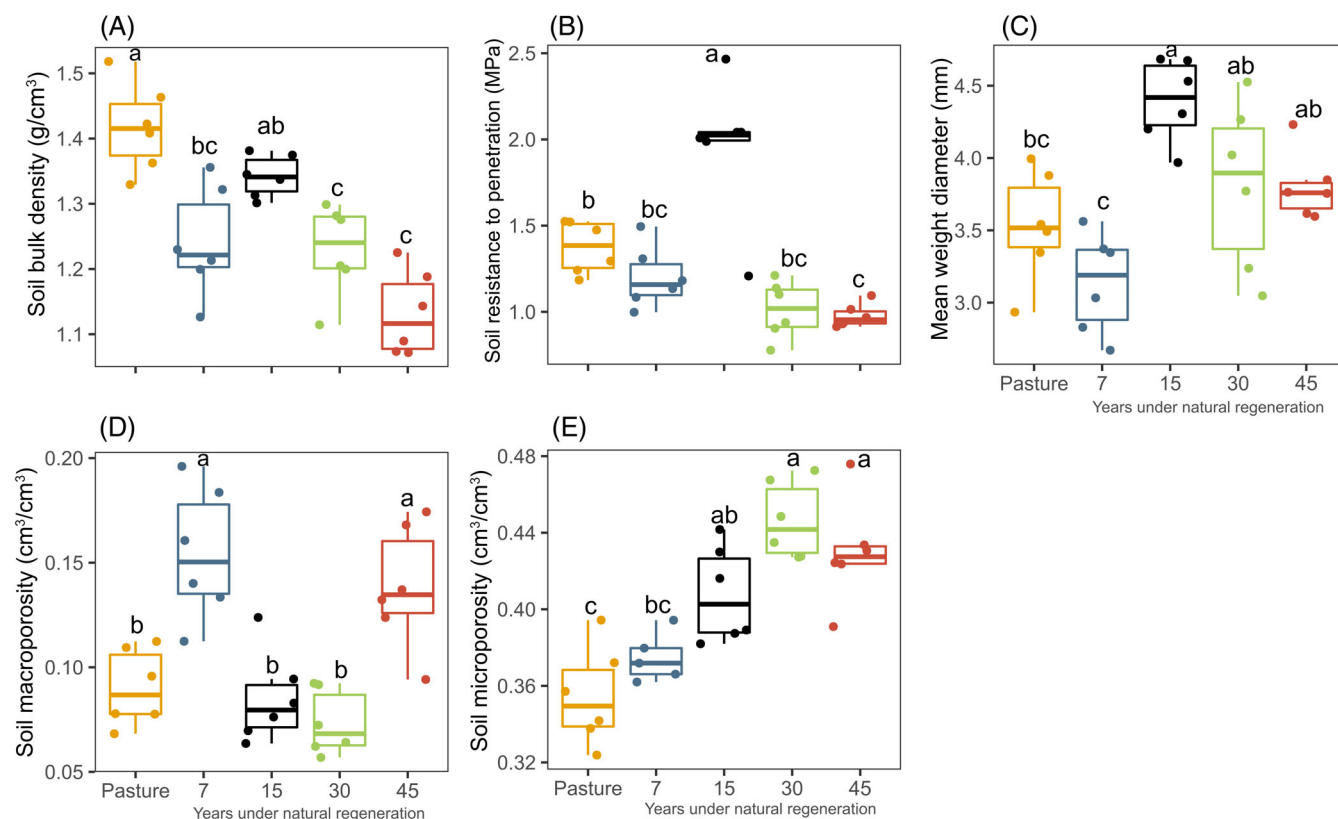


Figure 2. Box (25–75%, solid line shows median value) and whisker (min–max) plots for the soil physical properties bulk density (A), resistance to penetration (B), mean weight diameter (C), soil macroporosity (D), and soil microporosity (E) in the 0–40 cm soil depth along a chronosequence of natural regeneration of abandoned pastures in the Colombian Amazon. Different letters denote a statistically significant difference according to Tukey’s HSD ($p < 0.05$).

