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ORIGINAL ARTICLE

Impact of land conservation status on soil functionality in degraded versus old-growth forest in the Brazilian Atlantic Forest biome

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Abstract

Our aim was to assess the physical and biochemical properties of soil, the chemodiversity of dissolved soil organic matter (SOM), and the arbuscular mycorrhizal fungi (AMF) community associated with *Ocotea porosa* forests in the Brazilian Atlantic Forest biome. We evaluated (i) the physical and biochemical properties of soil using standard protocols, (ii) dissolved SOM chemodiversity and its optical characterization via Fourier-transform ion cyclotron resonance mass spectrometry, and (iii) AMF community structure and root colonization through morphological characterization. The highest values for Ca^{2+}, Mg^{2+}, SOM, S, P, K^{+}, Zn^{2+}, geometric mean diameter, weighted average diameter, microbial C biomass, microbial respiration, total glomalin, root colonization, oxalic and malic acids, carbohydrates, lipids, proteins/amino sugars, biological index, and fluorescence index were observed in the preserved plots. We also found differences in the AMF community associated with land conservation status: (i) *Acaulosporaceae* and *Gigasporaceae* were strongly correlated with the preserved plots. (ii) *Claroideoglomus claroideum*, *Funneliformis mosseae*, and *Rhizophagus intraradices* were more prevalent in the degraded plots. This has the potential to (i) increase soil C sequestration, (ii) mitigate climate change, and (iii) contribute to the preservation of an endangered, century-old tree species in the Atlantic Forest biome.

KEYWORDS
endangered tree species, host-AMF symbiosis, soil dissolved organic matter chemodiversity, soil physical and biochemical properties, subtropical cambisols

Highlights

- Preserved forests of *Ocotea porosa* showed higher levels of SOM, exchangeable cations, and enhanced physical properties than degraded forests.
- Microbial activity, total glomalin, and organic acids were notably higher in preserved forests, indicating more active soil biochemical processes.
- The chemodiversity of dissolved SOM, with significant contributions from carbohydrates, lipids, and proteins/amino sugars, was significantly higher in preserved plots.

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- Preserved and degraded plots exhibited distinct arbuscular mycorrhizal fungal (AMF) communities, with Acaulosporaceae and Gigasporaceae more prevalent in preserved plots, while degraded plots were associated with *Claroideoglomus claroideum*, *Funneliformis mosseae*, and *Rhizophagus intraradices*.

1 | INTRODUCTION

Ocotea porosa, commonly known as Brazilian walnut or "imbuia," is an endangered tree species native to the Brazilian Atlantic Forest biome.[1,2] This species primarily grows in subtropical Cambisols in southern Brazil, particularly in Paraná, Santa Catarina, and Rio Grande do Sul. As a dominant and keystone species, *O. porosa* plays a crucial ecological role by supporting biodiversity, sequestering significant amounts of carbon in its biomass and soil, and influencing soil quality. It is typically found at elevations ranging from 500 to 1500 m, where it contributes to the ecological functions of Araucaria Forests, including timber production, habitat provision, and climate change mitigation.[3–5]

Despite its ecological significance, the Atlantic Forest biome faces intense anthropogenic pressures, such as slash-and-burn agriculture, logging, timber extraction, and invasions by exotic species like *Pinus* spp.[6] While rare old-growth *O. porosa* forests (>250 years old) are primarily confined to permanent conservation areas, degraded or secondary forests are common in marginal zones, abandoned agricultural fields, and forest glades, where they compete for resources with invasive species.[7,8] These disturbances not only threaten the survival of *O. porosa* but also degrade soil quality, which is vital for its establishment and performance.

Previous research has shown that human-induced disturbances can negatively affect soil fertility and structure in subtropical Cambisols.[9,10] However, there is a limited understanding of how land conservation influences key soil parameters in *O. porosa* habitats. Important factors include total glomalin, a protein that promotes soil aggregation [11]; low-molecular-weight organic acids, which play a role in nutrient weathering and exchangeable cations [12]; dissolved soil organic matter (SOM) chemodiversity, which provides insights into labile and recalcitrant carbon pools in the rhizosphere [13]; and the structure of arbuscular mycorrhizal fungi (AMF) communities, which enhance nutrient uptake and stress tolerance.[14] The interactions among these factors and their combined influence on *O. porosa* conservation remain poorly understood.

Most studies have focused on AMF communities associated with other subtropical trees, such as *Araucaria angustifolia* and *Pinus taeda*,[6,14] or on the influence of soil management on dissolved SOM chemodiversity.[15,16] Research has also examined how root activity affects soil's physical and biochemical properties.[17] However, no studies have directly investigated the effects of land conservation on the interplay between soil parameters, AMF communities, and *O. porosa* performance.

This study addresses three key research questions: (1) How does land conservation influence soil physical and biochemical properties, including total glomalin, organic acids, exchangeable cations, and DOM chemodiversity, in *O. porosa* habitats? (2) What is the impact of conservation on AMF community structure, particularly in terms of species abundance, diversity, and root colonization? (3) How do these soil parameters interact with *O. porosa* performance in conserved and degraded forests? We hypothesized that land degradation disrupts soil homeostasis, leading to declines in soil fertility and physical properties. Specifically, degraded forests would exhibit lower microbial activity, organic acids, and total glomalin, as well as reduced AMF diversity and colonization. Conversely, preserved forests would maintain higher levels of these factors, creating a positive feedback loop that enhances soil functionality and supports *O. porosa* conservation.

To test these hypotheses, we conducted a field study comparing preserved (>250 years old) and degraded *O. porosa* forests within the subtropical Atlantic Forest biome. Soil samples were collected from adjacent sites to assess physical and biochemical properties, dissolved SOM chemodiversity, and AMF community structure. This research provides critical insights into the role of land conservation in maintaining soil ecosystem health and highlights its importance for the preservation of *O. porosa*, a species integral to the ecological integrity of the Atlantic Forest biome.

2 | MATERIAL AND METHODS

2.1 | Sites' description and sampling strategies

From January 2021 to December 2023, soil and root samples were collected from two forests with *O. porosa*—one preserved and one degraded—in Catanduvas and Fraiburgo, Santa Catarina, Brazil. The preserved forest, over 250 years old with minimal human activity, contained giant *O. porosa* trees. In contrast, the degraded forest experienced disturbances such as slash-and-burn, logging, timber extraction, cattle grazing, and invasion by Pinus species (Table 1). Catanduvas and Fraiburgo share similar soil and climate conditions: Cambisols and a humid subtropical climate (Cfa-type, according to Köppen's classification).

2.2 | Experimental design

We investigated the impact of degraded and preserved *O. porosa* forests on soil functionality at two sites, Catanduvas and Fraiburgo. Our study analyzed dissolved organic matter chemodiversity, physical and biochemical properties of soil, arbuscular mycorrhizal fungi diversity, and root colonization. We followed three main criteria for sampling: (i) delineating 10 permanent plots (100 × 100 m) with uniform stands in each forest; (ii) sampling soil near 25 trees per plot. We considered a target tree one that has reached reproductive maturity, achieved substantial structural development, and actively fulfilled its ecological role within the ecosystem. The selected trees had an average diameter at breast height ranging from 0.4 to 0.8 m, a height ranging from 13.0 to 18.0 m, and a basal area ranging from 18.0 to 20.0 m^2; and (iii) collecting three soil samples per tree at a depth of 0–20 cm. During the field experiment, soil samples (bulk and

TABLE 1 The main description of the studied sites and land conversation status in subtropical Cambisols in Fraiburgo and Catanduvas, Santa Catarina, Brazil.

