Impact of land use on the soil microbiota and soil abiotic traits in tropical and subtropical Brazilian ecoregions

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Abstract

Land uses influence soil microbiota and soil abiotic traits in the Brazilian Tropical and Subtropical ecoregions. Our aim was to test if different land uses may influence the soil microbiota and the soil chemical properties in agroforestry systems (AF), unassisted forest restoration (UFR), and natural ecosystem (Ne) located at Tropical and Subtropical ecosystems from North-eastern and Southern, Brazil, respectively. We have used the joint analysis of a series of experiments in a randomized block design. In the three land uses, we collected soil samples to determine arbuscular mycorrhizal fungi community, soil nematode, soil pH, available P, and soil organic carbon (SOC) from January 2018 to January 2022 using a semestral schedule. Soil microbiota richness in the AF and Ne was similar in the tropical ecosystem. The PCA analysis showed SOC, soil pH, Fungivores, Bacterivores, *Racocetra coralloidea*, *Dentiscutata scutata*, and *D. erythrophus* as the main factors contributing to the variance of the samples. Differences were associated with (1) the land uses by promoting different habitat, as we found difference on soil microbiota abundance, and diversity as affected by habitat simplification, and (2) changes in soil pH, SOC, and available P. These results contribute to a deeper view of the soil microbiota community composition in different land uses from two Brazilian ecosystems. Our work increases the understanding of the soil microbiota com-munity structure in the rhizosphere of AF and Ne in tropical and subtropical ecosystems.

Introduction

It is well documented that the land use (e.g., as a human activity that changes the structure of soil food web, and as complex adaptive systems) may influence soil microbiota ecological patterns through human-environment interactions (Lance et al. 2020). A solid soil food web is created by transforming the soil organic matter in a way that increase both habitat provision and nutrient cycling process (Souza et al. 2022). These two processes may promote the arbuscular mycorrhizal fungi and soil nematodes' community complexity (e.g., community ecological patterns). In this context, the Brazilian territory presents a wide range of biotic (e.g., plant species, land uses, soil organisms, etc.) and abiotic traits (e.g., soil type, climate type, etc.) that creates complex ecological networks. Inserted into this huge territory there are two main ecosystems: the tropical (by covering the North, Midwest, and Northeast Brazil) and subtropical one (by covering South, and Southeast Brazil). These ecosystems are very dissimilar considering their biocomplexity, organisms' self-organization, climate, and ecological patterns formation in space and time as well (Melo et al. 2021, Inague et al. 2021), and studies considering the influences of land uses on soil microbiota complexity into these ecosystems has remained unclear. Studies also considering soil ecology in huge territories using the joint analysis of a series of experiments are considered a hard task to accomplish, especially if these studies are performed in field conditions (Yamauchi et al. 2021, Wahdan et al. 2021), but they also integrate natural processes at appropriately broad human-environment interactions.

In our study, we examined the soil microbiota complexity (Arbuscular mycorrhizal fungi – AMF at species level, and soil nematodes at functional-group level), and soil abiotic traits (e.g., soil organic carbon, soil pH, and Olsen's P) in different land uses (e.g., 8-years agroforestry system, 10-years unassisted forest restoration, and natural ecosystem). Based on the soil quality and habitat provision hypothesis, we expected to find: i) ecological pattern variation at space as affected by the land use; and ii) the role of physical constraints (e.g., soil abiotic traits) when comparing the soil dynamics in the agroforestry system, and unassisted forest restoration with the natural ecosystem. Ecological patterns (e.g., abundance and diversity of soil organisms) depend on rootability and continuous input of litter (e.g., that determine the root activity into the rhizosphere and the main source of soil organic carbon, respectively (Melo et al. 2019). We must expect that land uses that promote both processes may increase soil microbiota abundance and diversity by providing habitat and energy supply.

Based on the nutrient content hypothesis, we expected to find high abundance, and diversity into the agroforestry system when compared to the unassisted forest restoration. There is evidence that agroforestry systems may support a solid soil food web and trophic structure based on the resource concentration hypothesis (Muchane et al. 2020). Into this context, in both tropical and subtropical ecosystems, soil traits are factors that can promote suitable conditions for soil microbiota activity (Laurindo et al. 2021, Forstall-Sosa et al. 2020). The agroforestry system can contribute to increase the soil organic carbon, and soil phosphorus availability, which directly can increase soil quality, ecosystem services, and provide food resources for the soil microbiota (Muchane et al. 2020, Nascimento et al. 2021).