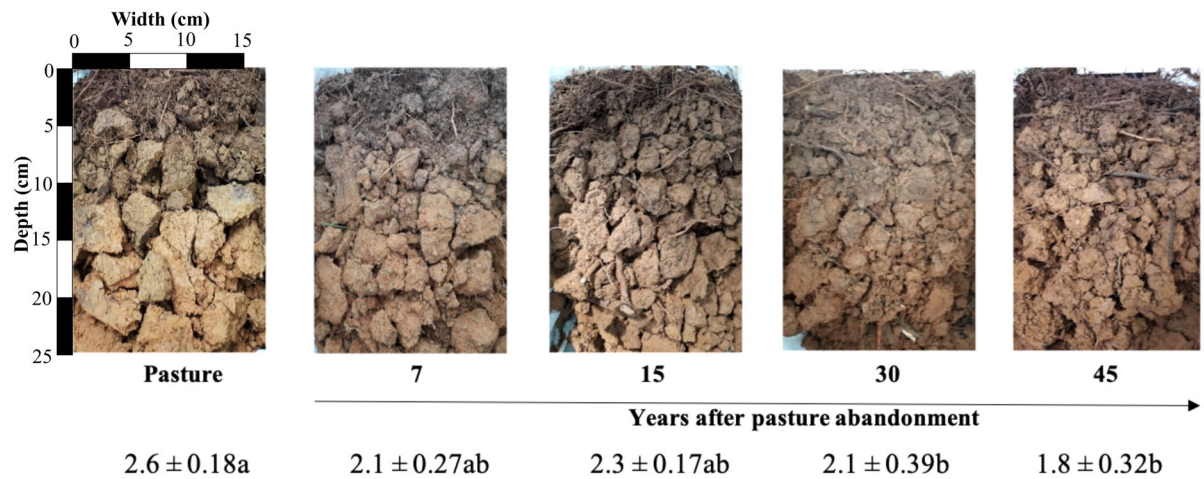


Figure 3. Representation of soil physical quality changes detected by the VESS method along a natural regeneration gradient in northwestern Amazon. The values below the pictures are the VESS scores (Sq) for the 0–25 cm layer. Lower VESS scores indicate better soil physical quality, characterized by a mixture of porous, easily breakable, and rounded aggregates, along with the presence of roots and signs of higher biological activity. In contrast, higher VESS scores reflect poorer soil physical quality, with large, angular, and hard-to-break clods, with very low visible porosity and an almost complete absence of roots.

properties. As observed in Figure 3, the natural regeneration process caused a significant improvement in the physical quality of the soil, with Sq values ranging from 2.6 in the pasture to 1.9 in areas with more than 30 years of natural regeneration.

Significant changes in soil chemical attributes related to soil acidity were detected along the chronosequence ($p < 0.05$) (Table 2). As natural regeneration progressed, soil pH decreased slightly, while the exchangeable H + Al concentration increased 2.3 times. The effective CEC increased under natural regeneration ($p < 0.05$), reaching a value 1.84 times higher after

45 years of forest regeneration. Soil acidification was also associated with lower Ca content in older forest regeneration soils. Soil BS decreased from 35.94 in pasture to 16.36 in the area under 45 years of natural regeneration ($p < 0.05$). There was no clear pattern of changes in soil micronutrients (Cu, Zn, Mn, and Fe).

Natural regeneration of the forest led to a significant increase in soil C stocks within the 0–40 cm soil profile, with levels reaching up to 65 Mg/ha in the 45-year-old forest regeneration area, compared to 34 Mg/ha at the pasture site (Fig. 4). However, it should be noted that the highest rate of C accrual

Table 2. Mean values of soil chemical properties (0–40 cm) and enzymatic activity (0–10 cm) along a chronosequence of natural regeneration of abandoned pastures in the Amazon region. The means followed by the same letter did not differ among themselves according to Tukey ($p < 0.05$); values in parentheses denote the standard error of the mean. Al + H, potential acidity; BS, base saturation; Ca, calcium; CEC, cation exchange capacity; Cu, copper; Fe, iron; K, potassium; Mg, magnesium; Mn, manganese; P, phosphorus; pH, active acidity; SOC, soil organic carbon; Zn, zinc.