	Catanduvas		Fraiburgo	
Characteristics	**Degraded**	**Preserved**	**Degraded**	**Preserved**
	Site characteristics			
Altitude (m.a.s.l.)	962.6 (11.5)	958.7 (23.1)	1040.4 (18.9)	1058.6 (17.2)
Clay (g kg^{-1})	47.4 (7.3)	39.7 (1.5)	39.9 (3.5)	46.8 (3.9)
	Dendrometric characteristics			
DBH (m)	0.6 (0.1)	1.5 (0.2)	0.5 (0.1)	1.2 (0.2)
Tree dominant height (m)	16.9 (0.9)	21.30 (1.3)	18.2 (1.2)	19.3 (2.3)
Trees' density (trees ha^{-1})	425 (32)	858 (15)	321 (8)	911 (23)
Mean basal area (m^2 ha^{-1})	18.3 (0.9)	47.4 (1.8)	21.2 (1.2)	51.3 (0.9)
	Diversity indices			
Species richness	49 (2)	93 (1)	58 (3)	98 (2)
Shannon index	1.54 (0.21)	3.54 (0.80)	1.58 (0.12)	3.61 (0.50)
Simpson index	0.80 (0.09)	0.53 (0.04)	0.83 (0.05)	0.61 (0.02)
Pielou index	0.63 (0.10)	0.90 (0.08)	0.79 (0.09)	0.91 (0.03)
	Relative frequence (%) of species with importance value index (IVI) ≥ 10%			
Araucaria angustifolia	1.2 (0.2)	5.5 (0.3)	2.4 (0.1)	5.8 (0.2)
Aspidosperma polyneuron	-	4.0 (0.5)	1.5 (0.1)	4.8 (0.4)
Cariniana legalis	-	1.2 (0.3)	-	1.8 (0.2)
Cecropia pachystachya	5.4 (0.2)	1.2 (0.1)	6.0 (0.5)	1.9 (0.2)
Croton floribundus	6.0 (0.5)	1.4 (0.2)	5.8 (0.2)	1.2 (0.3)
Dicksonia sellowiana	-	3.5 (0.6)	-	3.0 (0.8)
Eugenia uniflora	-	2.0 (0.2)	1.8 (0.4)	2.0 (0.3)
Ficus organensis	1.0 (0.1)	2.2 (0.2)	-	2.4 (0.1)
Guazuma ulmifolia	3.4 (0.3)	1.4 (0.1)	2.7 (0.2)	1.3 (0.4)
Gymnanthes klotzchiana	-	2.1 (0.2)	-	1.9 (0.2)
Ocotea porosa	4.2 (0.1)	7.8 (0.6)	3.9 (0.3)	8.3 (0.5)
Mimosa scabrella	10.2 (0.8)	-	11.3 (1.2)	-
Schinus terebinthifolia	8.2 (0.2)	-	6.7 (0.5)	-
Trema micrantha	6.7 (0.2)	-	4.5 (0.6)	-

Note: Standard deviation in parentheses.
Abbreviation: DBH = diameter at breast height.

rhizospheric soil) were collected 12 times, in other words, every 90 days from January 2021 to December 2023. We separated bulk from rhizospheric soil using a standardized protocol from Barillot et al.[18] Samples of bulk soil were used for dissolved organic matter and physical characterization, while rhizospheric soil was used for biochemical characterization, AMF community structure, and root colonization.

2.3 | Dissolved organic matter preparation and optical characterization

Soil dissolved organic matter (DOM) was extracted by shaking 60 g of dry soil in 0.1 L of deionized water at 25°C for 24 h. The mixture was then centrifuged and filtered through 0.45 μm polyether sulfone filters. To prevent microbial degradation, the supernatant was sterilized with UV radiation before being stored at 4°C for optical analysis.[19] For optical measurements, 5 mL of supernatant was analyzed using UV-Vis and three-dimensional excitation–emission matrix (3D-EEM) fluorescence spectroscopy (Hitachi F-7000, 0.01 m quartz cuvette). Total dissolved organic carbon was measured following the methods by Kothawala et al. [20] and Ohno.[21] The solution was acidified to pH 2.0 with phosphoric acid. Emission scans were conducted from 250 to 500 nm in 2 nm increments, and excitation scans from 230 to 500 nm in 5 nm increments. Both slit widths were set to 10 nm, with a scan speed of 1200 nm/min.

To evaluate the colored and fluorescent fractions of soil DOM, we employed a range of optical and fluorescence indices. The optical indices included specific ultraviolet absorbance at 254 nm (SUVA254), which indicates DOM aromaticity, and the spectral slope

(S250-600), which provides information on apparent molecular weight.[22] For fluorescence indices, we used the fluorescence index (FI) to determine microbial contributions to DOM, calculating it based on the ratio of emission intensities from 380 to 430 nm and 450–500 nm at excitation wavelengths of 310 and 370 nm.[23] Additionally, the biological index (BI) was used to reflect microbial activity in DOM. This was calculated as the ratio of the peak area under the emission spectra of 435–480 nm to that under 300–345 nm plus 435–480 nm at an excitation wavelength of 254 nm.[24]

2.4 | FT ICR MS analysis

The analysis of soil dissolved organic matter (DOM) samples was performed using a Solarix XR FTICR MS, which features a 9.4-T refrigerated, actively shielded superconducting magnet, and an ESI ion source operating in negative ion mode. For solid-phase extraction, Varian Bond Elut PPL cartridges (1 g per 6 mL) were utilized, followed by rinsing with 6 mL of methanol to ensure consistent sampling concentrations for FT ICR MS analysis. Detection parameters were set with a mass range of m/z 150–1200 Da and an ion accumulation time of 0.7 s. Peaks were identified based on the following criteria: a signal-to-noise ratio of at least 6, elemental compositions of $C \geq 3$, $H \geq 1$, $H/C \leq 2.2$, $N \leq 2$, $O \geq 1$, $O/C \leq 1.2$, and $S \leq 2$.[25–27]

The relative intensity of each molecule was obtained by normalizing the molecular intensity to the sum of all detected intensities in FT ICR MS measurements. The identified compounds were grouped into major categories for VK diagram analysis based on their molecular formulas. These groups were defined by their aromaticity index (AI), H/C, and O/C ratios, including aliphatic compounds ($2.2 \geq H/C \geq 1.5$), combustion-derived condensed aromatics ($AI > 0.66$), highly unsaturated and phenolic compounds ($AI < 0.5$ and $H/C < 1.5$), and vascular plant-derived polyphenolics ($0.66 \geq AI > 0.5$). Further classification of aliphatic compounds included carbohydrates, lipids, and proteins/amino sugars.[28–30]