The Brazilian tropical and subtropical ecosystems are characterized by dissimilar dry and wet periods at short-time scales (Laurindo et al. 2020, Lucena et al. 2021). This promotes the soil microbiota ecological patterns in different ways. AMF species are influence by soil water content and rootability, while the soil nematodes are influenced by soil organic carbon and rhizodeposition (Laurindo et al. 2021, Silva et al. 2021, Fu et al. 2020, Raiesi et al. 2020). In this context, the land uses with high plant diversity in both tropical and subtropical conditions might play a significant role in the soil microbiota diversity, and their ecosystem services (Teixeira et al. 2021). Previous studies suggested that in the natural ecosystem the high plant diversity combined with a high rate of litter deposition are positively correlated with acid soil with high values of soil organic carbon when compared with unassisted forest restauration, and agroforestry systems that presents in general soils with pH ranging from 5.8 to 6.5 and low plant diversity that limits the rate of litter deposition on soil surface (Hu et al. 2020, Yao et al. 2021). So, we must consider a positive plant-soil interaction, and a continuous energy fluxes created by the litter deposition in the natural ecosystem (Silva et al. 2021, Nascimento et al. 2021). While in the agroforestry system, plant species increase the H^+ extrusion process that changes plant nutrient uptake, and the release of organic acids (e.g., rhizodeposition) into the rhizosphere (Laurindo et al. 2021). There are many works that demonstrate that different land use may change soil traits in both tropical and subtropical ecosystems (Akinde et al. 2020, Singh et al. 2021, Yinga et al. 2020, Reichert et al. 2021), but the mechanisms underlying these changes and their consequences on soil microbiota complexity remains unclear.

In this study, we examined the AMF and soil nematode complexity, and soil abiotic traits in an agroforestry system, an unassisted forest restoration, and a natural ecosystem under tropical and subtropical ecoregions at the South, and Northeast Brazil using the joint analysis of a series of experiment in randomized block design from January 2018 to January 2022. Our study addressed the following questions: i) the land use may influence the AMF and soil nematode complexity at local scales? and ii) soil abiotic traits may be affected by land use, and in turn may indirectly affect soil microbiota ecological patterns? To accomplish these questions, we combined: a) soil sampling to extract AMF spores, and soil nematodes as described by Laurindo et al. (2021); and b) determination of soil chemical properties to characterize the soil ecosystem as described by Nascimento et al. (2021). All these tasks were done in the three land uses (e.g., agroforestry system, unassisted forest restoration, and natural ecosystem) in both tropical, and subtropical ecosystems. Our aim here was to test if different land uses (e.g., agroforestry system, unassisted forest restoration, and natural ecosystem) may influence the soil microbiota complexity and the soil traits in the South and Northeast Brazil.

Material And Methods

Study systems, climatic conditions, and soil types

This study was carried out in two ecosystems (e.g., tropical vs. subtropical), using soil data from three long-term field experiments following an agroforestry system, an unassisted forest restoration, and a natural ecosystem using the joint analysis of a series of field experiments in randomized block design. To characterize the tropical ecosystem, we collected soil samples in two experimental stations located at the experimental perimeter of EMEPA (State Research Company of Paraiba) in Alagoinha, Paraiba, Brazil (6°57’00” S, 35°32’42” W, altitude of 317 m above sea level), and at the Experimental Station “Chã-de-Jardim”, in Areia, Paraiba, Brazil (06º 58’12” S, 35º42’15” W, altitude of 619 m above sea level). While for the subtropical ecosystem, we collected soil samples into the experimental station from the Federal University of Santa Catarina, Campus of Curitibanos, Santa Catarina, Brazil (27°16’58” S, 50°35’04” W, altitude of 987 m above sea level) (Fig. 1). The climate types in the studied sites were classified as tropical Aw-type, tropical As-type, and subtropical Cfb-type following the Köppen-Geiger climate classification, with average annual precipitations of 995, 1500 and 1676 mm, respectively. The soil types of the studied sites were classified as Regosol (WRB 2015).

Experimental design

The results of this study were obtained from January 2018 to January 2022 using the joint analysis of a series of experiments. Soil samples were collected as described by the Tropical Soil Biology and Fertility method (Anderson and Ingram 1993), following a semestral schedule. We followed an ecological gradient to characterize the studied land uses, during each studied year. The treatments consisted of three different land uses: a) agroforestry system, b) unassisted forest restoration, and c) natural ecosystem. For more details about land uses, see Forstall-Sosa et al. (2020), Laurindo et al. (2021), Nascimento et al. (2021). For each land use, fifty soil samples (0.0-0.2 m) were collected per semester, and divided in two groups, where one of them was to characterize soil microbiota community composition and the remaining to characterize soil chemical properties. The following sampling criterion has been established: each tree species should be larger than 3 cm in diameter near soil surface and no other individuals from a different native tree species should occur at a distance lower than 3 m from the sampling point (Daubenmire 1968, Caifa and Martins 2007, Costa and Araujo 2007, Pinheiro and Durigan 2012).

Arbuscular mycorrhizal fungi (AMF) taxonomic structure and soil nematodes identification

To sample AMF spores and soil nematodes, we used the wet sieving technique using sieves with 710, 250, and 37µm (Gerdemann and Nicolson 1963) followed by sucrose (20/60%) centrifugation (Jenkins 1964). First, extracted AMF spores, sporocarps, and soil nematodes were examined in water under a dissecting microscope. They were separated based on their spore morphology (e.g., Acaulosporoid, Gigasporoid, Glomoid, or Radial-Glomoid for the AMF spores) and functional groups (e.g., Bacterivores, fungivores, herbivores, omnivore, and predators for the soil nematodes functional groups). For AMF species, we considered spore walls and presence of layer's ornamentation, germination shield or orb, peridium, small bulbs on subtending hypha, and inner walls. On the other hand, mouth parts, and body traits for soil nematodes were considered during the identification.