Soil properties	Pasture	Years under natural regeneration			
		7	15	30	45
pH (CaCl ₂)	4.71 (0.02) a	4.52 (0.03) b	4.71 (0.03) a	4.58 (0.02) b	4.50 (0.04) b
CEC (cmol/kg)	5.44 (0.22) b	6.23 (0.29) b	9.92 (0.26) a	8.73 (0.39) a	10.05 (0.27) a
H + Al (cmol/kg)	3.60 (0.22) c	4.54 (0.24) c	7.87 (0.26) ab	6.95 (0.42) b	8.38 (0.22) a
P (mg/kg)	2.51 (0.11) b	2.44 (0.07) b	3.08 (0.06) a	3.26 (0.10) a	2.34 (0.14) b
K (cmol/kg)	0.09 (0.005) c	0.08 (0.003) c	0.11 (0.002) b	0.14 (0.006) a	0.150 (0.01) a
Ca (cmol/kg)	1.33 (0.03) ab	1.22 (0.03) b	1.39 (0.04) a	1.09 (0.03) c	1.06 (0.03) c
Mg (cmol/kg)	0.31 (0.01) b	0.32 (0.01) ab	0.36 (0.01) a	0.30 (0.008) b	0.30 (0.009) b
BS (%)	35.94 (1.68) a	29.20 (1.30) b	20.72 (0.64) c	19.41 (0.61) c	16.36 (0.32) d
Fe (mg/kg)	396.64 (43.01) abc	486.11 (14.95) a	313.64 (25.92) c	426.17 (10.93) ab	355.70 (38.78) bc
Mn (mg/kg)	1.66 (0.29) bc	1.18 (0.18) c	5.20 (0.49) a	2.61 (0.32) b	3.24 (0.56) ab
Cu (mg kg ⁻¹)	1.06 (0.09) b	1.15 (0.11) b	1.83 (0.11) a	1.301 (0.06) b	1.39 (0.14) ab
Zn (mg/kg)	0.90 (0.06) a	0.86 (0.07) a	0.89 (0.04) a	0.58 (0.009) b	0.82 (0.04) a
SOC (g/kg)	8.70 (0.44) c	8.49 (0.52) c	13.54 (0.48) b	14.97 (0.37) ab	16.39 (0.58) a
Phosphatase (μg p-nitrophenol [PNP] g ⁻¹ hour ⁻¹)	84.35 (21.74) b	121.37 (11.28) a	144.72 (14.56) a	139.26 (32.14) a	131.97 (21.94) a
β-Glucosidase (μg PNP g ⁻¹ hour ⁻¹)	102.52 (11.43) a	107.09 (31.62) a	112.72 (34.39) a	143.69 (32.14) a	131.97 (21.94) a