To determine the molecular characteristics of DOM, double-bond equivalence (DBE) and the nominal oxidation state of carbon (NOSC) were calculated, representing the number of double bonds/rings and the biogeochemical reactivity of molecules, respectively. The relative abundance of each compound group was calculated by summing the relative intensities of all compounds within each group. The averages of AI, O, DBE, H/C, NOSC, and O/C ratios were computed for each sample based on the relative intensity of each molecule.[26,27]

2.5 | Physical and biochemical analysis of soil

To characterize the physical properties of the soil, we examined aggregate characteristics such as the weighted average diameter (WAD, mm) and the geometric mean diameter (GMD, mm).[31] Soil bulk density was measured using a metallic cylinder method,[32] while clay content was determined through particle size analysis as outlined by Teixeira et al.[33] For biochemical characterization, several parameters were analyzed at each sampling point, including total glomalin content [34] and concentrations of oxalic and malic acids, determined following the procedure by Mimmo et al.[35] Microbial biomass carbon was assessed using the fumigation-extraction method, and microbial respiration ($C–CO_2$) was measured through the incubation technique.[36] Soil pH was measured in a soil–water suspension with a 1:2.5 ratio. Available phosphorus was extracted using the Mehlich-1 method and quantified colorimetrically. Exchangeable cations Al^{3+}, Ca^{2+}, and Mg^{2+} were estimated using the potassium chloride extraction method, while $K+$ and Na^{+} were determined using Mehlich-1 extraction.[37] Soil organic carbon (SOC) content was measured by rapid oxidation with potassium dichromate as described by Okalebo et al.[38]

2.6 | AMF community structure and root colonization

To address methodological concerns related to AMF morphological identification, we implemented a multistep approach to ensure accuracy. Fresh AMF spores were first extracted and identified from soil samples collected from the field experiment. The identified AMF community was then inoculated into *O. porosa* plants grown in plastic pots containing autoclaved substrate. After 4 months, the AMF spores were re-extracted and reidentified. This inoculation and reidentification process was repeated three times, with the AMF community reinoculated in each cycle. The final AMF community reported in this study was identified during the last bioassay, ensuring that the spores originated exclusively from the rhizosphere of *O. porosa*. The controlled pot experiment eliminated potential interactions with other species, providing robust and reliable results for both spores and root colonization by AMF. We extracted AMF spores from each soil sample using wet sieving and sucrose centrifugation techniques as outlined by Gerdemann and Nicolson [39] and Jenkins,[40] respectively. The spores were observed in water under a dissecting microscope and then separated based on their morphology. Identification of AMF species was performed using the International Culture Collection of Arbuscular Mycorrhizal Fungi database (http://invam.caf.wvu.edu) with the aid of a microscope. Root colonization by AMF was evaluated by collecting fine roots of *O. porosa* with a diameter of less than 2 mm, which was cleaned, acidified, and colored following the protocol described by Laurindo et al.[6] The assessment of root colonization was conducted using the grid intersection method outlined by McGonigle et al.[41]

2.7 | Statistical analysis

Prior to analysis, all variables were tested for normality and homoscedasticity using the "shapiro.test" and "bartlett" functions, respectively in the "stats" package. We used the analysis of variance (ANOVA) using the "aov" function (in the "stats" package) to compare the influence of land conservation on soil physical and biochemical properties, SOM chemodiversity, and AMF community composition. First, an explanatory ANOVA was performed to explore all data variability among the land conservation, sampling period, and plots on all studied variables. In this explanatory analysis, we considered land conservation ($df = 1$), sampling period ($df = 11$), and plots ($df = 9$), and their interactions as sources of variation in a three-way

ANOVA. Data from sampling points were nested by plots. We did not find any significant differences or dissimilar trends among sampling periods, plots, or their interaction with any of the studied variables. Additionally, repeated measures ANOVA was not applied, as the seasonal variation exhibited consistent trends aligned with those observed in land conservation. Thus, we conducted a one-way ANOVA, considering land conservation as a source of variation. Here, sampling period, plots, and sampling points were used as replicates. Differences between the means were determined by using Bonferroni's test at the 5% level, and the results were statistically analyzed using the R 4.3.2 program. We used the Euclidean distance by using the "vegan" package. Additionally, we performed a principal component analysis (PCA) to show the dissimilarities between the sites and land conservation status and between the physical and biochemical properties of soil, dissolved SOM chemodiversity, and AMF community composition. Permutational multivariate analysis of variance (PERMANOVA) was used to separate and quantitatively evaluate the effects of sites and the land conservation status on all studied variables by using the "adonis2" function.[42]

We conducted a structural equation modeling (SEM) analysis to investigate the inherent relationships among AMF diversity, soil organic matter chemodiversity, and soil properties. Variables included in the SEM were selected based on their significance ($p < 0.001$) in prior PCA. Multiple combinations of AMF diversity, soil organic matter chemodiversity, and soil properties were tested, and the most plausible model was reported to elucidate the primary driving factors of soil functionality in degraded versus preserved forests. The measurement model was constructed using confirmatory factor analysis to determine the number of factors and their associated observed indicators based on loading scores. Factorability was confirmed using the Kaiser–Meyer–Olkin (KMO) test and Bartlett's test, evaluating eigenvalues, cumulative variance, and factor loadings. The final model represented a single-level analysis that integrated hierarchical AMF diversity, soil organic matter chemodiversity, and soil properties for each plot. The SEM analysis was performed using the "psych," "lavaan," "semTools," and "MASS" packages in R, with the maximum likelihood estimation method used for parameterization [43]. Model fit was assessed using three indices: (i) the comparative fit index (CFI > 0.95), indicating the alignment between data and the hypothesized model; (ii) standardized root mean square residual (SRMR < 0.08), reflecting discrepancies between sample and model covariance matrices; and (iii) root mean square error of approximation (RMSEA < 0.06), which measures the model's fit to the data set.

3 | RESULTS

3.1 | How did land conservation influence soil physical and biochemical properties in old-growth and degraded forest? What were the main physical and biochemical factors of soil influencing data variance?

We found significant differences between the land conservation of *O. porosa* on soil pH, exchangeable cation (Ca^{2+}, Mg^{2+}, Al^{3+}, and K^{+}), $H^{+}+Al^{3+}$, soil organic matter (SOM), S, P, micronutrients (Cu^{2+} and Zn^{2+}), bulk density, geometric mean diameter (GMD), weighted average diameter (WMD), microbial C biomass, microbial respiration, total glomalin, and oxalic and malic acids (Table 2). For clay and B, we did not find any significant difference between the degraded and preserved status. In the degraded plots, we observed the highest values of soil pH, Cu^{2+}, and bulk density. For Ca^{2+}, Mg^{2+}, Al^{3+}, $H^{+}+Al^{3+}$, SOM, S, P, Zn^{2+}, GMD, WMD, microbial C biomass, microbial respiration, total glomalin, oxalic acid, and malic acid, the highest values were observed in the preserved plots (Table 2).