Next, AMF spores were mounted in polyvinyl alcohol lacto-glycerol (PVLG) with or without Melzer's reagent as described by Souza (2015). For AMF species identification, we used the method described by Schenck and Pérez (1990), and by consulting the online AMF collection of the Department of Plant Pathology, the University of Agriculture in Szczecin, Poland (http://www.agro.ar.szczecin.pl/~jblasxkowski/), and the International Culture Collection of Arbuscular Mycorrhizal Fungi Database—INVAM (http://invam.caf.wvu.edu).

For soil nematodes the identification was based on the descriptions provided by Buchan et al. (2013), to separate free-living nematodes from soil components (e.g., organic matter and clay). We counted the soil nematodes under a binocular microscope. Next, the soil nematodes were fixed with a 4% hot (70ºC) formaldehyde solution. Finally, nematode identification using trophic groups was carried out according to Yeates et al. (1993). We assessed both AMF and soil nematode community structure based on the following parameters: abundance (number of individuals 100 g soil^{-1}), diversity (Shannon's index), species richness, and dominance (Simpson's index).

Soil chemical properties

To characterize soil chemical properties (e.g., soil pH, soil organic carbon, and Olsen's P), we collected fifty soil samples at 0.0–0.2 m soil depth following a semestral schedule. The samples were air-dried and passed through a 2–mm sieve. Soil pH was determined in a suspension of soil and distilled water (1: 2.5, v:v, soil: water suspension) following the methodology described by Black (1965). The soil organic carbon was determined by rapid dichromate oxidation method (Okalebo et al. 1993) and the soil available P was determined colorimetrically following the protocol described by Olsen et al. (1954), using a spectrophotometer at 882 nm by extraction with sodium bicarbonate for three minutes.

Statistical analyses

All statistical analyses were performed on the sample-level, which are nested within land uses. Prior to our analysis, we tested all variables for normality using the “shapiro.test()” function. Next, we used the “Moran.I” function (“ape” package) as described by Gittleman (1990) to find spatial autocorrelation. Here, if the analyses had indicated that the variables were spatially dependent to the sampling points, we must describe the site-effect level (e.g., dispersed, random, or clustered), and to use a nested analysis. However, none of the variables measured in our study were found to have any spatial relationship (e.g., no site-effects) with the sampling point. Since the Shapiro-Wilk test indicated non-parametric data and our samples were spatially independent, it enables us to use the “kruskal.test()” function at “stats” package to compare soil microbiota community structure and soil chemical properties among the land uses and studied ecosystems. We used the Tukey’s test (“stats” package) to compare soil microbiota community structure and soil chemical properties. We performed a principal component analysis (“princomp()” function at “stats” package) to outline the dissimilarities among soil microbiota community, soil chemical properties, and the studied land uses. All statistical analyses were done using R Studio Team (R Core Team 2018).

Results

Arbuscular mycorrhizal fungi (AMF) community composition

We identified field-collected spores from 25 AMF species. They can be distributed in two Orders: Diversisporales (two families) and Glomerales (two families) (Table 1). Three AMF species from Acaulosporaceae: *Acaulospora brasiliensis*, *A. denticulata*, and *A. tuberculata*; One AMF from Ambisporaceae: *Ambispora gerdemannii*; three AMF species from Claroideoglomeraceae: *Claroideoglomus claroideum*, *C. etunicatum*, and *C. lamellosum*; ten AMF species from Gigasporaceae: *Dentiscutata cerradensis*, *D. erythrophus*, *D. heterogama*, *D. scutata*, *Gigaspora albida*, *G. decipiens*, *G. gigantea*, *G. margarita*, *Racocetra coralloidea*, and *Scutellospora calospora*; eight AMF species from Glomeraceae: *Funneliformis caledonius*, *F. mosseae*, *Glomus multicaule*, *Glomus* sp., *Rhizophagus aggregatum*, *R. clarus*, *R. intraradices*, and *S. coremioides*. Across all the soil samples, *C. claroideum* was the most abundant identified AMF species on the tropical ecosystem under all land uses. On the other hand, we found *F. mosseae* was the most abundant identified AMF species on the subtropical ecosystem under all land uses (Table 1).

Table 1

Abundance of arbuscular mycorrhizal fungi species (spores 100 g soil^{-1}, mean ± standard deviation) among the land uses at tropical and subtropical ecosystems, Brazil.

