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Soil Quality Restoration during the Natural Succession of Abandoned Cattle Pastures in Deforested Landscapes in the Colombian Amazon

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Abstract: Successional processes in abandoned pastures in the Amazon region have been well-documented for the floristic component; however, soil succession has been poorly studied. This study assessed the physical, chemical and biological responses of soils in the Amazon region during the natural succession process in two main landscapes of the Colombian Amazon. Soil data on soil physico–chemical (bulk density, macroaggregates, pH and minerals) and biological (soil macrofauna) composition were evaluated along chronosequence with four successional stages: (i) degraded pastures, (ii) young (10–20-year-old), (iii) middle-age (25–40-year-old) and (iv) mature forests, in two different landscapes (hill and mountain). Individual soil variables and a synthetic indicator of soil quality (GISQ) were evaluated as tools for natural succession monitoring. The results corroborated the negative impact that cattle ranching has on Amazon soils. After 10 years of natural succession, the physico–chemical and biological soil components were widely restored. Less soil compaction and organic carbon occurred in older successional stages. Soil macrofauna richness and density increased along the chronosequence, with an evident association between the macrofauna composition and the macroaggregates in the soil. None of the individual soil properties or the GISQ indicator discriminated among natural succession stages; therefore, new soil quality indicators should be developed to monitor soil quality restoration in natural successions.

Keywords: degraded pastures; secondary succession; natural restoration; soil macrofauna; soil macroaggregation; soil physical and chemical properties

1. Introduction

The Amazon Forest is one of the largest tropical rainforests in the world and plays an important role by providing a wide variety of ecosystem services [1–4]. However, the expansion of the agricultural frontier has promoted an extensive deforestation process, causing the loss of 2.3 million ha of primary forests in 2020 [5], with a large section in Colombia. The establishment of pastures for livestock production has caused annual forest losses of 138,000 ha, resulting in the second deforestation hotspot in the Amazon Basin [6]. The land-use change, with overgrazing of pastures and poor soil management has induced significant physical, chemical and biological degradation of soils [7–10], leading to unproductive pastures that are subsequently abandoned. The Amazon ecosystem has a high resilience [11] and considerable potential of natural regeneration [12–14]. Once grazing ceases and pastures are abandoned, a natural regeneration (also called regrowth or natural succession) take place.

In general, when abandoned agricultural areas go into secondary succession, changes in the soil properties are expected, but the alterations on soil functioning are complex and seem to be ecosystem dependent [15,16]. Contrasting results have been reported in recent years. While the successional stage has been found to influence the soil organic carbon (SOC) content in the Brazilian Atlantic Forest [17,18] and the Lose Plateatu in China [19], this crucial indicator of soil quality did not reach the same level of natural forests even after 40 and 60 years of natural succession in a semi-arid environment and sub-humid Mediterranean area, respectively [16,20].

Successional processes of abandoned pastures in the Amazon region have been well-documented for the floristic component [21–23]. However, comprehensive studies on changes in soil properties and soil quality during this process are lacking. The soil is a complex matrix composed by solid, liquid and gaseous phases, with a biotic component and multiple natural and anthropic functions [24]. Most soil studies have focused their attention in chemical (total organic matter/carbon, pH and available P) or physical (bulk density or soil water storage) variables as soil quality indicators [25–27]. Soil organic matter/carbon is a ubiquitous soil quality indicator. It could change with soil management and land use, but those changes are not easy to track and relate with soil quality, especially along the successional pathways [25].

Recently, soil biological indicators have been proposed [26–28] as they play crucial roles in soil function [29–32]. Most soil studies have used soil biomass and soil respiration as soil quality indicators, but the analysis of those parameters are limited as they require standardized techniques at the laboratory. Soil macrofauna could be a proper biological indicator of soil quality as measurements can be carried out even in the field [33]. A recent report indicated that, although inventories of soil biological groups are becoming more robust around the world, the function and role that biological communities play in soil quality and soil function [34] are still poorly understood. Edaphic organisms influence soil structuration directly [35–38], with their species composition affecting the functional structure of soils and improving soil fertility [39–41]; therefore, soil macrofauna can relate changes in soil physical and chemical variables with soil functioning [42]. Velasquez et al. [33] developed a General Indicator Soil of Quality (GISQ) in which to evaluate the physical state, the chemical fertility/quality and organic matter stocks of the soil, the aggregation and morphology of the topsoil, and the diversity and composition of soil macrofauna, to evaluate soil ecosystem services without defining an a priori criteria for soil quality, and that could be used to compare different plots, landscapes and sites.

Changes in the quality of Amazon soils associated to land use changes have been assessed by soil chemical indicators [43–45], soil physical indicators [43], soil biological indicators [46–49] and combinations of soil variables [33,41,48,49]. Pasture, as the most intense land use change, presents the most dissimilar conditions among other land uses, such as its microbial composition [50] and microbial activity [51]. Soil microbial communities seem not to be severely affected, while soil macrofauna does [47,52]. In addition, there are different soil macrofauna compositions in natural and anthropic soils due to management practices that modify soil conditions and edaphic biotic interactions [53].

Although several indexing strategies have been implemented for assessing and monitoring soil quality in different ecosystems around the world [42,54–60], none have been applied to a restoration process in Amazonian soil conditions. For example, the GISQ can discriminate well between mature forest and covers dominated by grasses (pastures and silvopastoral systems) [49] and between covers with different intensity of use [48], but it has not yet proven if it can also discriminate the soil quality among different successional stages. In the same way, how soil macrofauna communities are influenced by the soil quality of the Amazon region [48,61] and how sensitive they are to soil disturbances, and their relation to physical–chemical attributes and soil aggregation during the natural restoration of degraded pastures has not been widely addressed [45,62,63].

This study aimed to assess: (i) individual responses of soil physical, chemical and biological variables along the natural succession of abandoned pastures in two contrasting landscapes in the Colombian Amazon region, and (ii) evaluate individual and synthetic indicators of soil quality along the natural succession and their capacity to discriminate different successional stages along a natural restoring chronosequence.

2. Materials and Methods

2.1. Study Area and Sampling Design

This study was performed in Caquetá, located in the northwestern Colombian Amazon, specifically in the municipalities of Florencia (1°36′50″ N; 75°36′46″ W), Morelia (1°29′09″ N; 75°43′28″ W), Belén de los Andaquíes (1° 24′59.1″ N; 75°52′21.2″ W), and San José del Fragua (1°19′52″ N; 75°58′28″ W) (Figure 1), which encompass two main landscapes of the Colombian Amazon: hills, characterized by an undulated landscape originating from the Amazonian plains and usually used for cattle ranching and, therefore, covered by pastures with a high level of degradation [64], and mountains, part of the Andean–Amazonian transition, with high slopes usually covered by a combination of natural forests, pastures and agricultural landscapes [64].

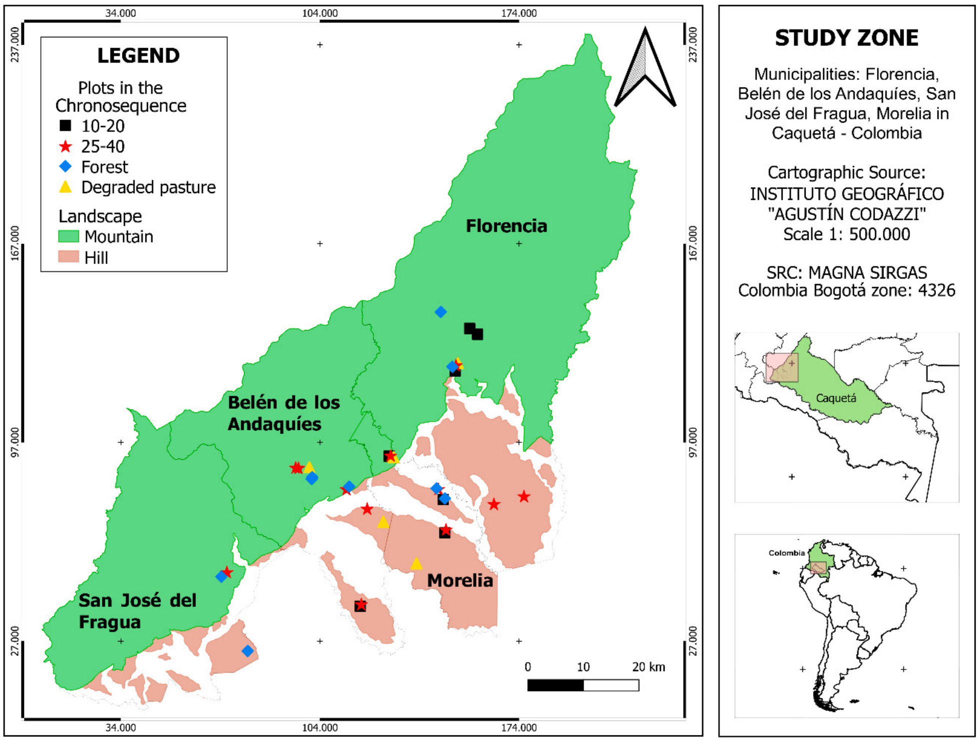

Figure 1. Location of the study sites (Caquetá state, Northwestern of the Colombian Amazon).

