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More than carbon: Soil organic carbon and cation exchange capacity as key indicators of chemical recovery in tropical montane Atlantic Forest soils

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Abstract

Purpose

Tropical montane Atlantic Forests are increasingly being converted into pastures and silvicultural systems, altering soil functioning and compromising long-term ecosystem resilience. However, soil indicators capable of diagnosing functional recovery across restoration pathways remain poorly defined, particularly in highly weathered tropical mountain environments.

Methods

This study evaluated whether soil chemical properties can discriminate among alternative recovery trajectories in a tropical montane Atlantic Forest landscape in the Serra do Mar, southeastern Brazil. Four land-use systems were assessed along a 0–60 cm soil profile: interior secondary forests (ISF), edge secondary forests (ESF), eucalyptus plantation, and pasture. Soil samples (n = 10 per land-use system) were analyzed for soil organic carbon (SOC), total nitrogen (N), pH, exchangeable nutrients, and cation exchange capacity (CEC).

Results

Forest restoration promoted substantial increases in SOC (+ 28%) and CEC (+ 28–44%) relative to anthropogenic land uses, with the highest values occurring in secondary forests. In contrast, pH and conventional fertility attributes showed limited capacity to distinguish restoration trajectories. Across the entire soil profile, SOC was strongly associated with CEC (r = 0.97), indicating that organic matter accumulation directly enhanced nutrient-retention capacity and soil chemical functioning. Notably, restored forests exhibited greater SOC, N, and CEC despite maintaining acidic conditions and elevated exchangeable Al concentrations.

Conclusion

These findings demonstrate that chemical resilience was driven primarily by the rebuilding of organic matter-mediated nutrient retention rather than by reductions in soil acidity. Our results provide preliminary evidence that soil organic carbon (SOC) and cation exchange capacity (CEC) have strong potential as indicators of chemical resilience across restoration pathways, and therefore should be considered in future studies aimed at assessing soil recovery and ecosystem resilience in high-altitude tropical soils of Brazil's Serra do Mar.

1 Introduction

Reliable indicators of soil condition, recovery, and resilience are fundamental for evaluating the impacts of land-use change and the effectiveness of ecological restoration. In tropical montane rainforests, soil properties are particularly informative indicators because the interaction among climate, topography, and pedogenesis regulates nutrient availability, soil acidity, exchangeable base cations, and the stability of reactive pools of C, N, and P (Benner et al. 2011; Nottingham et al. 2015). These soil-mediated processes underpin ecosystem functioning and biogeochemical regulation, making soils highly sensitive indicators of environmental change. However, tropical montane forests have been increasingly converted to production-oriented land uses, particularly eucalyptus plantations and pasture. Such transitions increase edge effects and microclimatic exposure in ecosystems strongly dependent on orographic moisture, with direct consequences for nutrient cycling, soil structural integrity, and the persistence of soil organic carbon (SOC) (Powers and Marín-Spiotta 2017; He et al. 2025). Globally, rainforest conversion has been associated with SOC losses of up to 50% in surface soils within approximately 25 years, with particularly pronounced declines in highly weathered tropical environments (Guo and Gifford 2002). These degradation processes often reduce cation exchange capacity (CEC), simplify nutrient cycling pathways, and weaken ecosystem resilience by impairing key soil functions that support productivity, nutrient retention, and long-term biogeochemical stability (Brady and Weil 2008).

SOC is a key regulator of soil functioning because it links litter inputs, microbial transformations, mineralization pathways, and ion-exchange mechanisms (Bhattacharyya et al. 2022). In tropical soils, SOC persistence is strongly influenced by interactions among organic matter inputs, mineralogy, organo-mineral associations, aggregate protection, and broader ecosystem controls (Oades 1988; Schmidt et al. 2011; Han et al. 2024). These mechanisms enhance nutrient retention and contribute to the maintenance of ecosystem functions even under conditions of rapid organic matter turnover (Li et al. 2024). Because SOC directly influences exchange surfaces and nutrient availability, it is closely associated with CEC, a widely used indicator of nutrient retention capacity and soil functioning. Together, these attributes integrate key processes associated with ecosystem recovery and resilience following disturbance.

In the montane remnants of the Atlantic Forest within the Brazilian Serra do Mar, soils are typically deep and enriched in reactive minerals, particularly Fe and Al oxides (Schaefer et al. 2023), which promote organo-mineral associations and long-term SOC stabilization (Torn et al. 1997; Shi et al. 2024; Totti et al. 2025). These mechanisms contribute to the maintenance of essential ecosystem functions, including nutrient retention, hydrological regulation, and carbon sequestration. Despite this intrinsic stabilization capacity, these soils are highly sensitive to anthropogenic disturbance and land-use change, exhibiting rapid declines in organic matter stability and soil functional integrity (Gomes et al. 2019; Guerrini et al. 2024). The expansion of pasture and homogeneous silviculture has intensified landscape fragmentation and altered soil dynamics (Ahirwal et al. 2021; Gómez et al. 2024), contributing to reductions in microbial biomass, aggregate stability, and nutrient retention, while accelerating carbon and nutrient losses through erosion and leaching (Bruijnzeel 2004; Broggio et al. 2024; Zeferino et al. 2023; Fachin and Thomaz 2025).

Conversely, forest restoration can promote the gradual recovery of soil functions through the reestablishment of organic matter inputs, nutrient cycling, and biogeochemical processes (Yang et al. 2025; Zhou et al. 2025). Naturally regenerating secondary forests frequently exhibit progressive increases in SOC retention and nitrogen accumulation along successional trajectories (Yu et al. 2023; Satdichanh et al. 2023). Likewise, reforestation and some silvopastoral systems have been associated with improvements in soil functioning and ecosystem recovery (Crouzeilles et al. 2017; Oliveira et al. 2024). Evidence from tropical forests indicates that restoration can increase SOC, total N, and CEC over time, although recovery trajectories remain strongly influenced by previous land use, management intensity, and environmental conditions (Mendoza-Vega et al. 2020; Fachin et al. 2021; Sniegocki et al. 2022).

Secondary forests and plantations generally accumulate less SOC than mature forests but may enhance stabilization of remaining carbon through changes in organic matter quality and organo-mineral protection (Don et al. 2010). Increasing plant diversity and belowground biomass can stimulate organic matter reactivation and restructure exchangeable ions, reinforcing soil functional integrity (Lange et al. 2015). Consequently, the balance among carbon losses, stabilization, and reactivation depends on restoration pathway, land-use legacy, and management intensity, generating distinct trajectories of soil functional recovery across tropical landscapes.

Despite growing evidence of ecosystem recovery following restoration, relatively little is known about which soil indicators can reliably diagnose functional recovery and resilience across contrasting restoration pathways in highly weathered tropical montane ecosystems. Most studies have focused on describing changes in individual soil attributes, whereas the identification and validation of indicators capable of integrating ecosystem responses to degradation and restoration remain limited (Doetterl et al. 2015). Because soil functional recovery emerges from the interaction among organic matter accumulation, nutrient retention, and biogeochemical cycling, indicators that integrate these processes may provide a more robust assessment of restoration outcomes than isolated fertility variables. Indicator-based approaches are increasingly required to evaluate restoration effectiveness, monitor ecosystem trajectories, and support evidence-based management and conservation decisions.

In the Atlantic Forest, conserved systems generally exhibit higher SOC, nutrient availability, and CEC than degraded land uses, reflecting stronger nutrient retention and more efficient ecosystem functioning (Zhao et al. 2023; Guerrini et al. 2024). These attributes are closely linked to ecosystem resilience because they regulate nutrient storage, exchange processes, and the maintenance of soil functions under environmental change, integrating organic matter dynamics with nutrient-retention capacity. However, their effectiveness as indicators for distinguishing alternative restoration trajectories in tropical montane landscapes has yet to be evaluated.

We hypothesized that the high production and accumulation of organic matter and soil organic carbon (SOC) along contrasting restoration pathways in tropical montane Atlantic Forest soils promote distinct trajectories of chemical recovery by influencing nutrient retention and cycling processes. In this context,

specific soil chemical attributes would provide more sensitive indicators of ecosystem recovery and chemical resilience than conventional fertility metrics such as pH and exchangeable base cations. Furthermore, we expected these responses to vary with soil depth, reflecting the vertical reorganization of soil functioning during restoration. Although based on a single case study, our objective was not to characterize regional soil conditions, but rather to evaluate whether SOC and CEC consistently emerge as integrative indicators of chemical resilience across contrasting restoration trajectories.