PCA showed a clear dissimilarity of physical and biochemical properties of soil between the land conservation status of *O. porosa* forest and all soil properties (Figure 1). Total glomalin, GMD, WAD, microbial C biomass, malic acid, microbial respiration, P, organic matter, S, Ca^{2+}, K^{+}, Al^{3+}, $H^{+}+Al^{3+}$, oxalic acid, bulk density, Cu^{2+}, pH, and Mg^{2+} were the main factors contributing with 73.91% of data variance. Additionally, PCA ordination showed that the total glomalin, GMD, WAD, microbial C biomass, malic acid, microbial respiration, P, organic matter, S, Ca^{2+}, and K^{+} were correlated with the preserved plots. On the other hand, Al^{3+}, $H^{+}+Al^{3+}$, oxalic acid, bulk density, Cu^{2+}, pH, and Mg^{2+} were correlated with the degraded plots. According to the PERMANOVA, land conservation had a greater (66.39%, $p < 0.001$) impact on the physical and biochemical properties of soil. For studied sites and the interaction sites × land conservation, we did not observe any significant impact on the physical and biochemical properties of soil (Figure 1).

3.2 | How did land conservation influence the chemodiversity of soil dissolved organic matter in forests of *O. porosa*? What were the main variables influencing data variance?

We observed significant differences between studied land conservation status for aliphatic compounds, biological index, macromolecules content (carbohydrates, lipids, and proteins/amino sugars), condensed aromatic compounds, fluorescence compounds (1–3 and 4) and index, H/C ratio, highly saturated and phenolic compounds, nominal oxidation stage of carbon, polyphenolic compounds, and $SUVA_{254}$ (Table 3). The highest significant values for aliphatic compounds, biological index, carbohydrates, fluorescence compounds, fluorescence index, H/C ratio, highly saturated and phenolic compounds, lipids, nominal oxidation stage of carbon, protein/amino sugars, and $SUVA_{254}$ were found in the preserved plots (old-growth forest). For condensed aromatic compounds, fluorescence compounds 4, and polyphenolic compounds, the highest significant values were found in the degraded plots. We did not observe any significant differences between the land conservation status for the O/C ratio (Table 3).

The dissolved soil organic matter chemodiversity shifted significantly between the land conservation (Figure 2). The first two PCA axes explained 88.72% and 10.60% of the total variation, respectively. Polyphenolic compounds, condensed aromatic compounds, biological index, aliphatic compounds, highly saturated and phenolic compounds, protein/amino sugars content, carbohydrates content, and lipids content were the main factors contributing to data variance. PERMANOVA was carried out to quantify the relative contributions of study sites, land conservation, and the interaction between sites and land conservation. Land conservation by itself explained 96.64% of the observed variation. For the other independent

TABLE 2 Physical and biochemical properties of soil as affected by land conservation in forests of *Ocotea porosa* at subtropical Cambisol, Santa Catarina, Southern Brazil.

Soil properties	Degraded status	Preserved status
Soil pH (1:2.5, v:v)	**4.03 (0.23) a**	3.85 (0.57) b
Ca^{2+} ($cmol_c\ kg^{-1}$)	2.02 (0.17) b	**3.87 (0.27) a**
Mg^{2+} ($cmol_c\ kg^{-1}$)	0.76 (0.09) b	**0.95 (0.06) a**
Al^{3+} ($cmol_c\ kg^{-1}$)	3.68 (0.12) b	**4.24 (0.26) a**
$H^{+}+Al^{3+}$ ($cmol_c\ kg^{-1}$)	22.59 (0.71) b	**37.21 (0.27) a**
SOM (%)	5.00 (0.62) b	**6.56 (0.27) a**
Clay (%)	47.4 (7.32) a	39.7 (11.5) a
S ($mg\ kg^{-1}$)	9.58 (0.54) b	**34.65 (0.17) a**
P ($mg\ kg^{-1}$)	8.50 (0.11) b	**12.62 (0.96) a**
K^{+} ($cmol_c\ kg^{-1}$)	0.23 (0.02) b	**0.43 (0.04) a**
Cu^{2+} ($mg\ kg^{-1}$)	**6.91 (0.16) a**	5.07 (0.18) b
Zn^{2+} ($mg\ kg^{-1}$)	2.28 (0.08) b	**6.34 (0.39) a**
B ($mg\ kg^{-1}$)	1.57 (0.86) a	1.45 (0.19) a
Bulk density ($g\ cm^{-3}$)	**1.28 (0.01) a**	0.98 (0.03) b
Geometric mean diameter (mm)	1.17 (0.03) b	**2.63 (0.04) a**
Weighted average diameter (mm)	1.82 (0.02) b	**3.02 (0.03) a**
Microbial C biomass ($mg\ kg^{-1}$)	132.52 (0.11) b	**539.04 (0.41) a**
Microbial respiration ($mg\ kg^{-1}\ h^{-1}$)	0.01 (0.004) b	**0.09 (0.008) a**
Total glomalin ($mg\ g^{-1}$ soil)	1.81 (0.32) b	**5.79 (0.52) a**
Oxalic acid ($\mu mol\ g^{-1}$)	37.58 (3.13) b	**80.19 (2.95) a**
Malic acid ($\mu mol\ g^{-1}$)	0.45 (0.08) b	**4.93 (0.53) a**

Note: Standard deviation in parentheses. Bold values represent the highest significant values. Within each line, the same small letters represent no significant differences by Bonferroni's test ($p < 0.05$).

variables, sites, and interactions, they did not exhibit any significant impact on dissolved soil organic matter chemodiversity (Figure 2).

3.3 | How did land conservation influence root colonization and AMF diversity in forests of *O. porosa*? What were the main AMF species influencing data variance?

For root colonization, the highest significant values (38.16% ± 2.89%) were found in the preserved plots (Table 4). The abundance of AMF spores varied significantly between the studied land conservation status. In total, nine AMF species were identified (*Acaulospora morrowiae*, *Cetraspora pellucida*, *Claroideoglomus claroideum*, *Funneliformis mosseae*, *Glomus coremioides*, *Glomus* sp., *Gigaspora gigantea*, *Gigaspora decipiens*, and *Rhizophagus intraradices*). By considering the presence of AMF species, *A. morrowiae*, *C. pellucida*, *G. gigantea*, and *G. decipiens* were exclusive for the preserved plots. In the degraded plots, we observed the highest significant abundance of *C. claroideum*, *F. mosseae*, and *R. intraradices*. For *G. coremioides*, and *Glomus* sp., we did not find any significant difference in their abundance between the degraded and preserved plots (Table 4).

Overall, 97.12% of the variation in the AMF community composition was explained by the 10 main driving forces: root colonization and the abundance of *F. mosseae*, *C. claroideum*, *R. intraradices*, *G. coremioides*, *C. pellucida*, *G. gigantea*, *A. morrowiae*, *G. decipiens*, and *Glomus* sp. (Figure 3). *F. mosseae*, *C. claroideum*, and *R. intraradices* significantly and simultaneously explained the variation in the degraded plots. Moreover, PCA demonstrated that root colonization, *G. coremioides*, *C. pellucida*, *G. gigantea*, *A. morrowiae*, *G. decipiens*, and *Glomus* sp. were correlated with the preserved plots. According to the PERMANOVA, land conservation had a greater (95.29%, $p < 0.001$) impact on AMF community composition. For studied sites and the interaction sites × land conservation, we did not observe any significant impact on soil physical and biochemical properties (Figure 3).

3.4 | What are the primary factors driving soil functionality in degraded versus preserved *O. porosa* forests?