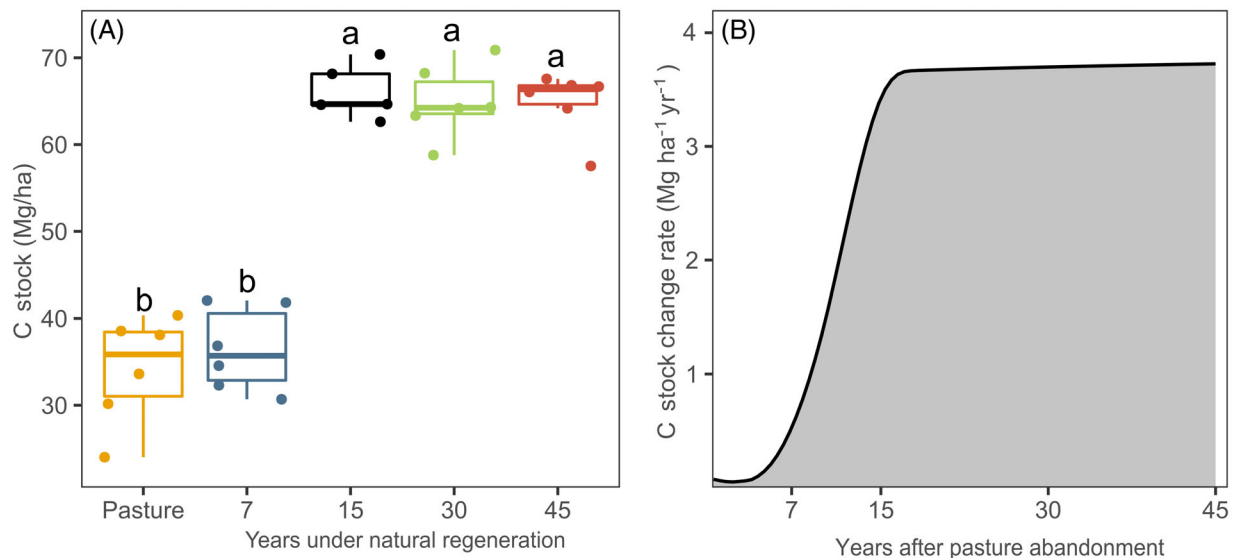


Figure 4. Soil C stocks (0–40 cm) (A) and rate of change in C stocks (B) along a chronosequence of natural regeneration of abandoned pastures in the Colombian Amazon. Means followed by the same letter do not differ according to the Tukey test ($p < 0.05$).

occurred from 7 to 15 years of forest restoration, while between 15 and 30 years, soil C accrual was slower and stopped after 30 years. The results make clear that after 15 years, the soil C reaches a new dynamic steady state (Fig. 4).

Measured soil enzyme activities did not respond strongly to forest regeneration. Acid phosphate was higher under forest regeneration than in pasture, while β -glucosidase did not change significantly between land uses.

Effects of Forest Regeneration of Abandoned Pasturelands on Soil Functions

The natural forest regeneration process on abandoned pasturelands substantially recovered five of the six soil functions evaluated (Fig. 5). After 15 years of pasture abandonment, a significant improvement in C sequestration, resistance to degradation, and biological activity soil functions ($p < 0.05$) was observed. The C sequestration function had the highest improvement, as the sub-index value increased from 0.48 in pasture to 0.88 after 15 years of natural regeneration. Likewise, the soil functions associated with plant growth and water and air flux regulation were rehabilitated to some extent, particularly after 30 and 45 years, respectively. Soil function related to nutrient storage and availability did not show significant differences among the study areas.

The above results were further confirmed by the overall index, which revealed a consistent pattern of soil multifunctionality restoration as forest regeneration progressed (Fig. 6). Soil multifunctionality index scores increased from 59% in the pasture area to 82% in the 45-year-old natural regeneration area, in which the index was 8% higher than the value for 15 years of pasture abandonment, but was not significantly different from the 30-year-old site.

Through a PCA, patterns of soil functions and time since pasture abandonment were explored in more detail (Fig. 7). The first

two components explained 77% of the variance, with C sequestration and biological activity soil functions showing the highest loadings on PC1 while plant growth and water and air flux regulation had the highest loadings on PC2. Soil function sub-indexes were also grouped into five clusters, separating both the pasture and the early stage of natural regeneration area (7 years) from the areas with more than 15 years of natural regeneration, with each ellipse showing a 95% confidence for a set of two-dimensional normally distributed data samples.

A significant relationship ($p < 0.05$) was found between plant growth and water and air flux regulation functions ($\rho = 0.57$), as well as between C sequestration with both nutrient storage and availability and resistance to degradation ($\rho = 0.50$ and 0.90 respectively). The sub-index of biological activity function was significantly correlated to the other soil functions except for water and air flux regulation ($\rho = 0.48, 0.71, 0.54$, and 0.60 for plant growth, C sequestration, nutrient storage and availability, and resistance to degradation, respectively). Nutrient storage and availability soil function sub-index was also correlated to resistance to degradation ($\rho = 0.44$).