AMF species	Agroforestry system	Unassisted forest restoration	Natural ecosystem
	Tropical ecosystem		
Acaulospora brasiliensis B.T. Goto, L.C. Maia & Oehl	-	6.82 ± 0.01 a	4.84 ± 0.12 b
A. denticulata Sieverd. & S. Toro	-	0.66 ± 0.11 a	0.33 ± 0.06 a
A. tuberculata Janos & Trappe	0.33 ± 0.06 b	5.00 ± 0.87 a	0.66 ± 0.11 b
Ambispora gerdemannii (S.L. Rose, B.A. Daniels & Trappe) Walker, Vestberg & Schussler	-	6.00 ± 0.61 a	5.32 ± 0.26 b
Claroideoglomus claroideum (N.C. Schenck & G.S. Sm.) C. Walker & Schüßler	11.25 ± 0.86 a	10.99 ± 0.70 a	17.99 ± 0.58 b
C. etunicatum W.C. Becker & Gerd.) C. Walker & Schüßler	2.99 ± 0.46 a	1.32 ± 0.68 b	2.33 ± 0.40 a
C. lamellosum (Dalpé, Koske & Tews) C. Walker & A. Schussler	-	1.15 ± 0.01 a	0.66 ± 0.01 b
Dentiscutata cerradensis (Spain & J. Miranda) Sieverd., F.A. de Souza & Oehl	-	0.66 ± 0.11 b	1.32 ± 0.17 a
D. erythrophus (Koske & C. Walker) C. Walker & D.R.)	-	3.46 ± 0.01 b	8.33 ± 0.61 a
D. heterogama T.H. Nicolson & Gerd.) Sieverd., F.A. de Souza & Oehl	-	4.33 ± 0.51 a	0.33 ± 0.06 b
D. scutata (Walker & Diedrich)	-	5.33 ± 0.23 b	8.00 ± 0.21 a
Funneliformis caledonius (T.H. Nicolson & Gerd.) C. Walker & A. Schüßler	-	1.66 ± 0.21 b	6.66 ± 0.38 a
F. mosseae (T.H Nicolson & Gerd.) C. Walker & A. Schüßler	7.66 ± 0.46 a	7.32 ± 0.49 a	0.33 ± 0.06 b
Gigaspora albida N.C. Schenck & G.S. Sm	-	0.66 ± 0.11 a	-
G. decipiens R. Hall & L.K. Abbott	2.99 ± 0.26 b	1.32 ± 0.22 c	4.33 ± 0.63 a

Different small letters at the same line represent statistically significant differences by land uses after Tukey’s test ($p < 0.05$).

*** Significative at $p < 0.001$ by unpaired t-test.

AMF species	Agroforestry system	Unassisted forest restoration	Natural ecosystem
G. margarita Becker & Hall	2.99 ± 0.31 a	1.99 ± 0.34 b	1.33 ± 0.18 c
Glomus multicaule Tul. & C. Tul	0.66 ± 0.11 b	2.33 ± 0.25 a	0.33 ± 0.06 b
Racocetra coralloidea Trappe, Gerd. & I. Ho) Oehl, F.A. Souza & Sieverd	1.66 ± 0.21 a	-	-
Rhizophagus aggregatum (N.C. Schenck & G.S. Sm.) Sieverd., G.A. Silva & Oehl	-	0.33 ± 0.06 b	1.33 ± 0.23 a
R. clarus (T.H. Nicolson & N.C. Schenck) C. Walker & A. Schussler	-	0.33 ± 0.06 b	5.33 ± 0.52 a
R. intraradices (N.C. Schenck & G.S. Sm.) Sieverd., G.A. Silva & Oehl	5.32 ± 0.67 a	4.00 ± 0.60 b	-
Scutellospora calospora (Nicol. & Gerd.) C. Walker & FE Sanders	11.32 ± 0.46 a	4.00 ± 0.01 b	-
Sclerocystis coremioides C. Walker & F.E. Sanders	0.66 ± 0.11 a	-	-
	Subtropical ecosystem		
A. tuberculata Janos & Trappe	-	-	0.33 ± 0.06 a
Claroideoglomus claroideum (N.C. Schenck & G.S. Sm.) C. Walker & Schüßler	4.66 ± 0.06 a	3.33 ± 0.25 b	2.33 ± 0.32 c
C. etunicatum W.C. Becker & Gerd.) C. Walker & Schüßler	-	0.33 ± 0.06 a	-
Dentiscutata cerradensis (Spain & J. Miranda) Sieverd., F.A. de Souza & Oehl	-	2.66 ± 0.21 a	0.66 ± 0.06 b
F. mosseae (T.H Nicolson & Gerd.) C. Walker & A. Schüßler	9.33 ± 0.06 c	20.00 ± 0.98 a	14.33 ± 0.56 b
Gigaspora albida N.C. Schenck & G.S. Sm	1.33 ± 0.06 a	1.33 ± 0.06 a	1.66 ± 0.21 a
G. gigantea T.H. Nicolson & Gerd.) Gerd. & Trappe	0.66 ± 0.06 b	1.33 ± 0.06 a	0.66 ± 0.11 b
G. margarita Becker & Hall	-	-	1.66 ± 0.15 a

Different small letters at the same line represent statistically significant differences by land uses after Tukey’s test ($p < 0.05$).