Soils in the study area are characterized by a low pH (between 4.5 and 5.8), with a high percentage of clay with kaolinite and quartz particles, classified as Oxisols and Ultisols (USDA soil classification), which show different grade of drainage limitation, aluminum saturation and low quantities of carbon, potassium, phosphorous and magnesium in the mineral horizons [65].

A random stratified sampling with optimum assignation established 14 and 19 plots of 50 × 50 m (0.25 ha) in hill and mountain landscapes, respectively. Then, a chronosequence composed of four successional categories was established in each landscape type: (i) degraded pasture, corresponding to degraded pastures with successional stages <3-year-old with shrubby vegetation, (ii) 10–20, corresponding to successional coverings between 10–20-year-old forests or young secondary forests, (iii) 25–40, corresponding to successional coverings between 25–40-year-old forest or intermediate secondary forest and (iv) forest (mature forest). A total of five, seven, twelve and nine plots were evaluated in the degraded pastures, 10–20, 25–40 and forest areas, respectively, in the two landscapes. The number of plots by successional category was different because of the availability of natural regrowth patches found in the study area that matched our selection criteria: the plots were identified from knowledge of owners of local farms about the sites-use history [17] and particular floristic attributes of the vegetation, such as the floristic composition, plant species density, truck diameter and basal area of plant species [66].

Degraded pastures included a mixed cover with degraded Brachiaria spp. grasses [67], weeds such as Urochloa decumbens (Poaceae), Homolepsis aturensis (Poaceae), Cyperus sp. (Cyperaceae), Scleria melaleuca (Cyperaceae) and Steinchisma laxum (Poaceae), and some shrub species. These areas presented the lowest plant richness, with 34 families and 103 species, with Melastomataceae (17), Annonaceae (9), Burseraceae (8), and Euphorbiaceae (7), as the most representative families, and plant species, such as Miconia elata (163), Miconia minutiflora (156) and Miconia lourtegiana (103).

Plots of 10–20-year-old forests were dominated by shrubs from the families Melastomataceae (27), Mimosaceae (20), Rubiaceae (18), Moraceae (15), Annonaceae (14), Euphorbiaceae (13), Lauraceae (13), Myrtaceae (10), Flacourtiaceae (9), and Arecaceae, Burseraceae, Caesalpiniaceae, Cecropiaceae, Fabaceae, and Fabaceae, with one species from each. The most abundant plant species were Siparuna guianensiss (138) Henriettea fascicularis (89), Adenocalymma aspericarpum (76), Piptocoma discolor (71) and Inga thibaudiana (69).

Plots of 25–40-year-old forests were characterized by pioneer tree species dominating the canopy, which included species from the families Rubiaceae (43), Melastomataceae (40), Mimosaceae (33), Moraceae (33), Fabaceae (30), Annonaceae (28), Lauraceae (27), Burseraceae (18), Clusiaceae (18), Euphorbiaceae (18) and Myristicaceae (17). The most dominant plant species were Tapirira guianensis (134), Siparuna guianensiss (120), Adenocalymma aspericarpum (114), Casearia arborea (87), Henriettea fascicularis (61), Matayba inelegans (49) and Guatteria punctata (49).

The forest corresponded to an old-growth or mature forest with the highest plant richness, a complex structure and diverse plant composition with trees, arborescent ferns and a well-developed understory and a well-stratified canopy. The richest plant families were Lauraceae (43), Rubiaceae (39), Melastomataceae (38), Fabaceae (36), Burseraceae (27), Sapotaceae (27), Moraceae (25), Mimosaceae (23), Annonaceae (22), Euphorbiaceae (19) y Chrysobalanaceae (16) Elaeocarpaceae (12), Meliaceae (12), Arecaceae (10), Myristicaceae (10), Sapindaceae (9), Caesalpiniaceae (8) Clusiaceae (7), Nyctaginaceae (7) and Lecythidaceae(6). The most abundant plant species were: Pseudosenefeldera inclinata (197), Wettinia praemorsa (135), Virola elongata (87), Ladenbergia muzonensis (56), Graffenrieda colombiana (50) and Geonoma maxima (47).

The degraded pasture, 10–20 and 25–40 categories were pooled and identified as "disturbed", and the forest was identified as "undisturbed" to compare the mean values of the soil biological, physical and chemical properties between both areas. Detailed information on the studied plots and soil samples is in Table S1 (Supplementary Materials).

2.2. Soil Sampling and Evaluation of Soil Quality

The soil sampling was performed in 2018 during the dry season (November to February). In each 50 × 50 m plot, five sampling points (the four corners and center of the plot) were established to collect different soil samples and evaluate the biological (soil macrofauna), morphological (macroaggregates) and physicochemical soil properties [48,60,68].

2.2.1. Soil Macrofauna

The soil macrofauna was collected following the methodology proposed by TSBF/ISO 23611–5 [69,70]. In each sampling point, a soil monolith of 25 × 25 cm and 30 cm depth was collected, which was stratified in four layers: litter, 0–10 cm depth, 10–20 cm depth and 20–30 cm depth. The soil macrofauna was extracted from each layer by hand-sorting all faunal individuals visible to the naked eye, which were preserved and labeled in a plastic vial with ethanol 80%. At the laboratory, all macrofauna individuals were cleaned, counted, separated by morphotype, and identified in taxonomic groups [29,71]. Additionally, the macrofauna density was calculated by quantifying the number of individuals m^{-2} of each biological group. All specimens were deposited in "Colección de artrópodos terrestres de la Amazonia Colombiana—CATAC" of the Sinchi Institute in the city of Leticia, Amazonas.

2.2.2. Soil Macroaggregation

The soil macro aggregates were evaluated following the methodology proposed by Velasquez et al. [60]. In each sampling point a soil monolith (10 × 10 × 10 cm) was collected and transported in a plastic container to the laboratory, where it was broken up and separated into aggregate morphologies [48,60], including (i) biogenic macroaggregates created by soil ecosystem engineers (earthworms, termites and ants), created by biological activity such as galleries, nests and coprolites; (ii) root macroaggregates created by roots, roots exudates and soil particles bonded together; (iii) physical macroaggregates created by bonded mineral particles, which usually present geometric shapes and edges in angles; and (iv) non-aggregated soil. Other soil components, including leaves, roots, and wood fragments, were also quantified to obtain the total percentage for the sample [48]. Macroaggregates were then dried at room temperature and weighed separately to determine the proportion (as percentage) of each macroaggregate in the soil sample.

2.2.3. Soil Physico–Chemical Properties

A small trench (30 × 30 × 30 cm) was opened in each sampling point to collect both undisturbed and disturbed soil samples at 10 cm increments until reaching a 30 cm depth (i.e., three soil layers), which were submitted to further analysis.

Different soil physical properties were evaluated through both in situ and laboratory methodologies. In the field, penetration resistance (MPa) was assessed by using an Eijkelkamp hand penetrometer. The laboratory soil samples were assessed for texture (sand, clay and silt) (as percentage) with Bouyoucos [72], bulk density (g cm^{-3}) based on the mass/volume relationship [73], total porosity (as percentage) based on the bulk density and particle density [74], soil moisture (as percentage) estimated after drying of a composed soil sample in a forced-air oven at 105 °C for 24 h [74] and structural stability index, SI (%), using the Equation (1), as proposed by Pieri [75]:

$$\mathrm{SI} = \frac{1.724\ \mathrm{SOC}}{(\mathrm{Silt} + \mathrm{Clay})} \times 100;\ 0 \leq \mathrm{SI} < \infty \quad (1)$$

where, soil organic carbon content (SOC) is the percentage of soil organic carbon, Silt and Clay correspond to particles size fractions expressed in percentages, and 1.724 converts SOC to soil organic matter. According to Pieri [75]: SI > 9% indicates stable structure, 7% < SI ≤ 9% indicates low risk of structural degradation, 5% < SI ≤ 7% indicates high risk of degradation, and SI ≤ 5% indicates structurally degraded soil.

Soil chemical properties related to soil fertility [48,60] such as pH (conductimetric method), cation exchange capacity (CEC) (meq 100 g^{-1}) (with ammonium acetate), electric conductivity (EC) (dS m^{-1}) (conductimetric method), available phosphorus (P) (mg kg^{-1}) (Bray II), exchangeable acidity (EA) (mg kg^{-1}) (KCl 1N/Volumetric), soil organic carbon content (SOC) (%) (Walkley and Black method), total nitrogen (N) (%) (Kjeldhal), calcium (Ca) (mg kg^{-1}), magnesium (Mg) (mg kg^{-1}) (with ammonium acetate and atomic absorption spectroscopy) and potassium (K) (mg kg^{-1}) (with ammonium acetate and atomic emission spectroscopy) were determined.