Discussion

Forest Regeneration of Abandoned Pasturelands Improves Soil Chemical, Physical, and Biological Indicators

The results reflect the soil compaction typically found in pastures areas under extensive management in the Amazon region (Polania-Hincapié et al. 2021; Rodríguez et al. 2021; Duran-Bautista et al. 2023) and suggest a recovery in the soil physical quality as the natural regeneration progresses. This process was accompanied by increments in SOC content, the CEC, and the intensification of soil acidification, supporting our hypothesis that secondary forest succession in abandoned pastures in the Amazon region positively affects SOC content, which

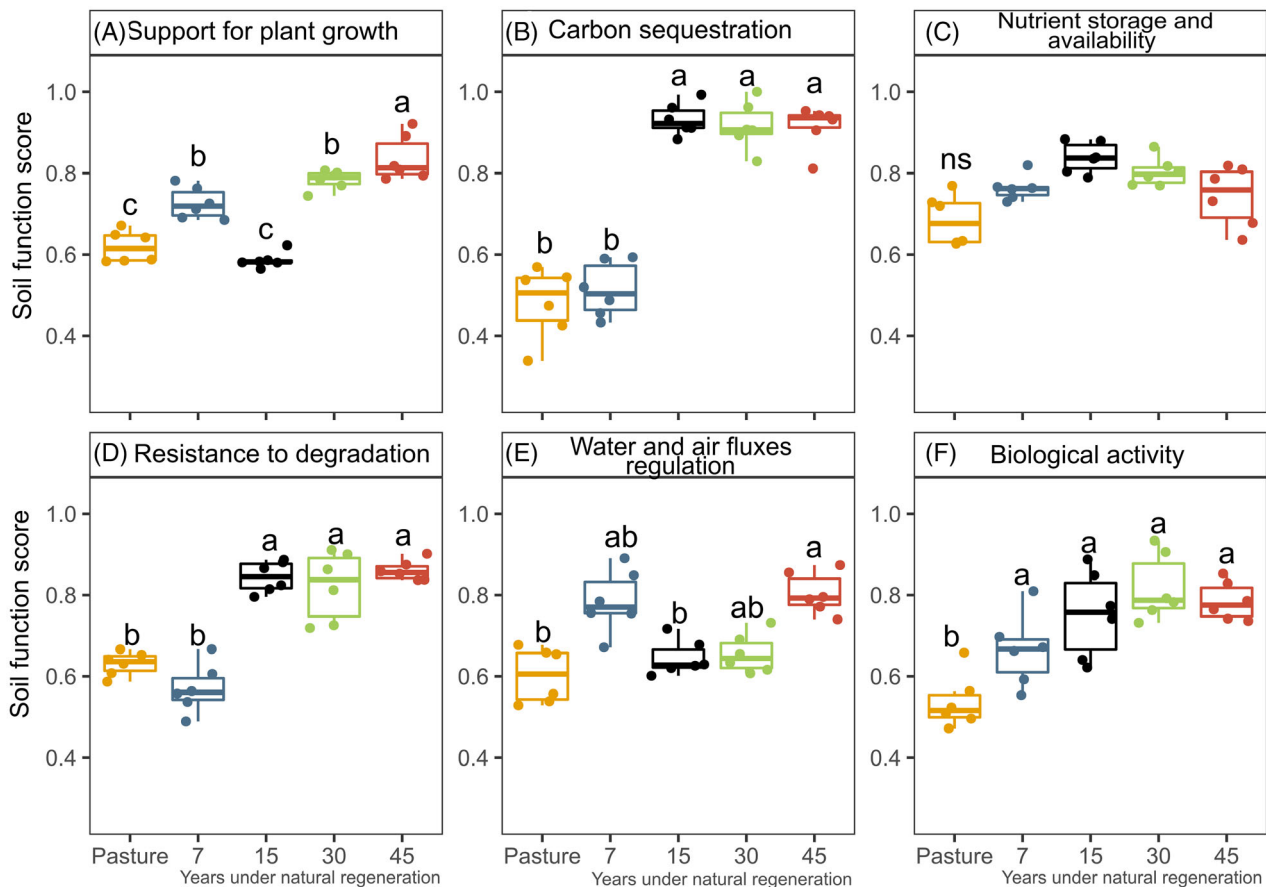


Figure 5. Box (25–75%, solid line shows median value) and whisker (min–max) plots for the soil functions sub-indexes (SF_{si}) support for plant growth (A), carbon sequestration (B), nutrient storage and availability (C), resistance to degradation (D), water and air fluxes regulation (E), and biological activity (F) assessed along a chronosequence of natural regeneration of abandoned pastures in the Colombian Amazon. Different letters denote a statistically significant difference according to Tukey's HSD ($p < 0.05$).

influences other soil properties and, consequently, the overall capacity of the soil to function.

The response of soil C stocks (0–40 cm) to forest restoration followed a sigmoid curve, in which there was a slow increase in the first 7 years followed by a sharp increase up to 15 years. After that, the change in SOC was minimum or even null, indicating that the C stocks in the soil reached a new steady state in the regenerated forest. Forest regeneration of pastures shifts the dominant plant functional groups, vegetation cover, height, and above- and belowground biomass (Rocha et al. 2016; Rodríguez-León et al. 2022), influencing the flux of C inputs into the soil. Changes in plant