The SEM model revealed three key pathways: (i) the AMF community (root colonization and the abundance of F. mosseae and C. claroideum) positively influenced soil functionality and interacted positively with soil properties and DOM chemodiversity; (ii) soil properties (pH, Cu^{2+}, Mg^{2+}, bulk density, and oxalic acid) positively impacted soil functionality and interacted positively with the AMF

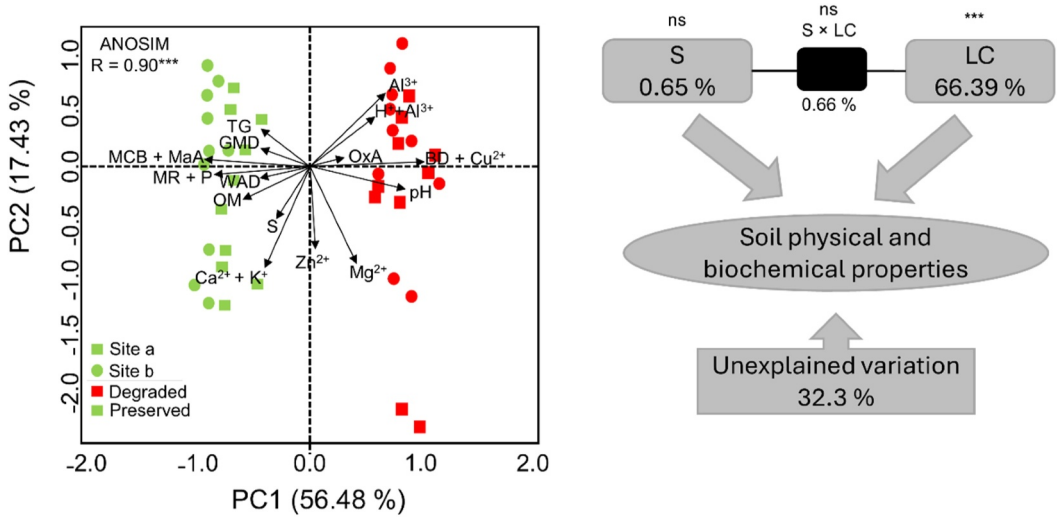


FIGURE 1 PCA scoreplot of the physical and biochemical data of the soil for the site (S) a and b for two land conservation (LC) statuses. The lengths of the arrows indicate the effects of physical and biochemical properties of soil, including Al^{3+}, $H^{+}+Al^{3+}$, oxalic acid (OxA), bulk density (BD), Cu^{2+}, pH, Mg^{2+}, Zn^{2+}, Ca^{2+}, K^{+}, S, organic matter (OM), microbial respiration (MR), weighted average diameter (WAD), microbial C biomass (MCB), malic acid (MaA), geometric mean diameter (GMD), and total glomalin (TG). Permutational multivariate analysis of variance (PERMANOVA) comparing the main and interactive effects of sites (S) and land conservation status (LC) on the physical and biochemical properties (999 permutations) of soil. Asterisks indicate significant differences at $p < 0.001$ (***), while ns indicate no significant differences. PCA = principal component analysis.

TABLE 3 The chemodiversity of soil dissolved organic matter (DOM) in the degraded and preserved plots with *Ocotea porosa* at subtropical Cambisol, Santa Catarina, Southern Brazil.

Variables	Degraded status	Preserved status
Aliphatic compounds (%)	10.28 (1.07) b	**20.43 (1.48) a**
Biological index	0.22 (0.04) b	**4.95 (0.26) a**
Carbohydrates (%)	2.64 (0.51) b	**29.41 (1.77) a**
Condensed aromatic compounds (%)	**35.67 (2.89) a**	20.28 (1.71) b
Fluorescence compounds 1–3	1.36 (0.27) b	**4.50 (0.37) a**
Fluorescence compounds 4	**−1.68 (0.20) a**	−5.27 (0.38) b
Fluorescence index	0.44 (0.13) b	**3.57 (0.29) a**
H/C ratio (%)	0.40 (0.02) b	**2.48 (0.16) a**
Highly saturated and phenolic compounds (%)	0.41 (0.02) b	**23.61 (2.41) a**
Lipids (%)	9.00 (0.24) b	**20.04 (1.43) a**
Nominal oxidation stage of carbon (%)	0.24 (0.04) b	**2.61 (0.07) a**
O/C ratio (%)	1.24 (0.03) a	1.26 (0.03) a
Polyphenolic compounds (%)	**32.17 (1.67) a**	21.86 (1.78) b
Protein/amino sugars (%)	1.96 (0.67) b	**41.73 (1.02) a**
Specific ultraviolet absorbance at 254 nm	1.67 (0.18) b	**3.83 (0.17) a**

Note: Standard deviation in parentheses. Bold values represent the highest significant values. Within each line, the same small letters represent no significant differences by Bonferroni's test ($p < 0.05$).

community and DOM chemodiversity; and (iii) DOM chemodiversity (polyphenolic and condensed aromatic compounds) positively affected soil functionality and interacted positively with the AMF community and soil properties (Figure 4). The SEM analysis identified the primary drivers of soil functionality as high root colonization, soil pH, and Mg^{2+}, alongside low levels of polyphenolic and condensed aromatic compounds, *F. mosseae* and *C. claroideum* abundance, Cu^{2+}, oxalic acid, and bulk density (Figure 4).

4 | DISCUSSION

Overall findings on the influence of land conservation in soil physical and biochemical properties, dissolved SOM chemodiversity, and AMF community composition.

The findings of this study underscore the critical role of land conservation in maintaining soil functionality in *O. porosa* ecosystems within subtropical Cambisols. We approached land conservation from

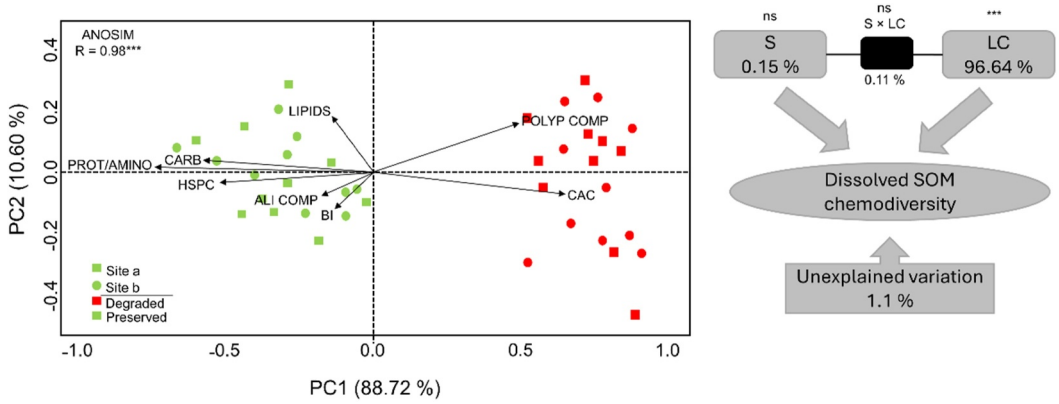


FIGURE 2 PCA scoreplot of the dissolved soil organic matter (SOM) chemodiversity data for the studied sites (S, site a and site b) for two land conservation (LC) statuses. The lengths of the arrows indicate the effects of the dissolved SOM chemodiversity, including polyphenolic compounds (POLYP COMP), condensed aromatic compounds (CAC), biological index (BI), aliphatic compounds (ALI COMP), highly saturated and phenolic compounds (HSPC), protein/amino sugar content (PROT/AMINO), carbohydrate content (CARBO), and lipid content. Permutational multivariate analysis of variance (PERMANOVA) comparing the main and interactive effects of sites (S) and land conservation status (LC) on the dissolved SOM chemodiversity (999 permutations). Asterisks indicate significant differences at $p < 0.001$ (***), while ns indicate no significant differences. PCA = principal component analysis.