2.2.4. Soil Quality Assessment

To perform an overall evaluation for the 0–30 cm soil surface, soil data from the 0–10, 10–20 and 20–30 cm layers were grouped to an average value for each physical and chemical property. Similarly, the soil macrofauna data from the litter, 0–10, 10–20 and 20–30 cm layers were grouped to an average value for each taxonomic group. The soil macroaggregation data for the 0–10 cm soil layer were analyzed to an average value for each property evaluated. Then, we calculated a sub-indicator of soil quality for each data set (macrofauna, macroaggregation, physical and chemical) following the methodology proposed by Velásquez et al. [60]. First, a principal component analysis (PCA) of each of the four data set was performed, and the variables that contributed more than 50% of the maximum variability captured for PC1 and PC2 of the PCA were selected. At the second stage, the values of each variable were multiplied by their weight factors (variability explained by the component and variable contribution) and summed, obtaining a sub-indicator of (i) biodiversity, (ii) macroaggregation, (iii) chemical and (iv) physical, according to the Equation (2):

$$Y = PC1 * (\alpha 1a + \beta 1b + \gamma 1c) + PC2 * (\alpha 2a + \beta 2b + \gamma 2c) \quad (2)$$

where Y is the sub-indicator value, PC is the captured variability (%) by the corresponding principal component, α, β and γ represent the contribution of the variables for their respective axes, and a, b and c, represent the variables values on their corresponding axes.

At the third stage, the values of the sub-indicators were normalized between 0.1 to 1, using Equation (3):

$$Y = 0.1 + ((x + b)/(a + b)) * 0.9 \quad (3)$$

where, Y is the transformed variable, x is the non-transformed variable, a is the maximum value of the variable, and b is the minimum value of the variable.

Finally, the General Indicator Soil of Quality (GISQ) was calculated from four sub-indicators of soil quality (biodiversity, macroaggregation, physical and chemical) using the same procedure for the sub-indicators calculation.

2.3. Statistical Analysis

The data were organized in four data sets: (i) macrofauna, (ii) macroaggregates, (iii) physical properties and (iv) chemical properties. To test the effects of landscapes and the successional categories as well as their interaction with the macroaggregates, physical and chemical soil properties, linear mixed-effects (LME) models were adjusted by considering plots as random effects. The normality and homoscedasticity were validated through exploratory analyses (QQ-plot and fitted-plot) of model residuals. Mean separation was carried out through an LSD Fisher test. Contrast of hypothesis was used to compare disturbed and undisturbed plots, using 5% significance. Macrofauna density was analyzed using generalized linear mixed-effects (GLME) models with negative binomial distribution and Poisson for taxonomic groups [48]. A PCA was done for each data set using a Monte-Carlo test (999 permutations) to evaluate significance (α = 0.05) in the stages of the chronosequence or landscapes. A PCA with a Monte-Carlo test (999 permutations) was performed on the matrix of sub-indicators and GISQ to relate them on the ordination plane with the successional categories and landscapes. In addition, LME models, Fisher's LSD tests and box plots were used to compare the sub-indicators and GISQ between successional categories and landscapes. Finally, a co-inertia analysis was performed with the Monte-Carlo test (999 permutations) [76,77] to test significance in the covariation of the data sets. The LME and GLME models were fitted with the functions lme (package nlme) [78] and *glmer* (package lme4) [79] from R v.4.0.3 language [80] using the interface in InfoStat v.2020 [81]. The box plots were visualized with the *ggplot* function in R package ggplot 2 [82]. The PCA, Monte-Carlo test and coinertia analysis were performed in the ade4 [83] and factoextra [84] packages from R.

3. Results

3.1. Changes in Soil Physico–Chemical Properties

The differences between the successional categories in the chronosequence were mainly related to the soil physical properties, such as penetration resistance and bulk density, which had higher values in the degraded pastures than the successional plots. Low values of SOC, N, EC and EA were also observed in the degraded pastures (Table 1).

Table 1. Soil physical and chemical properties (0–30 cm layer) along a chronosequence composed of four successional categories in two contrasting landscapes in the northwestern Colombian Amazon.

	Chronosequence				Landscape		Disturbed vs. Undisturbed	Chronosequence vs. Landscape
	Forest	**25–40**	**10–20**	**Degraded Pasture**	**Hill**	**Mountain**	***p*-Value**	***p*-Value**
Physical Properties								
Bulk density (g cm^{-3})	1.32 ± 0.02 b	1.35 ± 0.02 b	1.38 ± 0.03 ab	1.45 ± 0.03 a	1.35 ± 0.01 b	1.40 ± 0.02 a	0.0125	0.8855
Clay (%)	35.56 ± 0.33 a	39.44 ± 2.93 a	37.47 ± 3.76 a	29.50 ± 4.44 a	47.44 ± 2.25 a	23.54 ± 2.88 b	0.9834	0.6259
Sand (%)	55.17 ± 3.62 ab	51.08 ± 3.25 b	53.08 ± 4.14 ab	64.17 ± 4.87 a	43.93 ± 2.24 b	67.82 ± 3.33 a	0.8294	0.4442
Silt (%)	9.28 ± 1.10 a	9.47 ± 1.02 a	9.50 ± 1.28 a	6.33 ± 1.50 a	8.65 ± 0.56 a	8.64 ± 1.11 a	0.5304	0.4606
Total porosity (%)	44.77 ± 0.93 a	43.62 ± 0.84 a	42.37 ± 1.07 ab	39.30 ± 1.26 b	42.62 ± 0.57 a	41.41 ± 0.87 b	0.0126	0.8836
Soil moisture (%)	25.34 ± 1.59 a	23.38 ± 1.44 a	21.24 ± 1.82 ab	16.01 ± 2.14 b	23.3 ± 0.97 a	19.60 ± 1.48 b	0.0126	0.8837
SI (%)	7.13 ± 0.70 a	6.26 ± 0.98 a	5.95 ± 0.69 a	5.47 ± 0.85 a	4.33 ± 0.17 b	8.08 ± 0.79 a	0.1584	0.5881
Chemical properties								
pH	4.27 ± 0.07 a	4.50 ± 0.07 a	4.49 ± 0.09 a	4.50 ± 0.10 a	4.54 ± 0.03 a	4.34 ± 0.08 b	0.0186	0.4958
CEC (meq 100 g^{-1})	5.48 ± 0.72 a	7.00 ± 0.57 a	6.98 ± 0.77 a	5.25 ± 0.92 a	7.48 ± 0.61 a	4.87 ± 0.45 b	0.2826	0.9651
N (%)	0.13 ± 0.01 a	0.12 ± 0.01 a	0.12 ± 0.01 ab	0.09 ± 0.01 b	0.12 ± 0.004 a	0.11 ± 0.01 a	0.1291	0.7007
K (mg kg^{-1})	55.26 ± 6.54 a	54.52 ± 5.12 a	55.26 ± 6.54 a	34.81 ± 7.70 a	45.59 ± 3.71 a	49.37 ± 5.15 a	0.6806	0.6354
P (mg kg^{-1})	3.26 ± 0.27 a	3.13 ± 0.25 a	3.49 ± 0.31 a	2.80 ± 0.37 a	3.03 ± 0.17 a	3.30 ± 0.25 a	0.7077	0.5883
EC (dS m^{-1})	0.40 ± 10.04 a	0.25 ± 0.03 bc	0.32 ± 0.04 ab	0.17 ± 0.05 c	0.15 ± 0.01 b	0.42 ± 0.04 a	0.0011	0.0511
SOC (%)	1.49 ± 0.14 a	1.47 ± 0.08 a	1.41 ± 0.14 ab	1.06 ± 0.10 b	1.40 ± 0.09 a	1.32 ± 0.08 a	0.2628	0.6628
Ca (mg kg^{-1})	226.22 ± 6.35 a	236.89 ± 10.76 a	244.61 ± 8.94 a	232.42 ± 8.53 a	234.74 ± 6.60 a	235.33 ± 5.80 a	0.1731	0.2061
Mg (mg kg^{-1})	39.03 ± 1.23 a	42.97 ± 3.12 a	42.11 ± 1.53 a	36.81 ± 2.02 a	39.15 ± 1.55 a	41.31 ± 1.41 a	0.3862	0.4765
EA (mg kg^{-1})	342.40 ± 51.37 ab	478.25 ±49.77 a	377.54 ± 52.92 ab	315.89 ± 38.35 b	511.79 ± 37.02 a	245.25 ± 31.25 b	0.4159	0.8071

Values corresponded to mean and standard error. Values between rows in the chronosequence or landscape followed by the same letter do not differ statistically (Fisher's least significant difference LSD test, $p < 0.05$). Degraded pasture, 10–20 and 25–40: <3, 10–20 and 25–40 years of abandonment, respectively; forest: mature forest. The categories: degraded pasture, 10–20 and 25–40 were combined (disturbed) to compare to Forest (undisturbed).