functional composition and plant diversity, in turn, alter the biochemical and physical composition of litter inputs, and root exudates and turnover rate in ways that favor C sequestration (De Deyn et al. 2008). Although we did not assess the soil microbial communities in terms of biomass or diversity, the increase evidenced in soil acid phosphatase activity due to forest regeneration may correspond with more microbial biomass and associated mechanisms that can enhance C use efficiency. Previous studies indicate that microbial C use efficiency increases with increasing tree species diversity, suggesting a correlation between plant community traits

and soil C storage (Domeignoz-Horta et al. 2020; Duan et al. 2023).

This research offers valuable policy insights, indicating that natural revegetation can serve as an effective nature-based solution to increase soil carbon stocks in the Amazon region. Payment for Ecosystem Services (PES) certification contracts for regeneration sites should extend beyond 15 years, given the time required to reach soil saturation capacity. Moreover, the study findings can inform the establishment of baselines and achievable carbon stock limits for regional soils.

On the other hand, while soil organic matter surfaces generate negative electric charges that increase soil CEC, and consequently, the conservation and availability of soil nutrients such as K (Ramos et al. 2018; Solly et al. 2020), the organic acids exuded by plant roots and those released through litter decomposition and biological activity contribute to soil acidification (Hinsinger et al. 2003; Jones et al. 2004; Guo et al. 2016), which likely contributed to the decrease in pH with forest restoration in our study.

The physical functioning of the soil was also altered by forest regeneration. Collectively, the increased C stocks and biological activity, the growth of shrub/trees roots, and the absence of