TABLE 4 Root colonization and spores of AMF (spores g soil^{-1}) were observed in the degraded and preserved plots with *Ocotea porosa* at subtropical Cambisol, Santa Catarina, Southern Brazil.

Variables	Degraded site	Preserved site
Root colonization (%)	16.00 (1.71) b	**38.16 (2.89) a**
AMF species (spores 100 g soil^{-1})		
Acaulospora morrowiae	-	**13.36 (1.75) a**
Cetraspora pellucida	-	**9.90 (1.41) a**
Claroideoglomus claroideum	**21.12 (3.12) a**	6.00 (1.12) b
Funneliformis mosseae	**48.90 (5.11) a**	16.80 (2.89) b
Glomus coremioides	14.4 (3.05) a	15.00 (2.38) a
Glomus sp.	3.50 (0.82) a	3.90 (1.68) a
Gigaspora gigantea	-	**8.80 (1.43) a**
Gigaspora decipiens	-	**4.10 (0.71) a**
Rhizophagus intraradices	**17.90 (1.97) a**	6.20 (1.00) b

Note: Standard deviation in parentheses. Bold values represent the highest significant values.

Abbreviation: AMF, arbuscular mycorrhizal fungi.

Within each line, the same small letters represent no significant differences by Bonferroni's test ($p < 0.05$).

the perspective of "habitat provision" and site-specific effects from the hypothesis of "site-effect" [6,44]. Preserved forests, characterized by old-growth *O. porosa* trees, exhibited enhanced soil physical and biochemical properties, including higher levels of total glomalin, organic acids, and exchangeable cations, as well as greater chemodiversity of dissolved SOM.[45,46] These factors collectively promote soil aggregation, nutrient cycling, and microbial activity, which are crucial for supporting the long-term health and productivity of these ecosystems.[6] Furthermore, the higher abundance and diversity of arbuscular mycorrhizal fungi (AMF) observed in preserved forests suggest a robust symbiotic relationship that enhances nutrient uptake, stress resilience, and plant performance.[47] These findings highlight how land conservation not only protects biodiversity but also safeguards key soil processes essential for the sustainability of *O. porosa* and other coexisting species.

We anticipated a strong influence of land conservation in *O. porosa* forest and the following soil properties: (i) higher aggregation (e.g., geometric mean diameter and weighted average diameter) and lower bulk density in the preserved site than the degraded plots. It promotes a better ecosystem for healthy roots, thus improving rhizobiome, root activity by releasing organic acids, nutrients and water uptake [12]; (ii) higher fertility and microbial activity in the preserved plots than the degraded plots.[48] The nutrient loss by runoff and leaching is reduced by improving physical properties and rhizobiome, thus creating favorable conditions to increase soil organic matter, exchangeable cations, and microorganisms' traits (biomass and respiration).[49] Additionally, the healthy rhizobiome improved the release and exchange of cations (Ca^{2+}, Mg^{2+}, K^{+}, and Zn^{2+}) from clay to soil solution by changing soil pH and the organic acids content near the roots [50]; (iii) overtime, a positive cycle of soil organic matter inputs in the soil system could improve the chemodiversity of dissolved organic matter,[51] thus creating positive feedback with soil microorganisms [47]; and (iv) a healthy root system with average soil physical and biochemical properties would improve root colonization by AMF and the abundance of diverse AMF species in the preserved plots.[52]

In contrast, degraded forests showed significant declines in soil functionality, including lower levels of total glomalin, reduced organic acid content, and a less diverse AMF community. These changes reflect a disruption of soil homeostasis, which can adversely impact nutrient availability, soil structure, and plant–microbe interactions.[50] The diminished soil functionality in degraded forests likely limits the growth and survival of *O. porosa*, further exacerbating its vulnerability and threatening the ecological integrity of the subtropical Cambisols. These results underscore the need for targeted conservation strategies to restore degraded areas and mitigate the impacts of anthropogenic activities. Practices such as reforestation with *O. porosa*, promotion of AMF diversity, and soil amendments to improve organic matter content could enhance soil recovery and ecosystem resilience.[53] By prioritizing land conservation and restoration efforts,

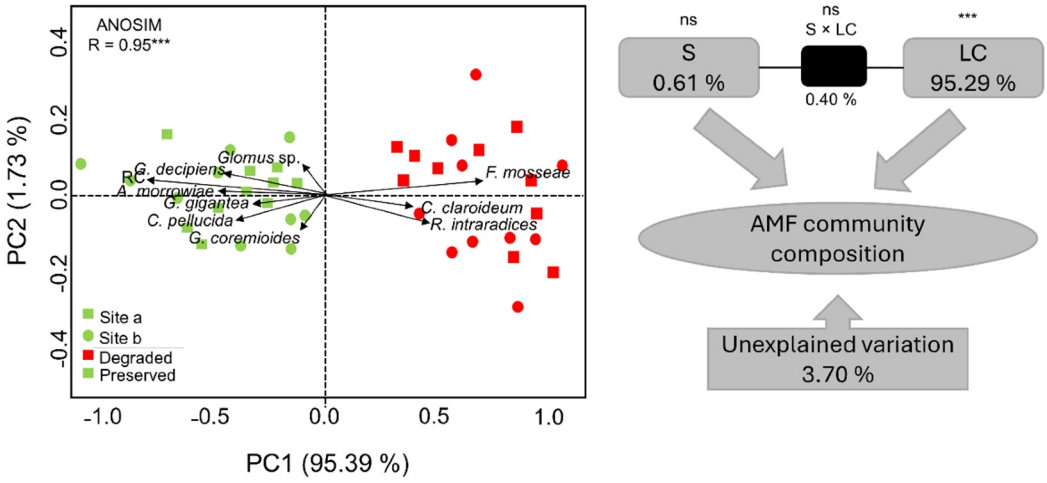


FIGURE 3 PCA scoreplot of the arbuscular mycorrhizal fungi (AMF) community composition data for the studied sites (S, site a and site b) for two land conservation (LC) statuses. The lengths of the arrows indicate the effects of the AMF community composition, including root colonization (RC), and the abundance of *Funneliformis mosseae*, *Claroideoglomus claroideum*, *Rhizophagus intraradices*, *Glomus coremioides*, *Cetraspora pellucida*, *Gigaspora gigantea*, *Acaulospora morrowiae*, *Gigaspora decipiens*, and *Glomus* sp. Permutational multivariate analysis of variance (PERMANOVA) comparing the main and interactive effects of sites (S) and land conservation status (LC) on the AMF community composition (999 permutations). Asterisks indicate significant differences at $p < 0.001$ (***), while ns indicate no significant differences. PCA = principal component analysis.