*** Significative at $p < 0.001$ by unpaired t-test.

AMF species	Agroforestry system	Unassisted forest restoration	Natural ecosystem
Glomus sp.	1.33 ± 0.06 c	4.66 ± 0.64 a	2.33 ± 0.40 b
Racocetra coralloidea Trappe, Gerd. & I. Ho) Oehl, F.A. Souza & Sieverd	-	0.66 ± 0.11 a	0.33 ± 0.06 a
R. clarus (T.H. Nicolson & N.C. Schenck) C. Walker & A. Schussler	2.33 ± 0.06 c	6.66 ± 0.66 a	3.00 ± 0.17 b
t-test (tropical × subtropical)	51.34***	87.55***	91.21***
Different small letters at the same line represent statistically significant differences by land uses after Tukey's test ($p < 0.05$).			
*** Significative at $p < 0.001$ by unpaired t-test.			

Soil nematode functional groups

In our field study, we observed significative differences ($p < 0.01$) on soil nematodes functional groups among the land uses (Table 2). The highest abundance of bacterivore, fungivore, omnivore, and carnivore were found on the tropical ecosystem under natural ecosystem, except the herbivores that presented the highest abundance in the agroforestry system. On the other hand, at subtropical ecosystem we found the highest values of all soil nematode functional group under the natural ecosystem (Table 2).

Table 2

Soil nematode functional group abundance (number of individual 100 g soil^{-1}, mean ± standard deviation) among the land uses at tropical and subtropical ecosystems, Brazil.

Land use	Bacterivore	Fungivore	Omnivore	Herbivore	Carnivore
Tropical ecosystem					
Agroforestry system	9.33 ± 0.33 c	9.00 ± 0.36 c	8.66 ± 0.41 c	**15.66 ± 1.11 a**	8.32 ± 0.35 c
Unassisted forest restoration	10.99 ± 0.55 b	10.66 ± 0.50 b	10.66 ± 0.50 b	4.00 ± 0.34 c	9.66 ± 0.55 b
Natural ecosystem	**15.99 ± 0.62 a**	**15.00 ± 0.70 a**	**15.00 ± 0.70 a**	9.66 ± 0.92 b	**14.66 ± 0.71 a**
Subtropical ecosystem					
Agroforestry system	4.00 ± 0.10 b	3.00 ± 0.05 b	3.00 ± 0.10 b	3.00 ± 0.10 b	3.00 ± 0.10 b
Unassisted forest restoration	3.33 ± 0.15 b	3.33 ± 0.15 b	2.66 ± 0.20 b	3.00 ± 0.17 b	1.66 ± 0.05 c
Natural ecosystem	**10.00 ± 0.69 a**	**10.00 ± 0.69 a**	**9.66 ± 0.72 a**	**9.66 ± 0.72 a**	**9.66 ± 0.72 a**
t-test (tropical × subtropical)	26.69**	17.71**	12.69**	29.60**	16.91**

Different small letters at the same column represent statistically significant differences by land uses after Tukey's test ($p < 0.05$).

** and *** Significative at $p < 0.01$ and $p < 0.001$, respectively by unpaired t-test.

Soil microbiota community structure - Ecological indices

We found significative differences between the studied land uses ($p < 0.01$) on soil microbiota community structure. For the richness, the highest values were observed at the tropical and subtropical ecosystem under the unassisted forest restoration (Table 3), while for the diversity (Shannon's diversity index), we found the highest values just in the agroforestry system at tropical and subtropical ecosystem conditions. We did not find significate differences on Simpson's dominance index among the land uses at tropical and subtropical ecosystems (Table 3).

Table 3
Species richness, Shannon's diversity index, and Simpson's dominance index (mean ± standard deviation) among the land uses at tropical and subtropical ecosystems, Brazil.

Land use	**Species Richness**	**Shannon diversity index**	**Simpson dominance index**
Tropical ecosystem			
Agroforestry system	11.00 ± 0.36 c	**2.32 ± 0.03 a**	0.88 ± 0.02 a
Unassisted forest restoration	**21.00 ± 0.20 a**	2.10 ± 0.04 b	0.86 ± 0.01 a
Natural ecosystem	17.67 ± 0.15 b	2.01 ± 0.01 b	0.81 ± 0.04 a
Subtropical ecosystem			
Agroforestry system	5.67 ± 0.05 c	**2.17 ± 0.07 a**	0.86 ± 0.03 a
Unassisted forest restoration	**12.34 ± 0.05 a**	2.07 ± 0.07 b	0.81 ± 0.03 a
Natural ecosystem	11.00 ± 0.01 b	2.11 ± 0.02 b	0.86 ± 0.01 a
t-test (tropical × subtropical)	23.01***	32.91***	21.09***

Different small letters at the same column represent statistically significative differences by the land use after Tukey's test ($p < 0.05$).