Accordingly, the objectives of this study were to: (i) identify the soil chemical indicators that best discriminate contrasting functional recovery trajectories across land-use and restoration pathways in a tropical montane Atlantic Forest landscape; (ii) evaluate the relative importance of SOC, CEC, soil acidity, and nutrient availability as indicators of soil functional recovery and resilience; and (iii) assess whether the diagnostic capacity of these indicators remains consistent throughout the soil profile or exhibits depth-dependent patterns of recovery.

In this preliminary assessment, we integrated indicators of soil acidity, mineral reactivity, C/N balance, and carbon and nutrient stocks across contrasting land-use and restoration pathways in a tropical montane Atlantic Forest landscape to evaluate how ecosystem recovery influences soil chemical functioning, nutrient cycling, and the development of chemical resilience.

2 Material and Methods

2.1 Study area

The experimental area is located in the municipality of Nova Friburgo (Fig. 1), in the upper reaches of the Boa Vista watershed, within the boundaries of the Macaé de Cima State Environmental Protection Area (APAMC). The site lies at a mean elevation of approximately 1,055 m a.s.l., at 22°19'08"S and 42°16'59"W, on a northwest-facing slope positioned in the upper portion of an interfluve in the Serra do Mar mountain range, locally referred to as Serra de Macaé de Cima, in the Lumiar district, Rio de Janeiro State, Brazil.

The regional climate is classified as Tropical Highland, with mean annual precipitation reaching up to 2,450 mm, largely concentrated during the austral summer (December-February) (Köppen 1948). Orographic effects combined with steep topography promote persistent atmospheric moisture and support a highly diverse Dense Ombrophilous Atlantic Forest.

Currently, the high-elevation ridges of the Serra do Mar are predominantly covered by secondary Atlantic Forest fragments, a pattern strongly influenced by the establishment of protected areas such as the Serra dos Órgãos National Park (PARNASO) and the Macaé de Cima Environmental Protection Area (APAMC) (Portes et al. 2020). The regional forest structure is characterized by a relatively closed canopy and a high abundance of ferns and palms, particularly species of the genus *Euterpe* (Fantini and Guries 2007).

The landscape has steep slopes and narrow valleys developed over clastic deposits (Marçal et al. 2015). Geomorphological dynamics are primarily driven by hillslope processes, bedrock incision, and fluvial reworking of coarse debris (Marçal et al. 2017). The dominant soils in the study area (Table 1) are low-fertility Oxisols, Inceptisols, and Entisols (corresponding to Ferralsols, Cambisols, and Leptosols in the WRB system), developed over Precambrian granites and gneisses of the São Fidélis geological unit (Tupinambá et al. 2013; Schaefer et al. 2023). In the study area, the C horizon typically occurs between 60 and 80 cm depth, however, in some locations soils reach up to 1.5 m and overlie Holocene colluvial deposits containing buried organic-rich horizons and charcoal fragments, recording recurrent fire activity, hillslope remobilization, and long-term carbon accumulation (Facadio et al. 2024; Ishimine et al. 2024).

2.2 Experimental design

Despite advances in experimental approaches, methodological constraints still limit the reproducibility of soil process studies (Costa et al. 2025). Here, two experimental sites with four vegetation types representing contrasting land covers were evaluated, including four secondary restoration forests (~ 40 years old) (Fig. 2): (2) interior secondary forest (ISF), (2) edge secondary forest (ESF), (2) eucalyptus plantation (~ 16 years old), and (2) pasture (~ 40 years old). All sites share a common land-use history involving slash-and-burn practices over the past century. The experimental areas are located adjacently on convex hillslopes (20% gradient). Each plot (~ 1 ha) is positioned at the base of a rocky escarpment in the upper interfluve, under well-drained conditions.

Edge secondary forest (ESF) has a smaller basal area (28.9 m^2 ha^{-1}) and stem density (2,366.7 individuals ha^{-1}), but higher surface coarse woody debris stocks (30.64 m^3 ha^{-1}). The dominance of pioneer and early secondary species reflects strong wind exposure, increased mechanical mortality, reduced root anchorage, and constraints on successional recovery. In contrast, the interior secondary forests (ISF) showed higher basal area (34.5 m^2 ha^{-1}) and mean stem density (3,150 individuals ha^{-1}), with a predominance of late secondary and climax species, characterizing a structurally more stable system, more resistant to disturbance, and representative of a locally advanced successional stage (Coelho-Netto 2026).

Table 1
Soils Characteristics B-Horizon. (20–50 cm)

Soil parameter	ISF	ESF	Eucalyptus	Pasture
Clay (g kg^{-1})	32	31	24	30
Silt (g kg^{-1})	13	18	21	21
Sand (g kg^{-1})	55	51	55	49
Organic matter[2] (g kg^{-1})	17.7	22.2	17.2	16.0
Soil type	Inceptisols	Inceptisols	Inceptisols	Inceptisols

[2]Walkley and Black (1934). (n = 10). ISF - interior secondary forests; ESF -edge secondary forest.

To ensure comparability among sampling points despite this heterogeneity, soil sampling was standardized to a maximum depth of 60 cm. In each land-use type, soil samples were collected using a hand auger at 10 randomly distributed points along the slope. Samples were obtained at six depth intervals: 0–10, 10–20, 20–30, 30–40, 40–50, and 50–60 cm.

The following chemical properties were determined: soil organic carbon, total nitrogen, pH, available phosphorus, exchangeable potassium, calcium, magnesium, aluminum, and cation exchange capacity (CEC). Soil chemical analyses were conducted using standard procedures. Soil pH was measured in $CaCl_2$ solution. Available phosphorus was extracted using the Mehlich-1 solution (0.05 mol L^{-1} HCl + 0.0125 mol L^{-1} H_2SO_4) (Mehlich 1953). Exchangeable potassium was quantified by flame photometry, while calcium, magnesium, and aluminum were extracted with 1 mol L^{-1} KCl. Cation exchange capacity was determined using the KCl-N method. All chemical analyses followed Brazilian standardized protocols aligned with internationally recognized soil analytical procedures (Embrapa 1997).

For complementary physical characterization, sand content in each plot was determined after chemical dispersion with 1 mol L^{-1} NaOH and sieving through a 2 mm mesh (Day 1965). Soil organic matter content (g kg^{-1}) was quantified using the Walkley and Black wet oxidation method (Walkley and Black 1934).

2.3 Statistical analyses

For each land-use type (n = 10 per area), soil chemical variables were evaluated at six depth intervals (0–10, 10–20, 20–30, 30–40, 40–50, and 50–60 cm). Data distributions were tested for normality, and transformations were applied when necessary to reduce skewness and stabilize variance. Soil depth intervals were not subjected to inferential statistical comparisons because they represent a continuous vertical gradient within the same pedological profile and are therefore characterized by structural dependence and spatial autocorrelation. Consequently, depth layers were not considered independent

experimental units. Analyses of soil depth focused on describing the vertical distribution of soil properties and interpreting observed patterns in terms of pedogenetic processes and ecosystem functioning. For comparisons among land-use types, profile-level values integrating all depth intervals were calculated and subsequently analyzed using one-way analysis of variance (ANOVA), these comparisons should be interpreted as differences among land-use conditions within a controlled hillslope system rather than as replicated treatment effects. To identify the variables explaining the greatest proportion of variability in the dataset and to evaluate the influence of vegetation cover on soil properties, Principal Component Analysis (PCA) was performed. Pearson's correlation analysis was used to quantify the strength and direction of linear relationships among selected variables. Finally, hierarchical cluster analysis using Ward's linkage method was applied to assess similarity patterns among variables and spatial variation in soil chemical properties within each land-use type. The results were visualized using dendrograms (McGarigal et al. 2000).