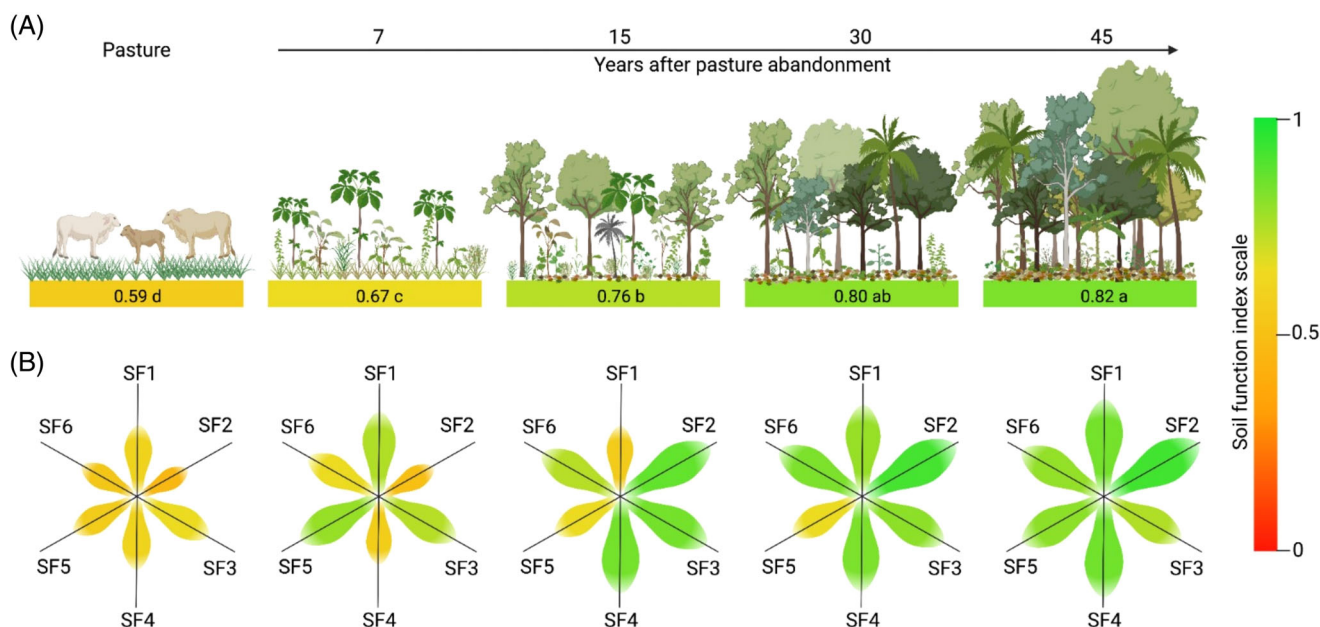


Figure 6. Soil multifunctionality changes along a chronosequence of natural regeneration of abandoned pasturelands in the Colombian Amazon. Values in panel (A) represent the overall index values for pasture and each stage of natural regeneration. The values in panel (B) represent the index values for each soil function, where SF1 represents plant growth, SF2 C sequestration, SF3 nutrient storage and availability, SF4 corresponds to resistance to degradation, SF5 to water and air flux regulation, and SF6 is biological activity. Means followed by the same letter do not differ according to the Tukey test ($p < 0.05$).

cattle trampling are the main drivers of improved soil structure and reduced compaction (Cherubin et al. 2019; Polanía-Hincapié et al. 2021). Increases in soil organic matter are frequently

associated with a more stable and complex structure (Blanco-Canqui & Ruis 2018; Li et al. 2019). Organic components enhance aggregate formation and stabilization (Tisdall & Oades 1982), acting as agglutinants and playing an important role in soil structure resilience (Annabi et al. 2017). Our results suggest that aggregate stability and VESS scores become stable after 15 years of forest regeneration. Improvement in soil physico-chemical properties after 15 years of land abandonment was also reported by Lintemani et al. (2020).