***Significative differences at $p < 0.001$.

Soil chemical properties

In our study, we observed significative differences among the land uses on soil pH ($p < 0.001$), Olsen's P ($p < 0.01$), and soil organic carbon ($p < 0.001$). The highest values of soil pH, and Olsen's P were found on the tropical and subtropical ecosystem under the agroforestry system, while the highest values of soil organic carbon were found in the natural ecosystem at tropical and subtropical ecosystems (Table 4).

Table 4
Soil chemical properties (mean ± SD) among the land uses at tropical and subtropical ecosystems, Brazil

Land use	Soil pH	Olsen's P (mg kg^{-1})	Soil organic carbon (g kg^{-1})
Tropical ecosystem			
Agroforestry system	**5.43 ± 0.06 a**	**20.02 ± 0.18 a**	8.25 ± 0.05 b
Unassisted forest restoration	5.28 ± 0.01b	6.52 ± 0.06 b	7.11 ± 0.02 c
Natural ecosystem	5.30 ± 0.02 b	6.52 ± 0.01 b	**16.52 ± 0.01 a**
Subtropical ecosystem			
Agroforestry system	**5.56 ± 0.05 a**	**24.60 ± 0.03 a**	22.86 ± 0.06 c
Unassisted forest restoration	4.83 ± 0.01 b	5.90 ± 0.01 c	76.56 ± 0.11 b
Natural ecosystem	4.63 ± 0.01 c	6.66 ± 0.05 b	**101.96 ± 0.02 a**
t-test (tropical × subtropical)	14.64***	9.04**	114.81***

Different small letters at the same column represent statistically significant differences by land uses after Tukey's test ($p < 0.05$).

*** and ** significative differences at $p < 0.01$

Multivariate analyses

The PCA analyses showed that soil organic carbon, soil pH, Fungivores, Bacterivores, *R. coralloidea*, *D. scutata*, *D. erythrophus* were the main factors contributing to the data variance. Our results showed that Tropical ecosystem were dissimilar to the subtropical ecosystem. The analyses also showed the following aspects: i) negative correlation among *R. coralloidea* with soil pH, *D. scutata*, and *D. erythrophus*; ii) positive correlation between soil organic carbon, and *R. coralloidea*; and iii) positive correlation between Fungivores and Bacterivores. The two axes represent 79.53% of the data variance (Fig. 2).

Discussion

Our results emphasized the influence of the land use on soil microbiota complexity (e.g., number of spores and soil nematodes' abundance) during the three studied years. We must consider that land uses with high root growth (e.g., rootability) such as the agroforestry system and unassisted forest restoration, may promote the specific ecological patterns into the soil microbiota community that made them dissimilar to the natural ecosystem. It in turns increase the abundance of some AMF species and soil nematodes individuals (Terefe et al. 2021) and can create a disturbed plant-soil interaction (Tedersoo et al. 2018), by promoting some AMF species (e.g., *Claroideoglomus* and *Funneliformis*) and soil nematode groups (Fungivores, Bacterivores, Omnivores, and Carnivores). In our study, *F. mosseae* (Glomeraceae), and *C. claroideum* (Claroideoglomeraceae) showed the highest abundance in all land uses. Some studies have reported *Claroideoglomus* and *Funneliformis* (frequency of occurrence by 23.4 and 20.5%, respectively) as the most dominant AMF genera in different land uses in tropical, and subtropical ecosystems (Laurindo et al. 2021, Terefe et al. 2021, Lucena et al. 2018). These AMF species are considered as bioindicators of high human activity and soil degradation. These results agree with the host-specificity hypothesis (Souza and Freitas 2018), and it determines the ecological preference (e.g., more effective symbiosis) between the plant species within each studied land use, and the identified AMF species and soil nematode functional groups (Melo et al. 2020, Zhang et al. 2021). Thus, highlighting the role of land uses on structure of complex and dynamic microbial communities such as the AMF and soil nematode communities.

The soil nematode complexity is directly linked with the energy fluxes, soil organic carbon pools, and soil food web into the entire ecosystem at spatial scale (Kooch et al. 2020, Nielson et al. 2020). These soil organisms play important ecosystem services (e.g., nutrient cycling, soil carbon dynamic, net primary production, and herbivory control), through their food behaviour (Nisa et al. 2021). We found differences into the soil nematode ecological patterns among the studied ecosystems (e.g., agroforestry system, unassisted forest restoration, and natural ecosystem). It may show an important aspect linked to the land use and its capacity to provide feeding sources, and habitat to a wide range of soil nematode groups (Siebert et al. 2020, Yang et al. 2021). Bacterivores and Fungivores are soil nematode groups that can feed the organic matter decomposers (e.g., bacterial and fungi, respectively). Both functional-groups indirectly control the organic matter mineralization rate, nutrient cycling, and plant-soil interaction (Kou et al. 2020).