4 Results

4.1 Litter production

Litter stocks varied markedly among land-use types at the summit of the Serra do Mar. The interior secondary forests (ISF) exhibited the highest litter accumulation (986 g m^{-2}), exceeding ESF by 14.1%, eucalyptus plantations by 5.7%, and pasture by a factor of 25. In the restoration forests, litter inputs were structurally heterogeneous, consisting of leaves, branches, fruits, seeds, and miscellaneous organic residues. In contrast, eucalyptus stands were characterized by a more homogeneous litter layer, composed predominantly of sclerophyllous leaves with slower decomposition rates. Pasture systems, in turn, produced litter largely derived from grass residues, typically associated with rapid decomposition and lower carbon content.

These contrasts underscore the role of forested systems in maintaining continuous organic inputs and protecting the soil surface layer (0–20 cm). Litter accumulation in the interior secondary forests was up to 25 times greater than in pasture areas, highlighting the importance of vegetation structure and successional stage in regulating organic matter inputs and soil cover.

4.2 Soil acidity and cation exchange capacity

Soil acidity varied substantially among land-use types and along the soil profile. Mean pH values in the interior secondary forests (ISF) were approximately 10–15% lower than those observed in eucalyptus and pasture systems, with the largest differences occurring in the upper 10 cm, where pH was roughly 15% lower than in pasture. At greater depths, pH increased in ISF, reaching values that were 14% higher at 50–60 cm than at 0–10 cm. In contrast, pH variation with depth under other land uses was limited to less than 5% (Fig. 3).

Exchangeable aluminum concentrations were higher in forested systems (ISF and ESF) than in eucalyptus and pasture. In the top 10 cm, aluminum levels were approximately 50% greater in forest

soils relative to eucalyptus and pasture. Concentrations declined and stabilized with depth, decreasing by about 33% between 10 and 20 cm in forest soils, whereas little variation was observed in eucalyptus and pasture systems. The edge-influenced forests (ESF) maintained aluminum concentrations approximately 50% higher than the other land uses down to 40 cm (Fig. 3).

Cation exchange capacity (CEC) exhibited marked contrasts among systems. In the 0–10 cm layer, ESF displayed CEC values 60% higher than those of pasture and 45% higher than those of eucalyptus, while ISF exceeded pasture by 40%. Along the profile, CEC declined by approximately 50% in ISF between 10 and 60 cm, whereas ESF showed a more moderate reduction of 31%. Eucalyptus and pasture maintained consistently lower CEC values, remaining 20–30% below ESF throughout the profile (Fig. 3). Overall, soils were acidic and characterized by high Al^{3+} concentrations across all land-use types. Pasture soils exhibited the highest pH values, whereas the advanced secondary forests (ESF) showed the highest CEC (Fig. 4).

4.3 Soil organic carbon-nitrogen relationship and available ions

The relationship between soil organic carbon and nitrogen varied significantly among land uses and along the soil profile. In the upper 10 cm, ESF exhibited the highest concentrations, with carbon and nitrogen values approximately 14% and 19% greater, respectively, than those in ISF. Eucalyptus showed reductions of 25% in carbon and 31% in nitrogen relative to ISF, while pasture displayed decreases of approximately 10% in carbon and 53% in nitrogen (Fig. 3).

With increasing depth, carbon concentrations declined more sharply in ISF, decreasing by approximately 76% between 10 and 60 cm, whereas ESF showed a more moderate reduction of 42%. Eucalyptus and pasture exhibited intermediate declines, ranging from 56% to 63%. This pattern suggests differences in carbon accumulation and vertical distribution among land uses, potentially reflecting variation in residue inputs and decomposition dynamics (Fig. 3).

Nitrogen followed a broadly similar trend, with reductions of 31% in ISF and 34% in ESF between layers 10 and 60 cm. However, declines were more pronounced in pastures (53%), whereas eucalyptus exhibited only a 9% reduction, maintaining relatively stable nitrogen levels at depth despite lower initial concentrations (Fig. 3).

C/N ratios revealed contrasting patterns among land uses. ESF maintained higher carbon and nitrogen concentrations in surface layers, whereas ISF exhibited a steeper vertical gradient. Eucalyptus and pasture showed lower surface values, although eucalyptus retained nitrogen more uniformly throughout the profile. These patterns indicate differences in organic matter renewal and nutrient cycling, with implications for soil fertility.

Macronutrients (Ca, Mg, K, and P) exhibited pronounced variation among land-use types and along the soil profile. Calcium concentrations were highest in eucalyptus stands, with soil layer (0–10 cm) values

approximately twofold greater than those in ISF and 36% higher than in pasture. ESF also displayed elevated Ca concentrations, roughly twice those observed in ISF down to 20 cm. Although Ca declined with depth across all systems, eucalyptus consistently maintained concentrations 50–125% higher than ISF throughout the profile.

Eucalyptus showed markedly higher Mg concentrations in the shallow layer (0–30 cm), reaching values four to five times those of ISF. ESF and pastures exhibited intermediate levels, approximately two to threefold higher than ISF in the upper layers. However, differences diminished, and Mg concentrations converged toward low values (0.1–0.2 cmol dm^{-3}) > 30 cm depth.

Potassium concentrations were highest in pasture soils within the top 10 cm, approximately twice those in ISF and about 50% higher than in eucalyptus and ESF. This enrichment was largely confined to the surface layer (0–10 cm), as K declined sharply with depth and converged among land uses in deeper layers.

Phosphorus concentrations were greatest in pastures and ESF soils, with surface layer values approximately 100% higher than ISF and 14% higher than eucalyptus. At depth, ESF maintained relatively elevated P concentrations, reaching values 10% higher than ISF at 60 cm. Eucalyptus displayed relatively consistent P levels throughout the profile, remaining 30–70% above ISF, whereas pastures showed elevated P primarily at the surface layer and at 60 cm.

Across the entire soil profile (0–60 cm), significant differences were observed for pH, CEC, N, Ca, and P (Fig. 4). Soil pH was slightly higher in the Eucalyptus plantation and pastures, exceeding values in ISF by approximately 4% and those in the ESF by 3–4%, whereas ISF and ESF did not differ significantly. Cation exchange capacity (CEC) was highest in ESF, with values approximately 32% greater than those in eucalyptus and 44% greater than those in pastures. ISF exhibited intermediate values (approximately 21% lower than ESF) and did not differ significantly from the other land-use types. Nitrogen concentrations were significantly lower in pasture soils, while ISF, ESF, and eucalyptus showed increases of approximately 83%, 91%, and 57%, respectively, relative to pastures. Exchangeable Ca differed only between eucalyptus and ISF, with concentrations in eucalyptus being approximately 106% higher. Available P was lowest in ISF, whereas eucalyptus and pasture exhibited concentrations approximately 84% and 69% higher, respectively. ESF also showed elevated P levels (approximately 72% higher than ISF) and did not differ significantly from eucalyptus or pastures.

4.4 Multivariate structure of soil chemical gradients

Principal Component Analysis (PCA) revealed a highly structured multivariate pattern, with the first two components explaining 92.9% of total variance (Dim1: 53.4%; Dim2: 39.5%). The ordination identified two dominant and functionally contrasting soil gradients. Dim1 represented a chemical fertility gradient, strongly associated with base cations (Ca^{2+}, Mg^{2+}, K^{+}), available P, and soil pH. Positive scores along this axis reflect higher base saturation and surface nutrient enrichment.

Dim2 captured an organic–colloidal retention gradient, primarily driven by soil organic carbon (SOC), total nitrogen, cation exchange capacity (CEC), and exchangeable Al. Negative scores along this axis indicate greater organic matter accumulation and enhanced variable charge development. Land-use systems were clearly segregated along these functional axes. Pastures occupied the positive region of Dim1, closely associated with higher pH and potassium availability, reflecting surface fertility concentration. Eucalyptus aligned with calcium and phosphorus, also positioned within the fertility domain.

In contrast, restored forests diverged along Dim2. ESF clustered strongly within the organic–colloidal retention domain, closely associated with SOC, nitrogen, CEC, and exchangeable Al. ISF occupied a more isolated position, exhibiting lower overall chemical fertility while maintaining a moderate association with organic variables. Overall, the ordination demonstrates a structural dissociation between immediate chemical fertility and long-term chemical retention capacity, distinguishing anthropogenic systems from restoration trajectories.