In addition, the bulk density and penetration resistance were significantly higher in the disturbed areas, while the total porosity and moisture soil were higher in the undisturbed areas (Table 1). Significantly higher acidity and high CEC values were observed in the undisturbed areas.

The relationship between the soil physico–chemical properties, the landscapes and the successional categories was evaluated with PCA (Figure 2).

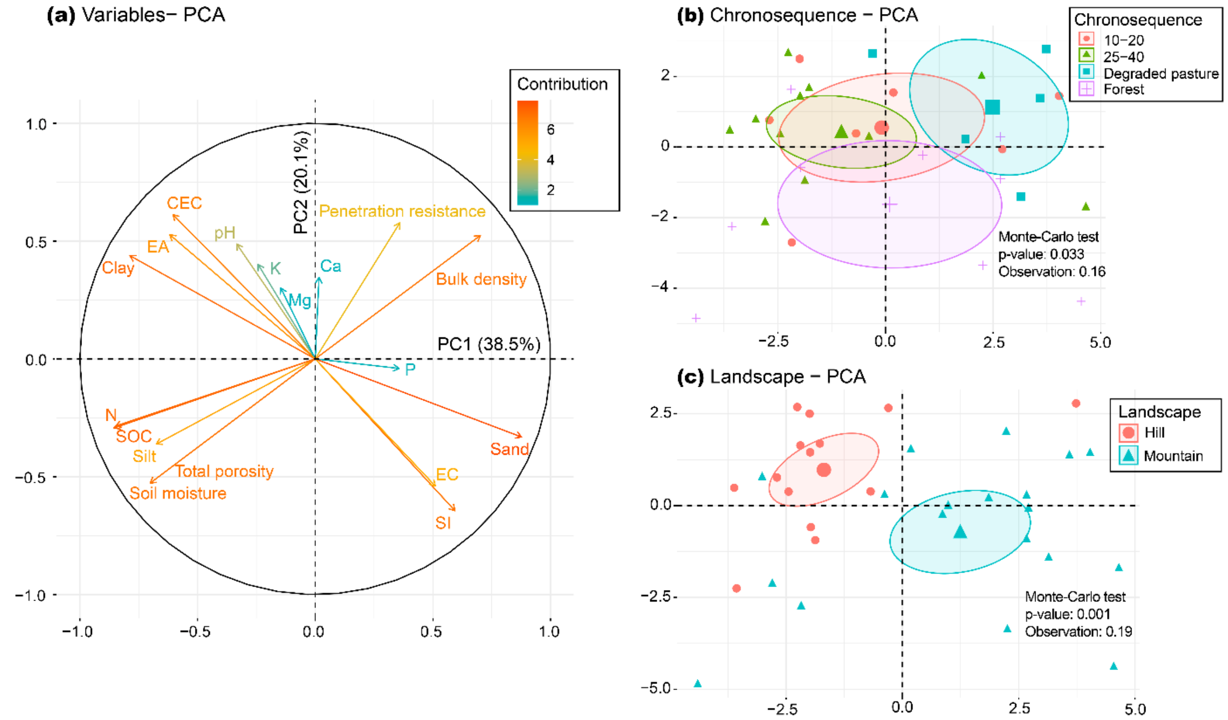

Figure 2. Principal component analysis (PCA) with the soil physical-chemical properties and the sampling plots projected on the ordination plane PC1/PC2. (**a**) Correlation circle of soil physical-chemical variables; the color of the vectors indicates the contribution of the variables to the PCs. (**b**,**c**), sampling plots grouped by chronosequence and landscape; 95% confidence ellipses. Degraded pasture, 10–20 and 25–40: <3, 10–20 and 25–40 years of abandonment; forest: mature forest.

The first two components explained 58.6% of the variance, with the physico–chemical composition of soils grouped into clusters clearly defined according to the landscapes (Figure 2c) ($p < 0.01$; 19% of explained variance) and the successional categories (Figure 2b), showing a significant effect from the chronosequence ($p < 0.05$; 16%).

The interaction between the chronosequence and landscape was not significant for any chemical and physical property ($p > 0.05$); therefore, the principal effects were interpreted directly (Table 1). The main differences between the landscapes occurred in the soil texture and soil acidity. Differences in soil texture were also reflected as differences in some physical properties, such as bulk density, total porosity, soil moisture and SI. Differences in the pH were also reflected as differences in some associated chemical properties, such as CEC, EC and EA.

3.2. *Responses of Soil Macrofauna Communities to Narural Succesion*

The linear mixed effects analysis showed that the interaction between the chronosequence and landscape was not significant for any soil macrofauna ($p > 0.05$), with the exception of some macrofauna groups (Araneae, Coleoptera larvae, Isoptera and Pseudoscorpionidae) (Table 2). Thus, in the hills, Araneae, Coleoptera larvae and Isoptera were significantly lower in the degraded pastures, while Pseudoscorpionidae was lower in the forest. In the mountains, the highest density of Pseudoscorpionidae was evidenced in the 25–40 category, while Isoptera was significantly higher in the forest as compared to the degraded pasture (Table S2; Supplementary Materials).

Table 2. Density of soil macrofauna communities (individuals·m^{-2}) in the 0–30 cm layer along a chronosequence composed of four successional categories in two contrasting landscapes in the northwestern Colombian Amazon.

Taxonomic Group	Chronosequence				Landscape		Disturbed vs. Undisturbed	Chronosequence vs. Landscape
	Forest	25–40	10–20	Degraded Pasture	Hill	Mountain	*p*-Value	*p*-Value
Araneae	107.93 ± 18.46 a	98.95 ± 13.86 a	96.55 ± 17.88 a	24.87 ± 6.27 b	62.18 ± 9.45 a	81.45 ± 9.50 a	0.0069	0.0003
Blattodea	37.17 ± 17.07 a	29.99 ± 11.27 a	29.21 ± 14.54 a	9.24 ± 5.61 a	20.79 ± 7.89 a	26.38 ± 8.26 a	0.2570	0.9621
Chilopoda	131.99 ± 24.86 a	99.12 ± 15.32 ab	110.22 ± 22.48 ab	60.22 ± 15.02 b	86.52 ± 13.52 a	107.70 ± 13.78 a	0.0613	0.0776
Coleoptera adults	98.34 ± 10.83 a	74.02 ± 6.79 a	94.26 ± 11.26 a	50.60 ± 7.56 b	80.25 ± 7.38 a	73.42 ± 5.60 a	0.0116	0.3860
Coleoptera-larvae	104.92 ± 20.41 a	86.16 ± 13.73 a	69.04 ± 14.61 ab	41.31 ± 10.90 b	55.52 ± 9.12 b	91.46 ± 12.08 a	0.0256	0.0235
Dermaptera	11.83 ± 4.63 a	2.67 ± 3.78 a	0.00 ± 5.00 a	8.00 ± 5.97 a	0.00 ± 3.78 b	11.25 ± 3.13 a	0.1415	0.3063
Diplopoda	98.34 ± 26.47 a	118.65 ± 26.05 a	126.21 ± 36.64 a	32.66 ± 11.54 b	90.49 ± 19.97 a	76.64 ± 14.08 a	0.4856	0.7487
Diplura	71.55 ± 31.77 a	55.23 ± 20.05 a	26.83 ± 13.02 a	16.65 ± 9.77 a	28.58 ± 10.55 a	46.49 ± 14.02 a	0.0871	0.2728
Diptera-larvae	6.67 ± 7.87 a	17.33 ± 6.43 a	8.67 ± 8.50 a	5.33 ± 10.16 a	4.00 ± 6.43 a	15.00 ± 5.33 a	0.6873	0.2184
Formicidae	1411.66 ± 139.70 a	1287.51 ± 104.08 ab	977.15 ± 104.68 b	656.26 ± 84.28 c	999.79 ± 81.01 a	1079.82 ± 72.51 a	0.0005	0.6544
Hemiptera	23.85 ± 7.70 b	42.86 ± 11.16 ab	95.20 ± 32.55 a	20.66 ± 8.66 b	39.07 ± 10.28 a	36.29 ± 7.87 a	0.1091	0.5139
Isopoda	40.00 ± 12.11 a	25.78 ± 9.89 a	30.67 ± 13.08 a	5.33 ± 15.64 a	28.22 ± 9.89 a	22.67 ± 8.20 a	0.1862	0.2600
Isoptera	4867.72 ± 1187.70 a	4806.44 ± 957.57 a	3648.65 ± 961.68 a	728.25 ± 229.81 b	3032.86 ± 604.81 a	2599.73 ± 429.56 a	0.0108	0.0369
Lepidoptera-larvae	15.92 ± 46.32 a	10.67 ± 37.82 a	140.33 ± 50.03 a	5.33 ± 59.79 a	72.67 ± 37.82 a	13.46 ± 31.36 a	0.5133	0.1868
Oligochaeta	214.00 ± 47.61 a	115.44 ± 21.08 b	276.09 ± 66.27 a	416.60 ± 120.18 a	255.54 ± 46.37 a	209.35 ± 31.54 a	0.6926	0.9039
Opiliones	39.19 ± 12.20 ab	53.18 ± 13.47 a	19.60 ± 6.71 b	23.55 ± 9.80 ab	23.66 ± 6.19 a	41.46 ± 8.74 a	0.4179	0.1224
Orthoptera	9.33 ± 3.84 a	10.67 ± 3.13 a	8.00 ± 4.14 a	2.67 ± 4.95 a	5.33 ± 3.13 a	10.00 ± 2.60 a	0.6274	0.3721
Pseudoscorpionida	18.50 ± 1.52 b	34.82 ± 1.72 a	22.63 ± 1.83 b	22.63 ± 2.16 b	27.36 ± 1.52 a	20.99 ± 1.17 b	0.0002	<0.0001
Symphyla	1.33 ± 3.86 b	6.67 ± 3.16 ab	0.00 ± 4.17 b	16.00 ± 4.99 a	7.33 ± 3.16 a	4.67 ± 2.62 a	0.1840	0.4342
Rychness †	14.99 ± 1.36 a	14.16 ± 1.09 a	8.08 ± 1.08 b	5.92 ± 1.14 b	10.06 ± 1.04 a	10.02 ± 0.81 a	<0.0001	0.6995
Density	7324.98 ± 937.89 a	7079.25 ± 740.13 a	5995.62 ± 829.30 a	2333.66 ± 386.24 b	5743.31 ± 600.78 a	4689.98 ± 406.72 a	0.0023	0.0609