Our results showed that in the natural ecosystem, the high diversity of plant species plus high temperatures promote the leaf litter diversification on soil surface and SOC pools. Into this condition, the decomposers' activity, and their abundance increase, thus promoting food sources for bacterivores and fungivores. It creates a positive plant-soil interaction into the soil nematode community structure (Silva et al. 2021). Omnivores and Carnivores are soil nematode groups that promotes the micro-regulation process by reducing herbivore nematodes and other protists' abundance. They also play an important role into the organic matter decomposition rate by controlling other soil organisms (e.g., Bacteria, Fungi, and even other soil nematodes) (Timper et al. 2021). They are extremely influenced by changes into the soil ecosystem promoted by land use and climate type because they are dependent of a complex soil food web (e.g., presence of other nematodes, and microbiota groups), such as we have found in the natural ecosystem (Wu et al. 2021).

Agroforestry systems that present a habitat simplification, low soil carbon pools, low soil water content, and some previous anthropogenic actions may decrease the abundance of these groups, especially Carnivore soil nematodes (Le Provost et al. 2021). The herbivores play an important role in the ecosystems by promoting the net primary production, because they feed roots, thus stimulating belowground growth (e.g., fine roots), and improving nutrient uptake (Gilarte et al. 2020). However, in the agroforestry system at Tropical conditions, we found a high abundance of herbivores through the low abundance of functional groups that act promoting micro-regulation (e.g., Carnivore and Omnivores). Here, we can consider it as a negative bioindicator by showing a soil food web disruption (Peralta et al. 2020, Ye et al. 2020).

The differences in soil microbiota ecological indices among the studied ecosystems were revealed by the significance on both soil microbiota richness and diversity. In this study, we did not find significance differences for dominance. We observed that on agroforestry systems at tropical ecosystems there was the highest values of soil microbiota richness and diversity. It is related to the specific ecosystem conditions (e.g., temperature and precipitation), and soil properties (e.g., soil pH, water availability, Olsen's P, and total nitrogen) from the Tropics (Nascimento et al. 2021). We must consider that tropical soils when compared to subtropical ones, can provide a better environment for a wide range of soil microbiota organisms (Silva et al. 2021). It also determines the composition and functioning of the entire soil food web (Chernov et al. 2021). On the other hand, we must consider that in the unassisted forest restoration we found the highest values of richness and diversity. According to studies from elsewhere (Laurindo et al. 2020) into this system we can found high rootability (e.g., root growth and activity) that increase the abundance and diversity of soil organisms, such as mycorrhizal fungi and soil nematodes. These soil organisms occur into the rhizosphere through biochemical signals (Souza 2015). On the other hand, we found the highest diversity in the agroforestry system. Here, we must consider that the agroforestry system promoted soil microbiota community structure through the rhizodeposition process (Lucena et al. 2021), by releasing C-rich compounds into the rhizosphere, thus promoting habitat provision for soil microbiota (Nascimento et al. 2021).

The differences in soil chemical properties between the studied ecosystems were modulated by plant diversity on different land uses (e.g., agroforestry system, unassisted forest restoration, and natural ecosystem). In our study, we observed that agroforestry system was useful to promote soil pH, and Olsen's P, whereas natural ecosystem promoted higher soil organic carbon. Overall, two different mechanisms may be involved at the increasing these soil chemical properties into these two conditions: i) rootability by fine roots production, and ii) H^+ extrusion in root zone (Melo et al. 2020, Gao et al. 2020). We cannot exclude that the increase in soil organic carbon is driven by rhizodeposition at high plant community diversity (Zarafshar et al. 2020, Zhang et al. 2021). Finally, the introduction of native tree species into an agroforestry system can cause changes in soil chemical properties as described by the island of fertility hypothesis (Nascimento et al. 2021). Furthermore, many tree species used in agroforestry systems are highly dependent on AMF species to adapt to soil phosphorus deficiencies (Muchane et al. 2020). Consequently, this changes the rhizobiome, and increases the phosphorus availability to plants (Dierks et al. 2021).

Overall, considering the PCA analysis the natural ecosystem was correlated to the highest abundance of Fungivores, Bacterivores, and soil organic carbon. Natural ecosystems usually present high plant diversity (Liu et al. 2020). It favours the habitat provision and source availability for the soil microbiota, thus increasing the functional-groups diversity (Chen et al. 2020). Changes into soil ecosystem may influence both habitat and the source availability, which can create a cascade of events thus creating a negative or positive plant-soil feedback (Singh et al. 2021). On the other hand, changes into habitat provision can promote the functional redundancy process (e.g., a negative plant-soil feedback). It can explain the AMF community and soil nematodes community changes in the studied ecosystems (Pyles et al. 2020). Different land uses with low plant diversity can promote soil quality loss and soil microbiota community disrupting (Wang et al. 2021). In turns, it reduces the AMF and soil nematode richness (Ossowicki et al. 2021). PCA analysis also showed that fungivore and bacterivores were the most representative soil nematode functional groups (Wilschut et al. 2020). Besides that, Gigasporaceae were the most representative AMF family. Gigasporaceae species (*D. scutata* and *D. erythropus*) predominates in soils with acid pH. Our results of soil organic carbon were inversely related to the soil pH, what explained the predominance of AMF species in tropical conditions. These results agree with the work done by Laurindo et al. (2021), that described the highest values of soil organic carbon, and Gigasporaceae abundance (e.g., *R. coralloidea*) in subtropical sites.