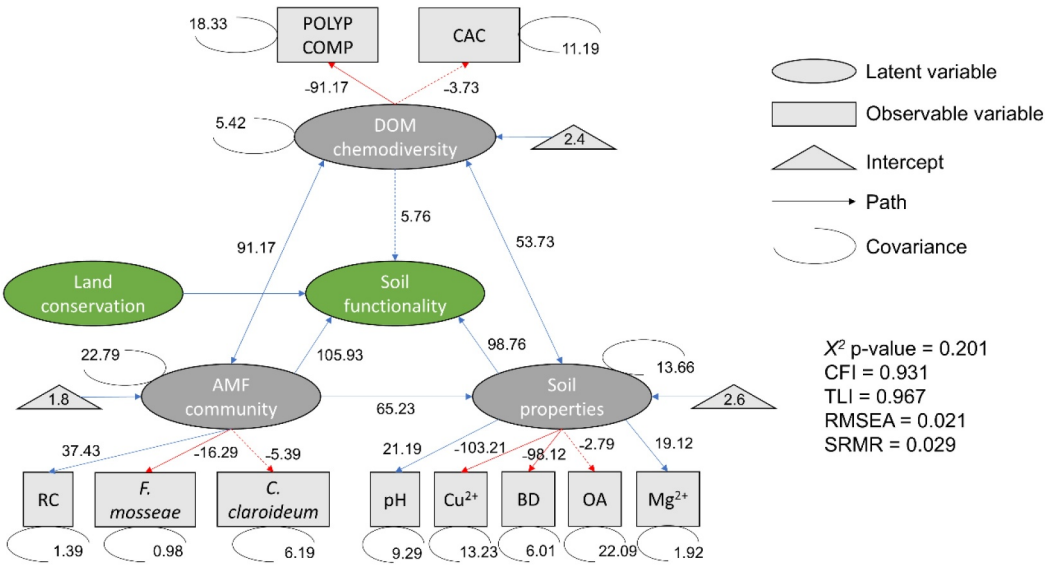


FIGURE 4 Structural equation model (SEM) indicating the inherent relationships among AMF community, dissolved soil organic matter (DOM) chemodiversity, and soil properties as affected by land conservation. Dashed and solid arrows represent significant effects at $p < 0.05$ and $p < 0.01$, respectively. Blue (positive) and red (negative) arrows represent paths that indicate the proportion of response variation explained by relationships with other variables. BD = bulk density, CAC = condensed aromatic compounds, OA = oxalic acid, POLYP COMP = polyphenolic compounds, and RC = root colonization. Values associated with arrows indicate standardized path coefficients.

it is possible to maintain the critical ecological functions provided by *O. porosa* ecosystems, ensuring their role in biodiversity conservation and climate regulation.[54]

4.1 | Land conservation influences the physical and biochemical properties of soil in old-growth and degraded forests of *O. porosa*

Our results revealed that the preserved plots provided a soil system dissimilar to that of the degraded plots, as evidenced by the higher values of geometric mean diameter, weighted average diameter, S, P, Ca^{2+}, Mg^{2+}, Zn^{2+}, Al^{3+}, $H^{+}+Al^{3+}$, soil organic matter, microbial C biomass, microbial respiration, total glomalin, oxalic acid, and malic acid.[55–57] Suitable contents of exchangeable cations, soil organic matter, organic acids, and microbial activity are commonly reported in well-conserved ecosystem, which aligns with our results from the preserved plots.[58] Conversely, we observed high values of bulk density, soil pH, and Cu^{2+} in the degraded plots. In such conditions, human activity played a crucial role in enhancing soil compaction (thus increasing bulk density), soil pH (by reducing root activity and the release of organic acids in a compacted soil), and Cu^{2+} (in the

preserved plots the active efflux, sequestration, and binding of Cu inside the cells by strong ligands are the main strategies used by *O. porosa* to resist this toxicity).[59–61] Our results suggest that after many years of land degradation in *O. porosa* forest, there is a negative shift from a preserved soil system to a degraded soil in terms of soil health and quality, that in turn may directly and indirectly affect *O. porosa* endangered conservation status. Some studies have interpreted such changes as habitat disruption and soil quality/fertility decline.[62,63]

4.2 | Land conservation influencing the chemodiversity of soil dissolved organic matter in forests of *O. porosa*

Our research revealed distinct differences in the impact of land conservation on soil composition. Preserved plots exhibited notable increases in various organic compounds, including aliphatic compounds, carbohydrates, and several fluorescence compounds, indicating a diverse array of dissolved organic matter. These findings suggest that land conservation promotes soil health and microbial activity over time.[13,64] Specifically, preserved plots showed higher levels of aliphatic and microbial-derived compounds, which play crucial roles in energy provision and nutrient availability for microorganisms and plants.[65] Scientific evidence has demonstrated the importance of natural ecosystems' conservation and dissolved SOM chemodiversity as key factors for biodiversity conversation and soil quality in tropical ecosystems.[66,67]

In contrast, degraded plots showed an increase in condensed aromatic compounds and a decrease in aliphatic compounds, indicating a shift toward less biologically active organic matter.[68] Our study also highlights the role of land conservation in reducing the accumulation of certain compounds, such as proteins and amino sugars, while promoting the decomposition of recalcitrant compounds.[69] The high bulk density and low microbial C biomass and microbial respiration in the degraded plots reduce O_2 supply and carbon substrate diffusion in the soil solution.[54] Additionally, the impact of land conservation on soil properties is influenced by changes in dissolved organic matter composition.[15] Furthermore, preserved plots exhibited higher microbial biomass and soil organic matter than degraded plots, suggesting a positive correlation between conservation efforts and soil health.[70] Conversely, degraded plots showed elevated levels of condensed aromatic compounds and polyphenolic compounds, likely due to the loss of soil aggregation and increased land degradation.[71] These findings underscore the importance of conservation efforts in maintaining soil quality and biodiversity in tropical ecosystems.

4.3 | Land conservation influencing the root colonization and AMF diversity in forests of *O. porosa*

In our study, certain AMF species showed indifference to the studied site (site a × site b) but were significantly influenced by the land conservation status (preserved × degraded). Our results indicated that the degraded plots altered the AMF community by increasing the abundance of *C. claroideum*, *F. mosseae*, and *R. intraradices*. This shift in the AMF community composition had a negative influence on root colonization by disrupting optimal pairings between AMF species from Acaulosporaceae and Gigasporaceae and the host plant.[53] For example, we observed a high abundance of *A. morrowiae*, *C. pellucida*, *G. gigantea*, and *G. decipiens* and high root colonization in the preserved plots. Here, we can presume that there is a positive relationship between these AMF species and the host plant, especially if we take into consideration the results of total glomalin and root colonization in the preserved plots.[72] In our experiment, we found strong evidence that these AMF species (*A. morrowiae*, *C. pellucida*, *G. gigantea*, and *G. decipiens*—exclusive from preserved plots) increased the percentage of root colonization and total glomalin. An improvement in the percentage of root colonization and total glomalin can enhance both plant performance and soil aggregation parameters, respectively.[11] The results of root colonization and total glomalin provided insights into the functionality of the symbiosis in both preserved and degraded plots.[73] For instance, the high root colonization indicates nutritional benefits to the host plant, while the total glomalin suggests a high positive influence in the geometric mean diameter, weighted average diameter, and bulk density.[74,75]