Values corresponded to mean and standard error. Values between rows in the chronosequence or landscape followed by the same letter do not differ statistically (Fisher's least significant difference LSD test, $p < 0.05$). Degraded pasture, 10–20 and 25–40: <3, 10–20 and 25–40 years of abandonment; forest: mature forest. The categories: degraded pasture, 10–20 and 25–40 were combined (disturbed) to compare to forest (undisturbed). † Per monolith.

Overall, a total of 19 soil macrofauna taxa were identified, with higher densities of Araneae, Coleoptera adults, Diplopoda and Isoptera in the forest, 25–40 and 10–20 than in the degraded pasture (Table 2).

The successional category affected the density and richness of soil macroinvertebrates. An increase in the number of individuals per m^{-2} in the 0–30 cm deep soil layer was detected, with values ranging from 2334 individual m^{-2} in the degraded pasture to the average value of 7202 individual m^{-2} in the 25–40 category and forest areas. The taxonomic richness was also lower in the degraded pasture than in the area with the most advanced stage of natural succession (25–40 category) and mature forest (Table 2).

Isoptera and Formicidae were the densest groups in the successional categories, representing 53.98 and 19.93% of the collected macrofauna, respectively. Differences in the density of taxonomic groups between the landscapes were only observed in Coleoptera-larvae, Dermaptera and Pseudoscorpionida (Table 2).

By grouping the sites according to disturbance, the Araneae, Coleoptera-adults, Coleoptera-larvae, Formicidade, Isoptera and Pseudoscorpionida groups showed significantly lower densities in the disturbed areas than in the undisturbed areas (Table 2).

A PCA analysis was performed to assess the relationship between the soil macrofauna taxonomic groups composition and the successional categories conforming the chronosequence in each landscape (Figure 3). The two first PCA axes explained 39.6% and 34.5% of the total variance of soil macrofauna species composition in the hills and mountains, respectively (Figure 3a,c). Formicidae, Dermaptera, Diptera-larvae, Oligochaeta, Coleoptera-adults, and Orthoptera were the taxonomic groups with higher contribution to the differentiation of successional stages in the hill areas. In contrast, in the mountain landscape, Diplopoda, Isopoda, Coleoptera adults, Dermaptera, Isopoda, Diplura, Araneaea, and Pseudoscorpionida contributed to the variance.

The soil macrofauna communities in the two landscapes were structured differently. The degraded pastures in the hills had a different soil macrofauna composition than the rest of successional categories ($p < 0.01$; 37% of explained variance) (Figure 3a,b). The successional 10–20 and 25–40 categories clustered together, showing a different composition from the mature forest. The mountains presented similar soil macrofauna composition along the chronosequence ($p > 0.05$; 18%) (Figure 3c,d), where the forests and middle-age succession (25–40) had the most similar soil macrofauna composition.

3.3. Soil Macroaggregation

Similar to the physico–chemical properties, the linear mixed effects analysis showed that the interaction between the chronosequence and landscape was not significant for any soil macroaggregation property ($p > 0.05$) (Table 3). The landscape and successional categories influenced the soil macroaggregation. The hills presented higher physicogenic macroaggregates and lower organic material than the mountains. Alterations in the physicogenic and root macroaggregates were observed because of the natural succession process, with higher values of these soil aggregates in the degraded pastures. In contrast, the largest proportion of biogenic macroaggregates was in the young and middle-age successional stages (25–40 and 10–20 study areas).

The non-macroaggregates and organic material were significantly lower in the disturbed areas than in the undisturbed one, while the biogenic macroaggregates were higher in the disturbed areas (Table 3).

PCA analysis of the data matrix performed by landscape type showed that the first two components of the PCA explained 79.8% of the soil aggregation variance in the hills, and 72.7% in the mountains (Figure 4a,c). Biogenic macroaggregates and non-macroaggregated explained most of the variance in both landscapes.

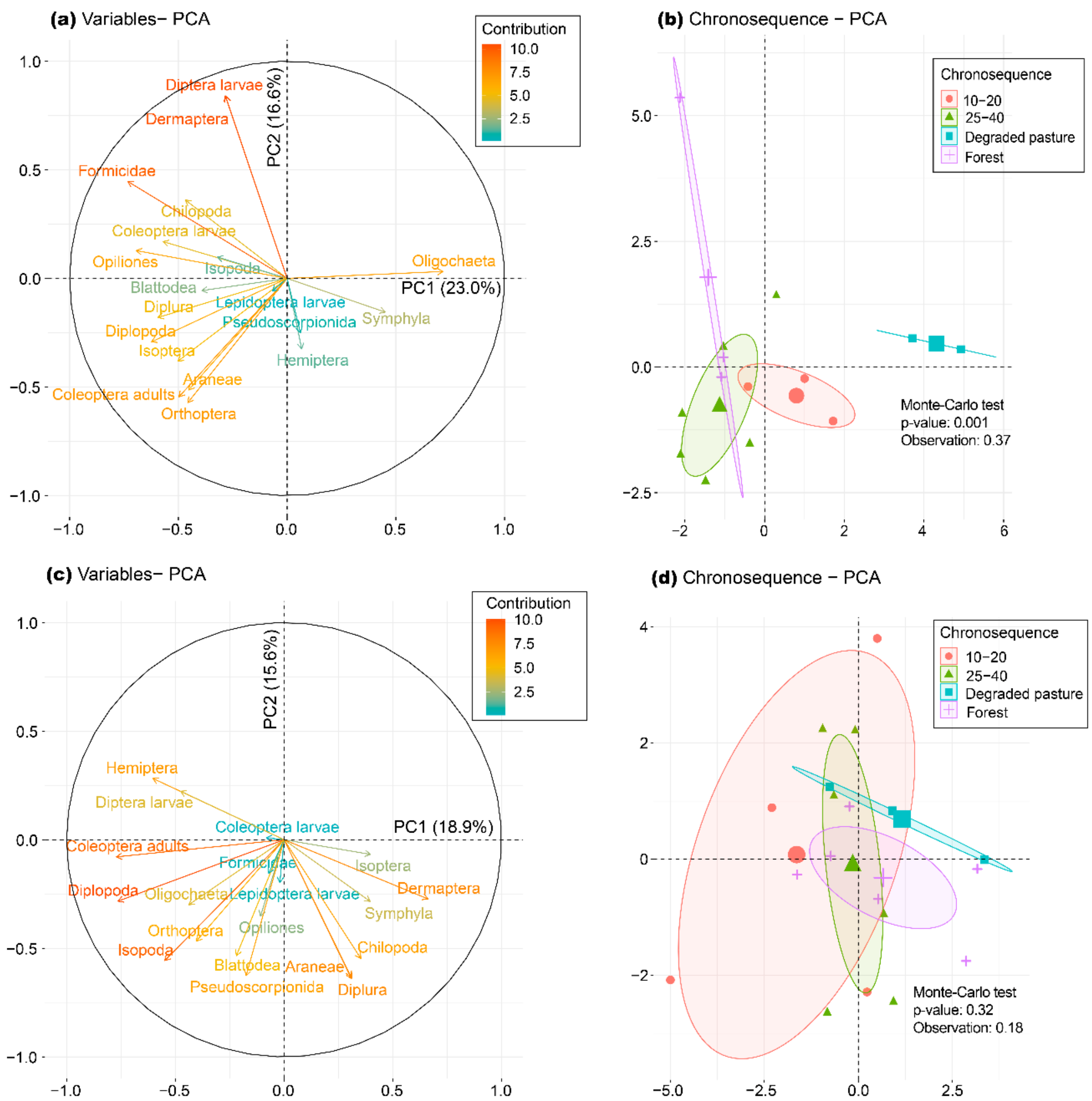

Figure 3. Principal component analysis (PCA) with the soil macrofauna taxonomic groups composition and the sampling plots projected on the ordination plane PC1/PC2. Correlation circle of soil macrofauna groups compositions; the color of the vectors indicates the contribution of the variables to the PCs, and sampling plots grouped by chronosequence: (**a**,**b**) hill areas, and (**c**,**d**) mountain areas; 95% confidence ellipses. Degraded pasture, 10–20 and 25–40: <3, 10–20 and 25–40 years of abandonment; forest: mature forest.