Dim1 represents a chemical fertility gradient associated with base cations and pH, whereas Dim2 reflects an organic–colloidal retention gradient driven by SOC, nitrogen, CEC, and exchangeable aluminum. The ordination highlights the functional divergence between anthropogenic systems (pasture and eucalyptus) and restoration trajectories (ISF and ESF), particularly the strong association of ESF with enhanced organic matter accumulation and nutrient retention capacity.

The Pearson correlation matrix (Fig. 6) highlights a strong clustering among exchangeable base cations. Phosphorus, potassium, and calcium were highly correlated ($r \geq 0.93$, $p < 0.05$), while magnesium showed consistent positive associations with these elements ($r = 0.72–0.88$, $p < 0.05$). Soil organic carbon (SOC) exhibited a very strong correlation with cation exchange capacity (CEC) ($r = 0.97$, $p < 0.05$), indicating the central role of organic matter in charge development. Aluminum was also positively correlated with CEC ($r = 0.71$, $p < 0.05$).

In contrast, soil pH showed a divergent pattern. It was positively associated with potassium and calcium ($r = 0.79–0.87$, $p < 0.05$), but negatively correlated with nitrogen, SOC, and CEC ($r = -0.61$ to -0.82, $p < 0.05$). Nitrogen, in turn, was positively related to SOC and CEC ($r = 0.61–0.77$, $p < 0.05$) and negatively associated with phosphorus and potassium ($r = -0.55$, $p < 0.05$). Additional moderate correlations were observed between magnesium and aluminum ($r = 0.60$, $p < 0.05$) and between SOC and aluminum ($r = 0.68$, $p < 0.05$).

Overall, these results indicate a clear co-variation among exchangeable bases and a contrasting relationship between pH and variables associated with organic matter and exchange capacity, suggesting that nutrient availability and retention in these soils are jointly regulated by base saturation and organic matter-driven charge dynamics.

The hierarchical clustering dendrogram (Fig. 7) revealed clear differentiation among land-use types. Pastures and eucalyptus formed a common cluster, associated with higher pH, Ca, P, and K values,

reflecting the influence of management practices and potential fertilization inputs. In contrast, ESF constituted a distinct group characterized by elevated nitrogen, soil organic carbon, CEC, and exchangeable aluminum, highlighting the role of organic matter accumulation in restoring soil fertility and CEC.

ISF emerged as the most isolated cluster, exhibiting lower values for most chemical variables, suggesting a slower or more nutrient-constrained regeneration trajectory. These patterns underscore the strong influence of land use on soil chemical attributes and are consistent with the Pearson correlation analysis.

5 Discussion

5.1 Soil organic carbon and cation exchange capacity emerge as key indicators of chemical resilience

The contrasting land-use and restoration pathways evaluated in this study were associated with distinct patterns of soil chemical organization in this tropical montane Atlantic Forest landscape. Rather than reflecting a single gradient of soil fertility, the results revealed two functionally distinct groups of indicators. The first was associated with short-term nutrient availability and base enrichment, represented primarily by pH, Ca, K, and P. The second was associated with long-term nutrient retention and chemical resilience, represented by SOC, CEC, N, and exchangeable Al. This distinction is particularly relevant in highly weathered tropical soils, where ecosystem recovery may not be adequately captured by conventional fertility metrics alone (Guerrini et al. 2024; Medeiros et al. 2025).

The multivariate analyses consistently supported this interpretation. PCA separated a fertility-related axis dominated by base cations and pH from an organic–colloidal retention axis dominated by SOC, CEC, N, and Al. Similarly, cluster analysis differentiated restored forests from eucalyptus and pasture systems and revealed distinct indicator profiles within the restored systems themselves. Together, these results suggest that restoration-associated soil recovery involves not only changes in nutrient availability but also the reorganization of nutrient-retention mechanisms mediated by soil organic matter. In this context, ESF was not positioned as an intermediate condition between forest and anthropogenic land uses, but as a chemically distinct system associated with enhanced charge development and nutrient retention.

The correlation structure further highlighted the existence of contrasting chemical domains. Negative correlations between pH and SOC, N, and CEC indicate that higher acidity was not necessarily associated with poorer soil functioning, but rather with stronger expression of variable-charge processes in organic matter-rich soils (Uehara and Gillman 1981; Sposito 2008). Conversely, the strong positive relationship between SOC and CEC confirms the central role of organic matter in sustaining exchange capacity in highly weathered tropical soils (Brady and Weil 2008; Qafoku et al. 2004). The negative relationship between N and P further suggests a trade-off between nutrient retention and nutrient

availability, reinforcing the functional distinction between immediate fertility and long-term chemical resilience (Lal 2004; Vitousek et al. 2010).

Among all evaluated relationships, the exceptionally strong SOC–CEC coupling ($r = 0.97$, $p < 0.05$) emerged as the clearest indicator of chemical resilience. This finding suggests that restoration-driven soil recovery was more strongly associated with organic matter accumulation and nutrient-retention capacity than with increases in pH or exchangeable base cations. Consistent with Zhao et al. (2021), SOC appears to function not only as a carbon reservoir but also as a key regulator of nutrient transformation and soil fertility.

Likewise, the positive association between Al^{3+} and CEC ($r = 0.71$, $p < 0.05$) suggests that part of the exchange complex may be associated with organo-aluminum interactions, whereas the negative relationship between pH and CEC ($r = -0.68$, $p < 0.05$) indicates that greater acidity may coexist with greater nutrient-retention potential in these variable-charge systems (Uehara and Gillman 1981; Sposito 2008). Together, these results challenge the conventional assumption that increases in pH necessarily represent improved soil functioning in highly weathered tropical environments.

The restored forest systems exhibited contrasting but complementary recovery trajectories. ISF showed higher litter accumulation and a steeper decline of SOC and N with depth, indicating strong nutrient concentration and cycling in surface horizons. In contrast, ESF exhibited higher surface CEC and greater concentrations of C and N, together with a smaller proportional decline in SOC throughout the profile. The persistence of SOC and CEC throughout the soil profile indicates that ESF followed a distinct pathway of chemical reorganization rather than a transitional stage between forest and anthropogenic systems. This pattern likely reflects greater structural dynamism associated with coarse woody debris accumulation, canopy openness, and pioneer species dominance (Lange et al. 2015; Satdichanh et al. 2023). Elevated N concentrations further suggest progressive recovery of nutrient pools during revegetation (Omidvar et al. 2021).

By contrast, eucalyptus and pasture exhibited lower SOC stocks and reduced CEC despite higher pH values and localized enrichment in exchangeable bases. Elevated Ca and Mg concentrations in eucalyptus, likely associated with nutrient return through litterfall, did not translate into greater exchange capacity (Laclau et al. 2003). Similarly, pasture soils showed surface K enrichment but lower N concentrations and weaker vertical incorporation of organic residues. These patterns indicate that higher base availability does not necessarily correspond to greater chemical resilience and are consistent with reductions in charge-retention capacity and buffering commonly reported after forest conversion (Lal 2004; Guo and Gifford 2002).

The vertical distribution of indicators further supports the hypothesis that recovery responses vary with soil depth. In restored systems, SOC, CEC, and exchangeable Al declined gradually throughout the profile, indicating that organic matter remains a major regulator of colloidal reactivity and nutrient retention (Judson et al. 2024; Totti et al. 2025). Elevated surface concentrations of C and N suggest stronger organo-mineral protection mechanisms (Guerrini et al. 2024; Han et al. 2024), while relatively stable C/N

ratios indicate a balance between organic inputs and decomposition characteristic of functionally reorganizing ecosystems (Ahirwal et al. 2021; Bhattacharyya et al. 2022). In contrast, the greater vertical homogenization of pH and reduced CEC variability observed in anthropogenic systems suggest simplification of soil chemical functioning.

These patterns must also be interpreted within the geomorphic context of steep tropical mountain landscapes, where topography influences organic matter redistribution, drainage pathways, and hydrological connectivity (Jandl et al. 2019). Forest conversion can intensify erosion and SOC depletion, reducing chemical resilience (Fachin et al. 2024), whereas restoration-associated vegetation cover and litter inputs favor carbon retention and the recovery of soil functions (Yang et al. 2025; Guerrini et al. 2024).