The relationship between AMF species and *O. porosa* in degraded and preserved plots may be influenced by soil pH and the content of exchangeable cations. In soils with pH lower than 4.0 and average contents of Ca^{2+}, Mg^{2+}, K^{+}, and Zn^{2+}, there was a high abundance of Acaulosporaceae and Gigasporaceae.[76] Conversely, in soils with pH higher than 4.0 and low contents of exchangeable Ca, Mg, K, and Zn, there was a high abundance of Claroideoglomeraceae and Glomeraceae.[77] These soil properties play important roles in the symbiotic relationship, such as the following: (i) Exchangeable cations are involved in depolarizing the AMF cell membrane [78]. (ii) The Cu/Zn ratio activates specific genes involved in the symbiotic phase between AMF species and host plants [79]. (iii) Soil pH enhances the activity in ionic channels and increases H^{+} extrusion, thereby improving electrochemical gradient in the rhizosphere.[80]

Our section on changes in soil dissolved organic matter chemodiversity and the AMF community demonstrated that differences among land conservation statuses were influenced by the physical and biochemical properties of soil.[45] Other studies reported the following: (i) Improved physical properties of soil create favorable conditions for a healthy rhizobiome, which can be positively correlated with microbial biomass, microbial activity, total glomalin, AMF diversity, and root colonization [81]. (ii) Improved biochemical properties of soil create favorable conditions to improve soil organic matter content, thus affecting the dissolved organic matter content and its chemodiversity [16]. (iii) Improved microbial activity and symbiotic relationship can positively impact the contents of both labile and recalcitrant compounds near the rhizosphere.[82] Considering that these soil compartments (physical properties of soil, biochemical properties of soil, dissolved SOM chemodiversity, and AMF diversity) are linked to each other and modulated by land conservation [62] through *O. porosa* growth and its nutritional status, we can presume that preserved forest of *O. porosa*—a multicentennial endemic plant species from Southern Brazil—has an important influence on carbon sequestration (by increasing soil carbon stock and above- and belowground biomass), thus helping to mitigate climate change.[57]

Studies involving the identification of AMF species and their relationship with soil physical, soil biochemical, and dissolved SOM chemodiversity as influenced by land conservation in forests of

endemic and endangered plant species from Brazilian flora are rare.[62] To our knowledge, this is the first report assessing the AMF community structure in forests of *O. porosa* from degraded and preserved plots. As previously hypothesized, the highest richness of AMF species was observed in the preserved plots,[47] mainly with giant trees in old-growth forests.[83] In this condition, we observed low bulk density, high soil organic matter, glomalin content, and root colonization, which can promote the abundance of exclusive AMF species from Acaulosporaceae (*A. morrowiae*) and Gigasporaceae (*C. pellucida*, *G. gigantea*, and *G. decipiens*).[84] In the contexts of *O. porosa* as an endangered plant species and climate change, AMF richness, root colonization, and total glomalin play a crucial role as bioindicators for soil conservation, C sequestration, and soil C stock.[85]

When we started our study in forests with *O. porosa*, we did not anticipate discovering strong evidence for changes in the entire soil functioning—from physical properties to the chemodiversity of dissolved SOM, and finally to the AMF community structure.[86] Other studies have reported changes in soil chemical properties and AMF diversity in *Araucaria angustifolia* and *Pinus* sp. [6,14] If we consider the carbon density (which takes into account the soil C stock, aboveground biomass, and belowground biomass [87]) in the land conservation status, there was a reduction of approximately 58.9% in carbon density in the degraded plots compared to the preserved plots. Previous studies have demonstrated positive interactions between soil C compartments and AMF diversity,[6,75] supporting the hypothesis proposed by Souza et al. [14] and Zhao et al. [12] that well-conserved ecosystems provide habitats for diverse communities of microorganisms. These microorganisms help plants and the climate by enhancing plant performance and sequestering C into the soil ecosystem, respectively.[67,85]

5 | CONCLUSION

The land conservation status of *O. porosa* forests influenced the physical and biochemical properties of soil, soil dissolved organic matter chemodiversity, and AMF symbiosis into subtropical Cambisols from Brazilian Atlantic Forest biome. Samples from the degraded plots showed higher soil pH, Cu^{2+}, bulk density, condensed aromatic compounds, fluorescence compounds 4, polyphenolic compounds, and the abundance of *C. claroideum*, *F. mosseae*, and *R. intraradices* than the preserved plots. Our findings suggest that land conservation positively affected the Cambisols functionality by increasing soil organic matter and its quality, exchangeable cations, physical traits of soil, organic acids, total glomalin, root colonization by AMF, and AMF species from Acaulosporaceae and Gigasporaceae with a potential to: (i) increase soil C sequestration; (ii) mitigate climate change; and (iii) preserve an endangered centenary tree species from Atlantic Forest biome. The results of our study highlighted the importance of considering the preserved old-growth forest of *O. porosa* with high impact on the soil functionality and its quality.

AUTHOR CONTRIBUTIONS

Conceptualization: Tancredo Souza and Marcelo Callegari Scipioni. Methodology: Tancredo Souza, and Marcelo Callegari Scipioni. Software: Tancredo Souza, Agnne Mayara Oliveira Silva. Data curation: Tancredo Souza. Investigation: Tancredo Souza, Marcelo Callegari Scipioni, Mário Dobner Júnior, Andressa Vasconcelos Flôres, Agnne Mayara Oliveira Silva, Josefa Bruna Lima dos Santos, Diego Silva Batista. Validation: Tancredo Souza, Marcelo Callegari Scipioni, Mário Dobner Júnior, and Andressa Vasconcelos Flôres. Formal analysis: Tancredo Souza. Supervision: Tancredo Souza and Marcelo Callegari Scipioni. Funding acquisition: Tancredo Souza, Marcelo Callegari Scipioni, and Diego Silva Batista. Visualization: Tancredo Souza, Marcelo Callegari Scipioni, Mário Dobner Júnior, Andressa Vasconcelos Flôres, Agnne Mayara Oliveira Silva, Josefa Bruna Lima dos Santos, Diego Silva Batista. Project administration: Tancredo Souza, and Marcelo Callegari Scipioni. Resources: Tancredo Souza, Marcelo Callegari Scipioni, Mário Dobner Júnior, and Diego Silva Batista. Writing—original draft preparation: Tancredo Souza, Agnne Mayara Oliveira Silva, and Marcelo Callegari Scipioni. Writing—review and editing: Tancredo Souza, Marcelo Callegari Scipioni, Mário Dobner Júnior, Andressa Vasconcelos Flôres, Agnne Mayara Oliveira Silva, Josefa Bruna Lima dos Santos, Diego Silva Batista. All authors have read and agreed to the published version of the manuscript.

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ETHICS STATEMENT

This study is original, and all relevant authors whose work relates to this research area have been appropriately acknowledged and cited.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data sharing is applicable with a formal and justified request for the corresponding author.

CONSENT TO PUBLISH

We confirm that this manuscript has not been published elsewhere and is not under consideration by another journal. All authors have approved the manuscript and agreed with submission to Biological Diversity. We have read and have abided by the statement of ethical standards for manuscripts submitted to Biological Diversity.

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