Table 3. Soil macroaggregates (%) in top layer (0–10 cm) along a chronosequence composed of four successional categories in two contrasting landscapes in the northwestern Colombian Amazon.

Soil Macroaggregates	**Chronosequence**				**Landscape**		**Disturbed vs. Undisturbed**	**Chronosequence vs. Landscape**
	Forest	**25–40**	**10–20**	**Degraded Pasture**	**Lomerío**	**Mountain**	***p*-Value**	***p*-Value**
Biogenic macroaggregates	19.72 ± 4.14 b	44.11 ± 3.38 a	33.40 ± 4.47 a	15.41 ± 5.35 b	24.52 ± 3.38 a	31.80 ± 2.80 a	0.0297	0.9865
Non-macroaggregated	49.86 ± 4.67 a	27.02 ± 3.82 b	41.26 ± 5.05 a	22.18 ± 6.03 b	36.50 ± 3.82 a	33.66 ± 3.16 a	0.0014	0.8059
Organic material	0.97 ± 0.15 a	0.65 ± 0.14 ab	0.44 ± 0.18 bc	0.04 ± 0.20 c	0.32 ± 0.05 b	0.73 ± 0.16 a	0.0029	0.2140
Physicogenic macroaggregates	19.64 ± 3.51 b	20.41 ± 2.87 b	16.55 ± 3.80 b	33.80 ± 4.54 a	27.05 ± 2.87 a	18.15 ± 2.38 b	0.3491	0.6347
Root macroaggregates	9.81 ± 2.60 b	7.81 ± 2.12 b	8.35 ± 2.80 b	28.58 ± 3.35 a	11.62 ± 2.12 a	15.65 ± 1.76 a	0.1079	0.8565

Values corresponded to mean and standard error. Values between rows in the chronosequence or landscape followed by the same letter do not differ statistically (Fisher's least significant difference LSD test, $p < 0.05$). Degraded pasture, 10–20 and 25–40: <3, 10–20 and 25–40 years of abandonment, respectively; forest: mature forest. The categories: degraded pasture, 10–20 and 25–40 were combined (disturbed) to compare to forest (undisturbed).

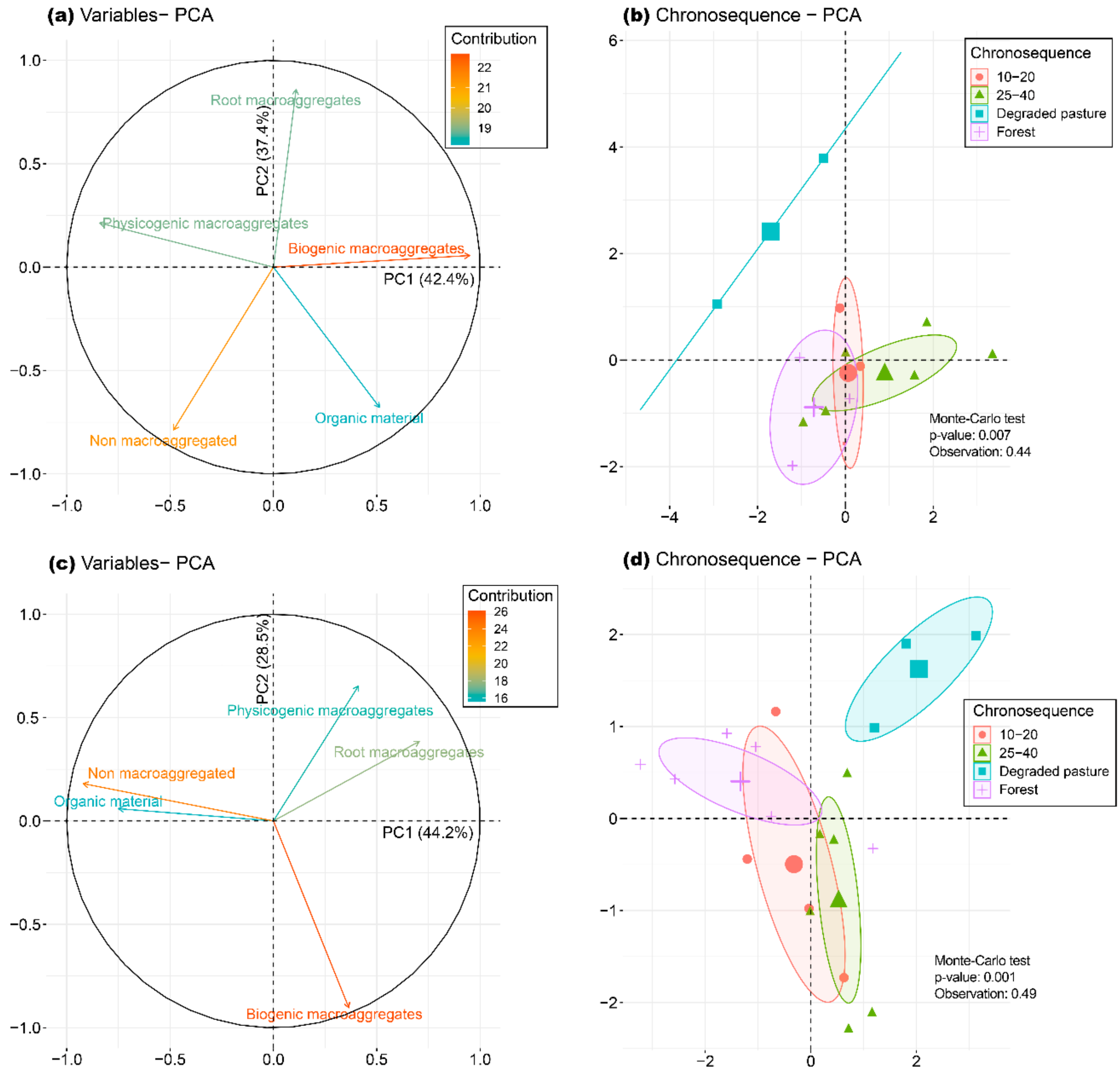

Figure 4. Principal component analysis (PCA) with the soil macroaggregation variables and the sampling plots projected on the ordination plane PC1/PC2. Correlation circle of soil macroaggregation variables; the color of the vectors indicates the contribution of the variables to the PCs, and sampling plots grouped by chronosequence: (**a**,**b**) hill areas, and (**c**,**d**) mountain areas; 95% confidence ellipses. Degraded pasture, 10–20 and 25–40: <3, 10–20 and 25–40 years of abandonment; forest: mature forest.

The successional categories clustered together according to the soil macroaggregate composition, following similar patterns in both landscapes. Clearly, the degraded pastures presented a different macroaggregate composition ($p < 0.01$), separated by PC1 in both landscapes (Figure 4b,d).

3.4. Soil Quality Indicator (GISQ)

After integrating 41 soil properties into four soil quality sub-indicators and then into a GISQ, an increasing trend of soil quality was verified when degraded pastures are abandoned, allowing the natural succession process (Figure 5). A lower GISQ was observed in the degraded pastures than in the areas with young, middle-age successional stages (10–20, 25–40 study areas) and forests.