5.2 Assessing restoration success through indicators of nutrient retention and soil functioning

The results indicate that contrasting restoration pathways can produce distinct expressions of soil chemical resilience even within the same landscape and under a shared land-use history. In particular, the divergence between ISF and ESF demonstrates that secondary forests do not necessarily converge toward a single functional state during recovery. Long-term monitoring of Atlantic Forest succession has shown that land-use legacies can generate asymmetric recovery trajectories, promoting different patterns of biomass accumulation, species turnover, and ecosystem functioning (Verly et al. 2026). In the present study, these differences were reflected in the soil indicator profiles. ISF was associated with a more conservative pathway characterized by stronger SOC and N accumulation, whereas ESF exhibited a more dynamic configuration associated with higher CEC and greater nutrient-retention capacity.

The differentiation between ISF and ESF is particularly relevant because edge-influenced forests are commonly interpreted as degraded or transitional environments. However, the indicator-based approach adopted here suggests a more complex interpretation. The strong expression of SOC-, N-, and CEC-related responses in ESF indicates that edge forests may function as active zones of biogeochemical reorganization rather than simply representing intermediate states between conserved forests and anthropogenic systems. Structural characteristics such as greater coarse woody debris stocks, canopy heterogeneity, and the contribution of pioneer species may contribute to enhanced organic matter turnover and nutrient redistribution (Lange et al. 2015; Satdichanh et al. 2023), generating soil conditions associated with high nutrient-retention capacity.

The comparison with eucalyptus plantations and pasture further highlights the limitations of conventional fertility metrics for assessing restoration outcomes. Both systems exhibited localized enrichment in exchangeable bases, yet neither showed the same expression of resilience-related indicators observed in restored forests. Elevated concentrations of Ca^{2+} and Mg^{2+} in eucalyptus stands likely reflect nutrient recycling through litterfall (Laclau et al. 2003), whereas surface K enrichment in pasture is consistent with rapid herbaceous biomass turnover (Jobbágy and Jackson 2001). However, these responses were not accompanied by equivalent increases in indicators associated with long-term

nutrient retention. Consequently, assessments based solely on pH or exchangeable base cations may overestimate recovery status in highly weathered tropical soils (Sposito 2008; Lima et al. 2022; Oliveira et al. 2024).

SOC and CEC are directly linked to nutrient retention, carbon stabilization, and the maintenance of exchange sites, they capture dimensions of soil functioning that are not reflected by short-term changes in nutrient availability. This distinction is particularly important in tropical montane environments, where steep slopes, intense rainfall, and highly weathered soils increase the vulnerability of nutrient pools and organic matter stocks (Jandl et al. 2019; Chadwick et al. 1999; Lin 2010; Uhlemann et al. 2024). Under these conditions, restoration success depends not only on restoring nutrient availability but also on rebuilding the mechanisms that sustain nutrient retention over time.

The practical implications are clear. Restoration strategies that promote continuous organic matter inputs, litter accumulation, vegetation structural complexity, and coarse woody debris retention are likely to strengthen soil chemical resilience and improve long-term ecosystem functioning (Wardle et al. 2004; Chazdon 2014). In contrast, simplified systems dominated by monocultures or herbaceous cover may maintain localized fertility while remaining functionally limited in terms of nutrient retention and resilience (Rocha Junior et al. 2020; Fachin et al. 2019). Consequently, monitoring programs in tropical montane landscapes should prioritize indicators capable of capturing these long-term functional attributes rather than relying exclusively on traditional fertility metrics.

Although this study represents a case study within a single, well-constrained hillslope system, it provides one of the first integrated assessments of soil chemical resilience indicators in tropical montane Atlantic Forest soils. By minimizing variability associated with climate, geology, topography, and land-use history, the study was able to isolate restoration-related patterns and identify strong and consistent linkages between SOC, CEC, nutrient retention, and ecosystem recovery. These findings provide compelling evidence that SOC and CEC are promising indicators of chemical resilience in highly weathered tropical mountain soils and establish an important foundation for future regional-scale validation across the Serra do Mar.

Conclusions

This case study evaluated how contrasting restoration trajectories and anthropogenic land uses are associated with soil chemical indicators in a tropical montane Atlantic Forest ecosystem. Distinct land-use trajectories produced contrasting soil functional states. Rather than converging toward interior secondary forests (ISF) or anthropogenic systems, edge secondary forests (ESF) developed a unique biogeochemical configuration characterized by the highest SOC, N and CEC values.

The strong correlation between SOC and CEC ($r = 0.97$) identified soil organic matter as a key regulator of nutrient retention capacity and chemical resilience. Despite persistent acidity and high exchangeable aluminum levels, restored forests exhibited greater SOC, N, and CEC than eucalyptus plantations and

pastures, indicating that soil functional recovery in this environment can occur independently of increases in pH or reductions in exchangeable aluminum.

These findings suggest that conventional fertility metrics alone may not adequately capture restoration-related changes in highly weathered tropical soils located on the upper slopes of the Brazilian Serra do Mar. Chemical recovery was also depth-dependent, with restoration-related responses concentrated in surface horizons and progressively reorganized throughout the soil profile. This pattern highlights the importance of considering vertical soil variability when assessing recovery trajectories and ecosystem resilience in this environment.

The strong coupling between SOC and CEC across contrasting restoration pathways highlights their potential as practical indicators of soil chemical resilience in tropical montane Atlantic Forest ecosystems. Extending this framework to a wider range of landscapes and soil conditions throughout the Serra do Mar represents a promising next step toward the development of robust indicator-based approaches for evaluating restoration outcomes and long-term ecosystem recovery.

Declarations

Author Contribution

P. A. F.: Conceptualization, Methodology, Investigation, Data curation, Formal analysis, Visualization, Writing – original draft.A. L. C-N.: Conceptualization, Supervision, Funding acquisition, Resources, Project administration, Writing – review & editing.

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Data Availability

The datasets generated and analyzed during the current study are available from the corresponding author upon reasonable request.