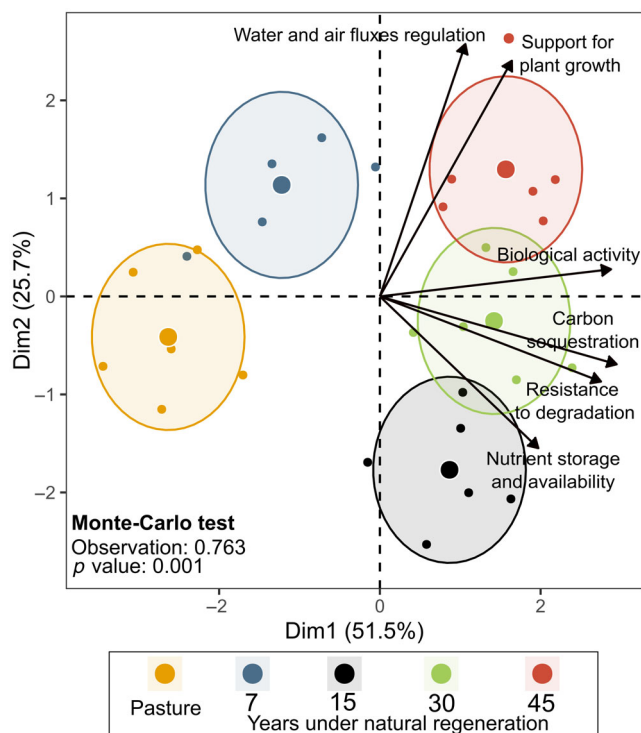


Figure 7. Principal component analysis for the sub-index of the soil functions assessed in this study linked to years of forest regeneration.

Recovery of Soil Multifunctionality Through Natural Regeneration of Abandoned Pastures

Evaluating soil indicators individually does not provide enough information about the responses of the holistic soil functioning to the natural regeneration process, leading to unclear conclusion that can hinder decision-making (Bieluczyk et al. 2023). By using an approach that integrates those indicators into soil functions scores, we were able to capture the changes in the complex interaction between soil physical, chemical, and biological process, providing evidence that the natural regeneration of the Amazon forest is an important driver for the recovery of degraded areas by improving both individual soil functions and soil multifunctionality. In this study, after 15 years of natural regeneration, five of the six soil functions assessed were restored, and a clear recovery trend was observed in the overall index of soil functioning along the chronosequence. The index value reached 76 and 80% of potential functioning capacity after 15 and 30 years of pasture abandonment, respectively, suggesting 15 years may be a critical threshold in the natural regeneration process to restore the overall soil multifunctionality.

Regeneration of degraded pastures likely increases soil multifunctionality through multiple mechanisms, including increased litter production and soil foodweb diversity and activity (Prescott & Grayston 2013); protection of the soil surface from physical disturbances, preventing surface sealing, and reducing soil erosion (Cherubin et al. 2019); and promotion of soil aggregation and stability (Demenois et al. 2018). The increase in litter production and the improvements in soil structural quality can, in turn, increase SOC storage (Six et al. 2004) by increasing C and nutrient inputs to soil and increasing C stabilization through chemical and physical protection from microbial decomposition (Dungait et al. 2012).

Significant relationships between most of the soil function sub-indexes suggest a synergistic relationship among soil functions. These relationships indicate that the delivery of these functions is governed by interdependent soil properties and that any positive or negative effect on one (or more) of the soil properties is likely to be reflected in the others, as previously reported in other studies performed in tropical regions (Lavelle et al. 2014; Oliveira et al. 2019; Rodriguez et al. 2021; Silva-Olaya et al. 2022a, 2022b).

This study provides empirical evidence that secondary forest succession is not only an effective and low-cost strategy to increase forest cover, but also to restore the multiple associated soil functions and the soil capacity to provide soil ecosystem services in the Amazon region. The approach used is a potential science-based tool for assisting decision-making on land use planning and the development of financial mechanism for forest landscape restoration in a region where more than 50% of pastures are in some stage of degradation (Motta-Delgado & Ocaña-Martínez 2018). Furthermore, this region is strategic and a priority for establishing large-scale forest restoration for C sequestration (and C credits in PES), which can help mitigate global climate changes.

Our results demonstrated that natural regeneration of degraded pastures in the Amazon region could play a critical role in achieving global targets for climate mitigation and biodiversity restoration, including the Paris Climate Agreement, 4 per 1000 (www.4p1000.org/), RECSOIL (<http://www.fao.org/3/ca6522en/CA6522EN.pdf>), and United Nations Sustainable Development Goals—SDGs (<https://sustainabledevelopment.un.org/sdgs>), and also could substantially contribute to the goals of the Global Decade on Ecosystem Restoration (2021–2030). Consequently, we encourage more studies to understand the dynamic of soil health (multifunctionality) recovery in other Amazon regions to support the development and implementation of public and private forest restoration plans in the coming decades.

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