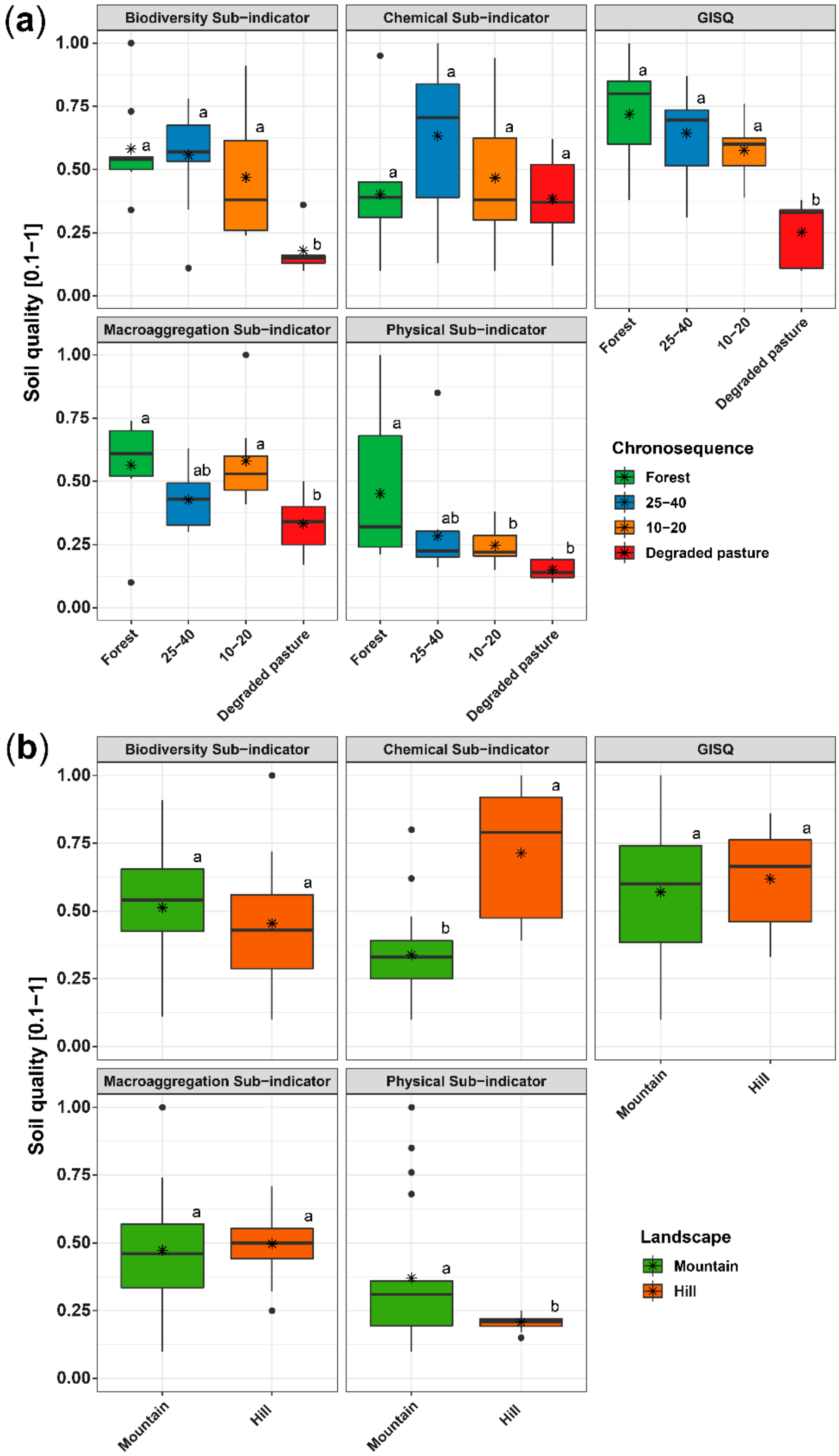

Figure 5. Soil quality sub-indicators and GISQ (general indicator of soil quality) according to successional stages of the chronosequence (Degraded pasture, 10–20 and 25–40 years of abandonment, and Forest) (**a**) and landscape (**b**). Mean values (*) between successional categories or landscapes followed by the same letter do not differ statistically (Fisher's least significant difference LSD test, $p < 0.05$).

Differences between the succession categories conforming the chronosequence were also detected in the soil quality sub-indicators physical, biodiversity (soil macrofauna species composition) and macroaggregation, which showed lower values in the degraded pastures than in the successional stages (Figure 5a). On the other hand, while a non-significant interaction between the chronosequence and landscape was observed for all soil quality sub-indicators ($p > 0.05$), the landscape affected the physical and chemical sub-indicators (Figure 5b).

A PCA of the soil quality sub-indicators and the GISQ ranked the study areas by landscape type and successional stage. The soil quality sub-indicators explained 75.28% of the variance in the first two axes (Figure 6a). GISQ and chemical sub-indicators were the indicators with the highest contribution to the ordination (Figure 6a). PC1 separated the degraded pasture with the lowest soil quality from the forest with the highest soil quality index (Figure 6b).

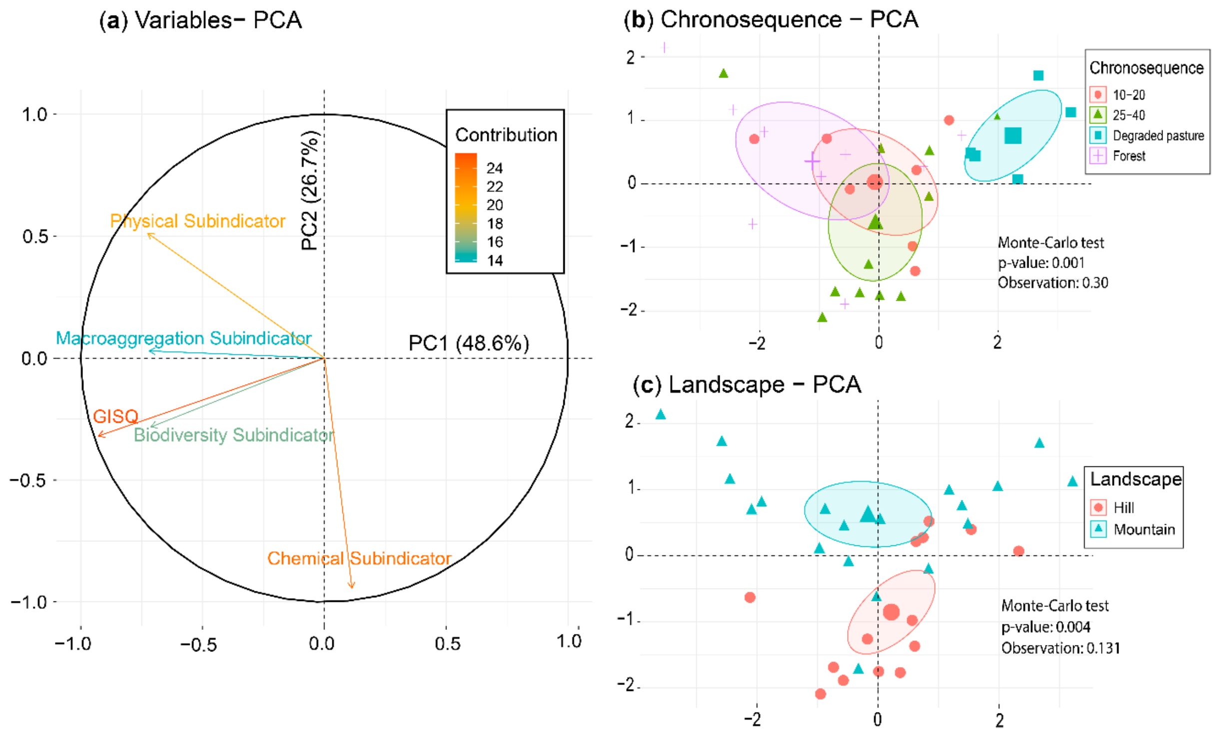

Figure 6. Principal component analysis (PCA) with the sub-indicators of soil quality, GISQ (general indicator of soil quality), and the sampling plots projected on the ordination plane PC1/PC2. (**a**) Correlation circle of the sub-indicators of soil quality and GISQ; the color of the vectors indicates the contribution of the variables to the PCs. (**b**,**c**), sampling plots grouped by chronosequence and landscape, respectively; 95% confidence ellipses. Degraded pasture, 10–20 and 25–40: <3, 10–20 and 25–40 years of abandonment; forest: mature forest.

The soils in the mountain landscape showed a higher physical quality, while a higher soil chemical quality was observed in the hills (Figure 6c). PC2 represented mainly the 25–40 category with a higher soil chemical quality.

3.5. Relationship between Data Matrices

A coinertia analysis between the data set matrices showed a significant relationship ($p < 0.05$) between the correlation coefficients, with percentages ranging between 14% and 53% (Table 4). The covariation showed that there were more biogenic macroaggregates where the macrofauna diversity was higher. However, Oligochaeta and Symphyla were more related to physical and root macroaggregation. Chilopoda, Dermaptera and Coleoptera larvae were more significant in the forest and old-growth successional stages (Figures S1–S6; Supplementary Materials).

Table 4. Matrix correlation coefficients (RV) between four data matrices (i.e., macrofauna, physical, chemical and macroaggregation) obtained from the coinertia analysis.

Coinertia Analysis	Projected Inertia		RV	*p*-Value
	Axis 1	Axis 2		
Macrofauna vs. Chemical	52.3	21.1	0.24	0.035
Macrofauna vs. Physical	51.6	39.1	0.23	0.036
Macrofauna vs. Macroaggregation	68.3	22.1	0.21	0.040
Chemical vs. Physical	79.6	16.7	0.53	0.001
Chemical vs. Macroaggregation	51.2	39.9	0.17	0.043
Physical vs. Macroaggregation	73.9	22.8	0.14	0.044

4. Discussion

Overall, the soil quality assessment reveled how the soil quality was improved throughout a natural succession of the degraded pastures in two different landscapes of the Colombian Amazon. The results evidenced that, although the physical and chemical composition soils varied among the landscapes, the soil quality indicator of mature forest and young/middle-age successional stages (25–40 and 10–20 study areas) was similar, with soil macroaggregation and macrofauna playing an important role in the soil quality improvement. Additionally, none of the individual variables or composed indicators could discriminate among different successional stages.