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Figures

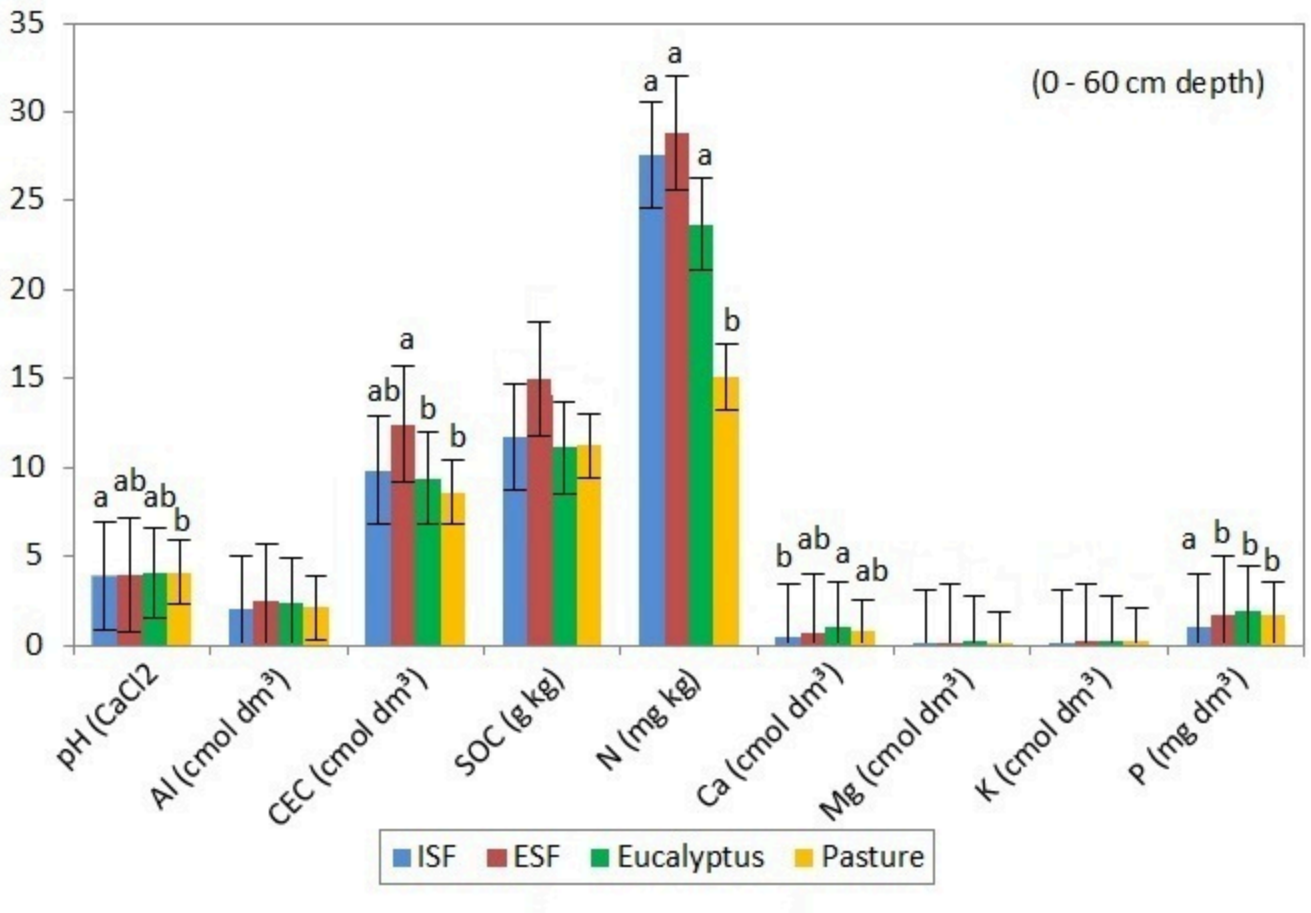


Figure 1

Principal Component Analysis (PCA) of soil chemical properties across contrasting land-use types.

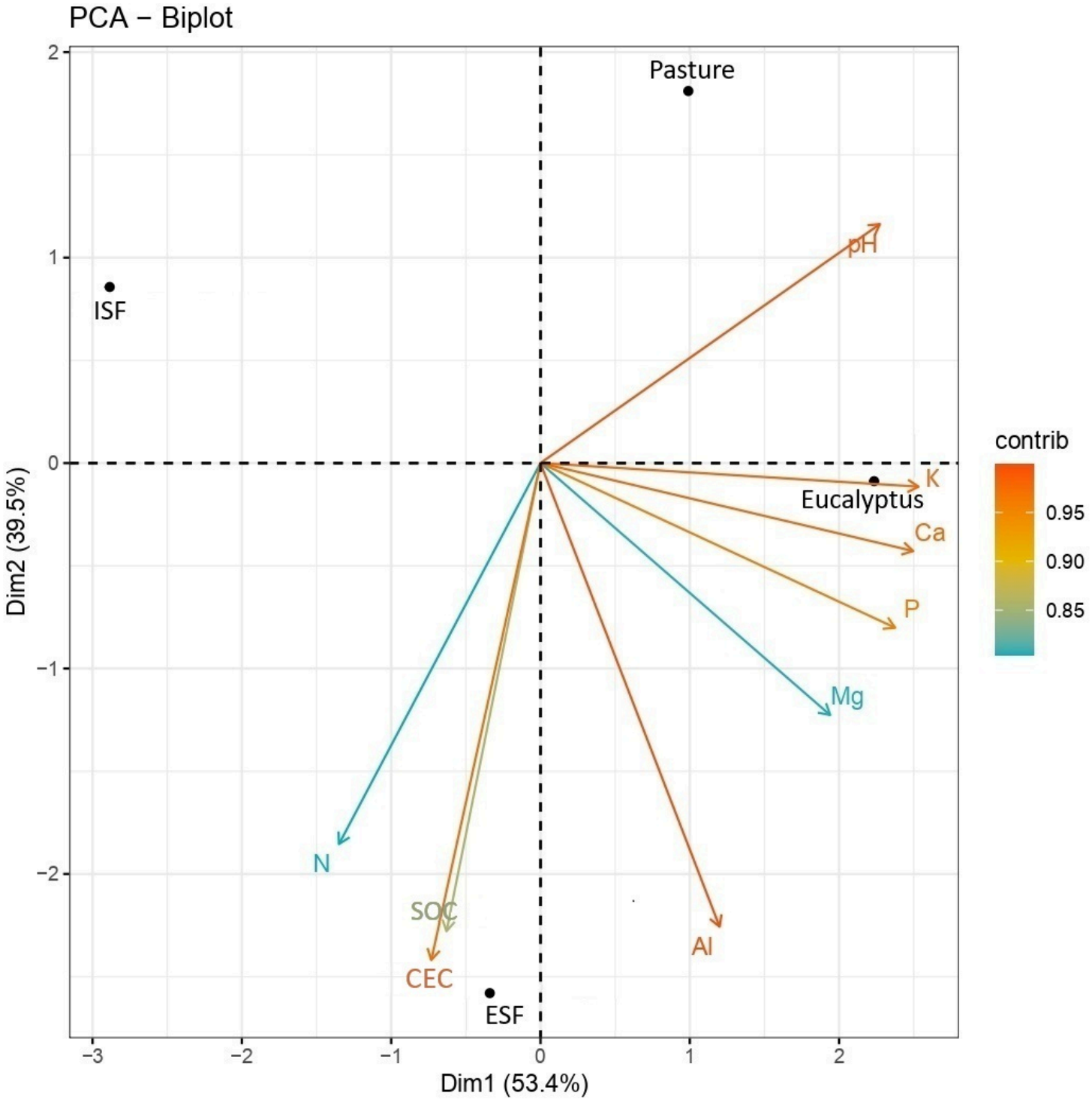


Figure 2

Overall variation in soil chemical properties across land uses over the 0–60 cm soil profile. ISF, interior secondary forests; ESF, edge secondary forests. Results of a one-way ANOVA followed by Tukey's post hoc test assessing the effects of land use on soil chemical properties. Bars represent mean values, and error bars indicate standard deviations. Different letters denote statistically significant differences among land uses at $p \leq 0.05$. Columns sharing the same letter, as well as columns without letter annotations, do not differ significantly.

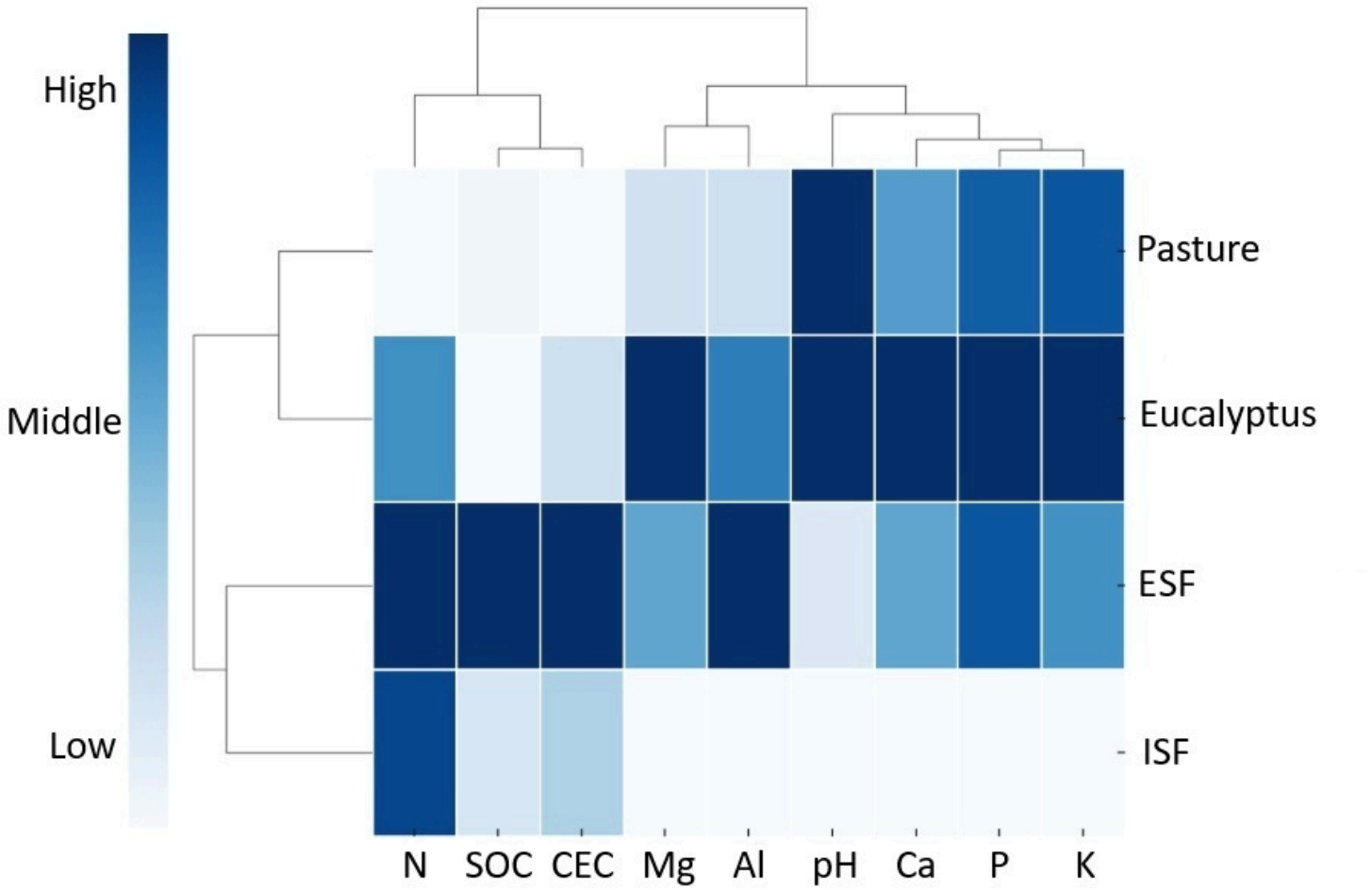


Figure 3

Hierarchical clustering of soil chemical properties and land-use types. ISF - interior secondary forests; ESF -edge secondary forests.

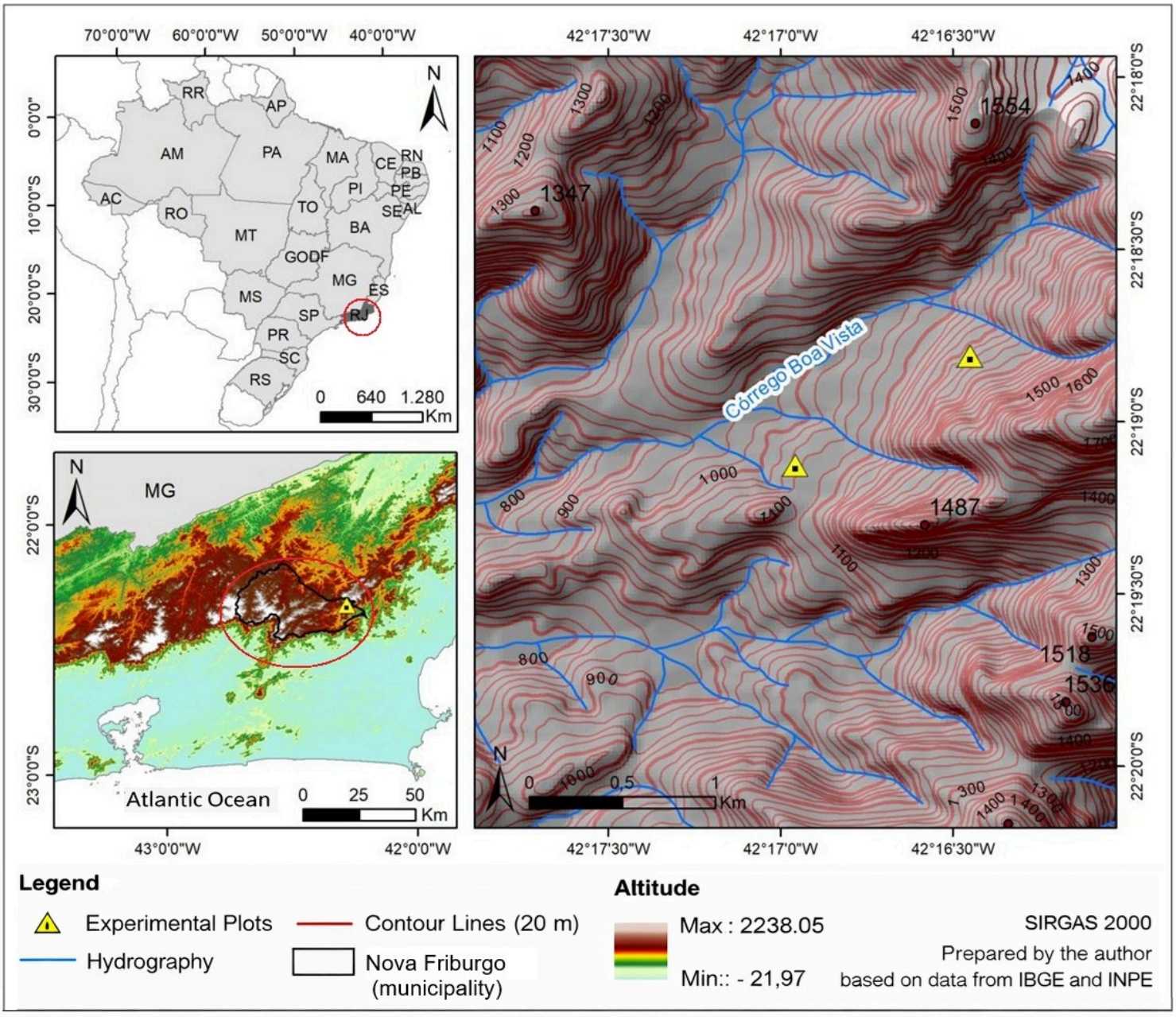


Figure 4

Location of the study areas (Adapted from Mendonça, 2023).