Soil is a fundamental component of ecosystems; therefore, enhancement and maintenance of soil quality is necessary to guarantee environmental sustainability and successful forest recovery [42,85]. Soil chemical properties in this study reflected the typical characteristics of Amazon soils, with high acidity and poor fertility from an intense weathering process. Alterations were observed mainly in the biological and physical indicators in response to pasture abandonment, denoting the impact of livestock production on soil quality. Long periods of grazing and cattle trampling have direct effects on soil structure by increasing soil compaction [86], thereby degrading the soil physical quality over time. Furthermore, the burning of pastures, a management practice commonly used to improve pasture soil quality [87] with short-term benefits [88], reduces the soil organic matter, soil biodiversity, nutrient content, soil moisture and aggregate stability [89–92], thus accelerating the soil degradation.

Despite the fact that the lowest soil macrofauna richness and density were observed in the degraded pasture, the soil engineers (Isoptera, Formicidae and Oligochaeta) exhibited higher densities that the other taxonomic groups. Formicidae are usually very abundant in deforested areas [38,93,94], with many species commonly reported in agricultural and urban ecosystems [95]. Earthworms are resistant towards degraded soils [31,61] and can change soil physical properties and biogeochemical processes [96]. Isoptera, although reported as very sensitive to soil disturbances [97–99], has some indicator species such as Apicotermitinae morphospecies that have been found in Amazon soils [100]. This study had abundant Apicotermitinae in the most degraded soils, which might indicate that, even in very degraded soils, the soil could hold part of that particular diversity, providing an important tool for restoration.

Macroaggregates are structural units that participate in the regulation of nutrient cycling and the organic matter dynamics [101], which also depend on the carbon availability and the biological activity [48,102,103], leading to improved soil quality [104]. The presence of higher physical and root macroaggregates in pastures might be the result of macroinvertebrates, together with the dense root system of pastures, that through mechanical reinforcement, promote soil aggregation, binding the soil and releasing exudates that acts as soil binding agents [105–107]. The presence of the large number of grasses, related to a high abundance of rhizophagous organisms [23], such as Coleoptera larvae and Symphyla was evidenced. However, contrary to the results reported by Rodríguez et al. [48], there was not a higher proportion of biogenic macroaggregates in the pastures with abundant earthworms. Particularly, in this study, degraded pastures included plots with successional stages <3-year-old with shrubby vegetation, and where the earthworm *Pontoscolex corethrurus* was abundant. This earthworm has been directly associated with pastures [108–111] and identified as a promotor of soil compaction [96,111,112], which could explain these results.

After some years of pasture abandonment, soil macrofauna tend to recover during the first 10 years [46,113]. Nevertheless, the recovery of edaphic macrofauna communities can continue for 50 years, with minor changes [38]. The fast natural recovery of degraded pastures is associated with a high activity of edaphic communities and a fast recovery of plant species [114]. The soil restoration process obtained naturally through succession was similar to the one reported through active restoration [48,49]. However, there were some differences in the type of soil macroaggregates associated with each successional stage In this study, the biogenic macroaggregates were more important in the successional categories with more soil engineer activity. The creation of nests and tunnels not only increases the biogenic macroaggregates proportion but also incorporates macronutrients into the soil, favoring soil fertility [115,116]. Rodriguez et al. [48] found that biogenic macroaggegates were more abundant in silvopastoral systems dominated by grasses, as well as in pastures. It seems that the natural recovery of vegetation, which includes a more diverse plant community with shrubs and pioneer trees, favor soil macrofauna activity and the formation of biogenic aggregates. Since more forested ecosystems are not preferred by *P. corethrurus*, the higher amount of biogenic macroaggregates in middle- and old-successional stages could be the product of other soil engineer communities, such as Isoptera [117].

Macroaggregates are a source of food for soil macrofauna and influence the density of groups. Detritivore organism densities were also shown to be greater in the soils with a high concentration of organic material (Forest and 25–40) [23,38,118], that corresponded to Isopoda, Diplura (Campodeidae), Diplopoda, Blattodea (non-Isoptera) and some Opiliones. Those organisms were also favored by a low pH [119] (Table 1). In addition, high densities of detritivore organisms increase the offer of food for predators (Araneae, Chilipoda, Diplura-Japigydae, and Dermaptera).

The coinertia analysis showed significant correlations between the macrofauna and other soil indicators (RV > 0.20), as reported in other studies in the Amazon region [48,49]. Our study confirmed that physico–chemical properties of the soil are determinant in the configuration of soil macrofaunal communities [41,49] and revealed how groups, such as Coleoptera, Blattodea and Dermaptera, can contribute positively with the restoration of the soil physical quality, soil stability and macroaggregation process. In addition, a strong positive association was evidenced between the Araneae, Diplura, Formicidae and Isoptera groups, and N and SOC indicators, and also between the Coleoptera-larvae and P content. The results showed the capacity of these organisms to improve soil chemical fertility by promoting increased nutrient availability in the soil [41,48].

As none of the individual soil physico–chemical or biological variables discriminate among the natural successional stages of the chronosequence, a synthetic multiparametric indicator was evaluated. The GISQ indicator and its sub-indicators showed a wide contrast between the pastures and successional categories, but not among successional stages. Differences in the GISQ and its sub-indicators have been reported among different land uses [33,48,49] and therefore, could differentiate contrasting successional stages (pastures vs. mature forests), but not intermediate stages. Other methodologies used other biological indicators to better discriminate between mature restoration stages [120,121]. In our study, there was a significant number of Diplura, used in methodologies, such as IBS-bf and in QBS-ar [122], as target groups. Additionally, in terms of the applied methodology, the use of narrow age-ranges along the natural succession could help to better discriminate the changes that occurred in the soil as the initial years of the natural succession is where the greatest changes occurred [123], and could be crucial for soil responses.

5. Conclusions

Different physical, chemical and biological changes occur in Amazon soils during recovery through natural succession. Soil physical and chemical changes are more influenced by the soil composition of the landscape in which the degraded pasture is located.

In the early stages, soil restoration was fast, then, changes occurred more slowly, with no differences among the soils in the successional stages and forests. Soil macroaggregates, as physical and structural variables of soil that impact in the porosity, water-holding capacity and soil fertility, were directly related to the macrofauna composition of the soils. Earthworms were more related to the degraded pastures with compacted soils and physical macroaggregates, while Isoptera and Formicidae were more related to the successional plots with more biogenic macroaggregates.

The degraded pasture presented the most negative physical, chemical and biological variables, and the lowest General Indicator Soil Quality (GISQ) and differed in all variables from the forest and subsequent successional stages. Signs of soil restoration became evident after the first 10 years of natural succession.

Regarding the impact of restoration strategies on the recovery of soil, our data indicate that there are no accurate indicators to monitor soil restoration in natural successions yet. New variables and soil quality indicators, more sensitive to soil changes will be required.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/agronomy11122484/s1, Figure S1: Coinertia analysis PC1/PC2 plane with the projection of macrofauna communities (a) and soil macroaggregates (b); Figure S2: Coinertia analysis PC1/PC2 plane with the projection of macrofauna communities (a) and soil physical properties (b); Figure S3: Coinertia analysis PC1/PC2 plane with the projection of macrofauna communities (a) and soil chemical properties (b); Figure S4: Coinertia analysis PC1/PC2 plane with the projection of soil chemical properties (a) and soil macroaggregates (b); Figure S5: Coinertia analysis PC1/PC2 plane with the projection of soil chemical properties (a) and soil physical properties (b); Figure S6: Coinertia analysis PC1/PC2 plane with the projection of soil physical properties (a) and soil macroaggregates (b). Table S1: Details of plots and soil samples collected and analyzed; Table S2: Density of soil macrofauna communities (individuals·m^{-2}) in the 0–30 cm layer for the significant interaction between chronosequence and landscape.

Author Contributions: Conceptualization, C.H.R.-L. and C.P.P.-V.; methodology, C.P.P.-V. and D.C.; software, A.S.; validation, A.S. and C.P.P.-V.; formal analysis, A.S.; investigation, C.H.R.-L., C.P.P.-V., D.C., L.K.M.-V. and Y.R.V.-D.; resources, C.H.R.-L.; data curation, C.P.P.-V., D.C., L.K.M.-V., Y.R.V.-D. and A.S.; writing—original draft preparation, C.H.R.-L., C.P.P.-V. and L.K.M.-V.; writing—review and editing, C.H.R.-L., C.P.P.-V., A.S. and A.M.S.-O.; visualization, A.S. and L.K.M.-V.; supervision, C.H.R.-L., C.P.P.-V. and A.M.S.-O.; project administration, C.H.R.-L.; funding acquisition, C.H.R.-L. All authors have read and agreed to the published version of the manuscript.

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