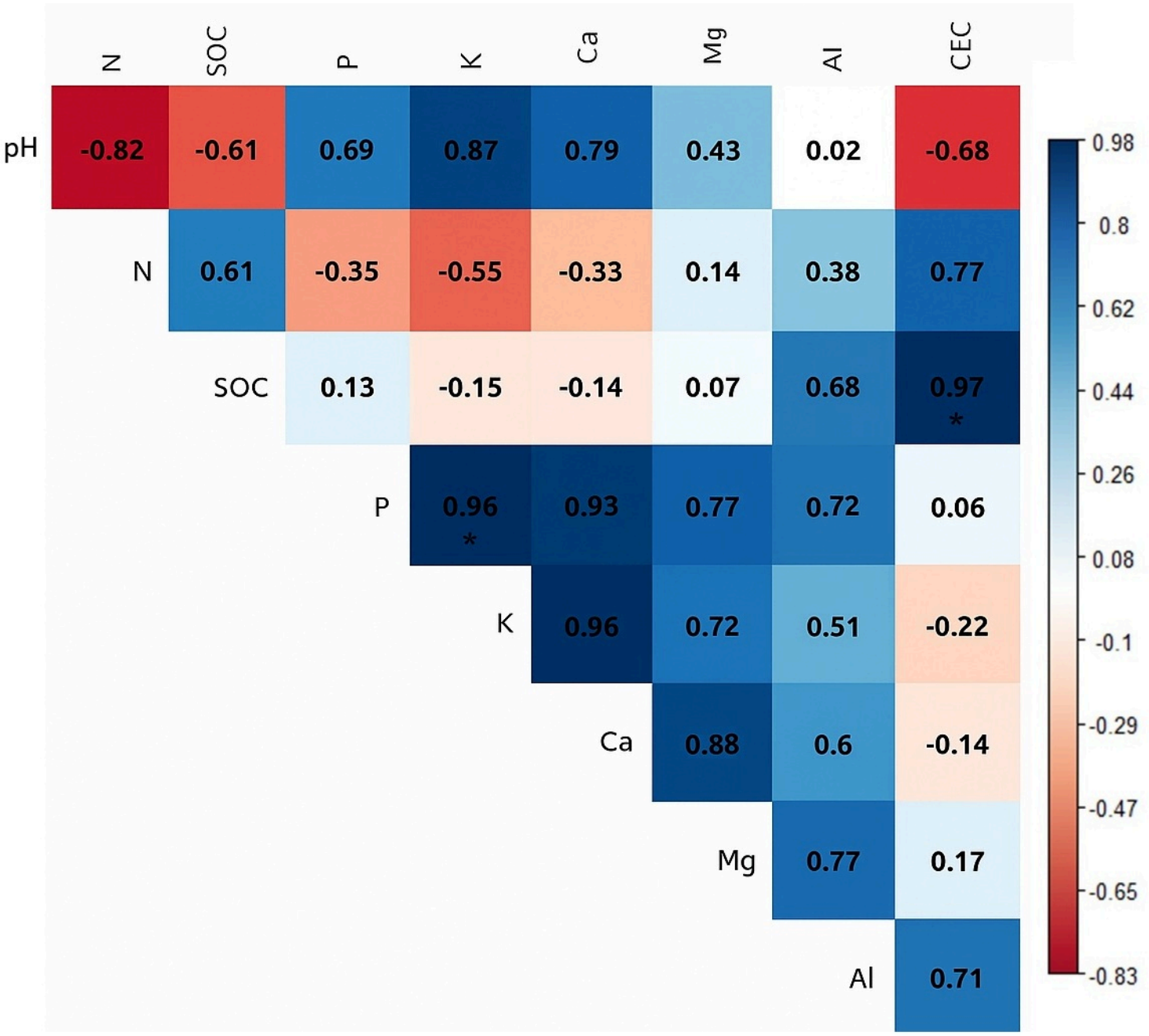


Figure 5

Pearson correlation matrix of soil chemical properties.

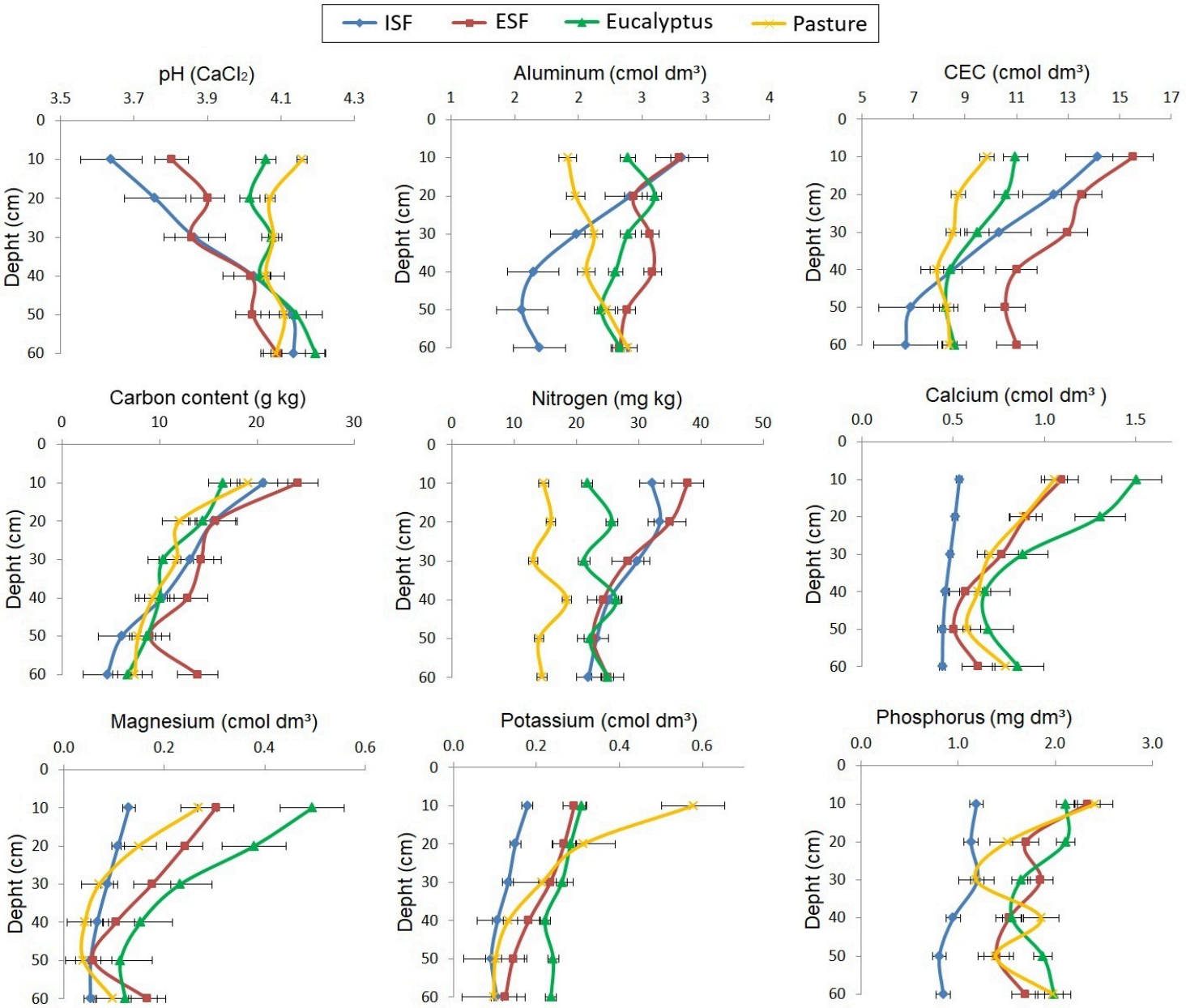


Figure 6

Soil chemical properties across land-use types and soil depths. ISF - interior secondary forests; ESF - edge secondary forests. Mean values for each land-use system.

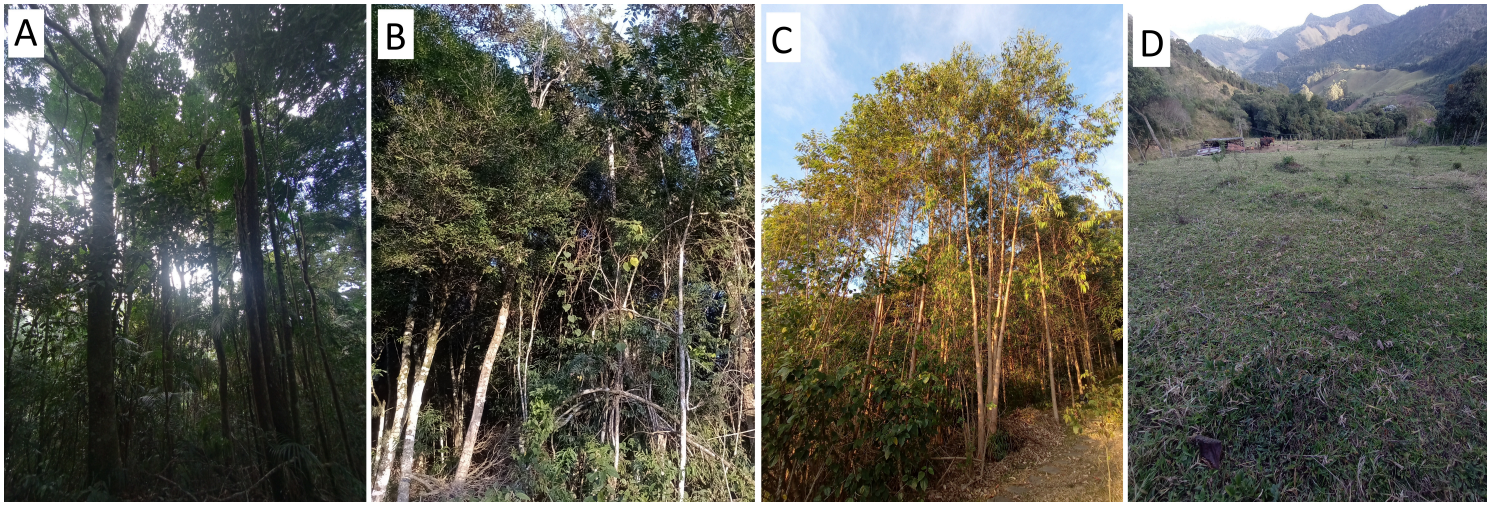


Figure 7

Land-use types: (a) interior secondary forests (ISF); (b) edge secondary forest (ESF); (c) eucalyptus plantation; (d) pasture.