Our study revealed that the soil microbiota complexity and soil abiotic traits were influenced by the land use. Soil organic carbon, soil pH, Fungivores, Bacterivores, *Racocetra coralloidea*, *Dentiscutata scutata*, and *D. erythrophus* were the main factors contributing to the data variance. Our work increases the understanding of the soil microbiota complexity in the rhizosphere of agroforestry systems and unassisted forest restorations in tropical and subtropical ecosystems. We provided evidence that land uses strongly influence both AMF and soil nematode complexity at local scales. Also, our results demonstrated how agroforestry system can affect soil microbiota assemblage and the soil abiotic traits when compared to a natural ecosystem. Differences in soil microbiota ecological patterns were associated with (1) the land uses by promoting different habitat provision, as we found difference on soil microbiota abundance, richness, and diversity, (2) changes in soil properties such as, soil pH, soil organic carbon, and available P, and (3) rhizodeposition by differences on soil organic carbon content into the land uses as observed into the PCA analysis. The most abundant AMF species in all the soil samples were *Claroideoglomus claroideum*, *Funneliformis caledonius*, and *F. mosseae*. This study shows the importance to consider how land uses can affect soil abiotic traits, and how these traits may influence soil microbial ecological patterns at spatial scale.

Declarations

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Compliance with Ethical Standards

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Ethical approval: This article does not contain any studies with huma participants or animals performed by any of the authors.

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Figures

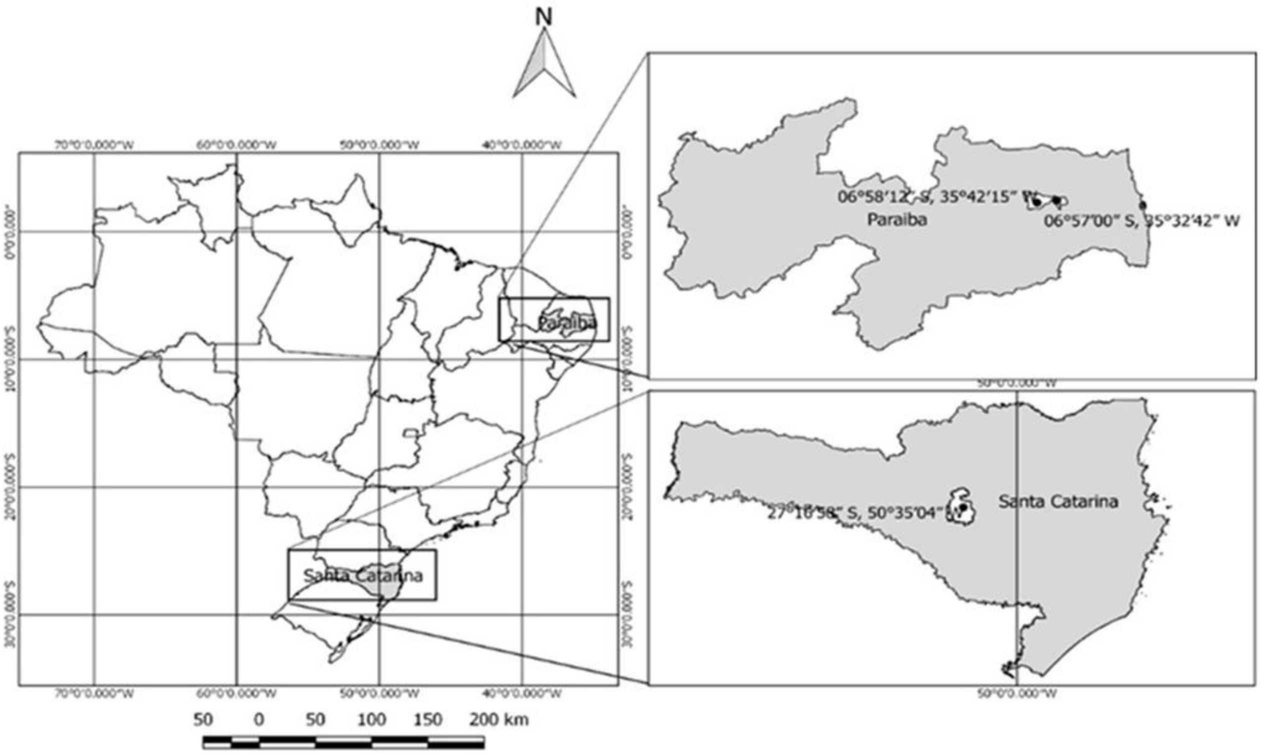

Figure 1

Geographical distribution of the sampling sites, and their main geographic characteristics from the Tropical ecosystem (As- and Aw-climate type, Paraiba), and subtropical (Cfb-climate type, Santa Catarina).

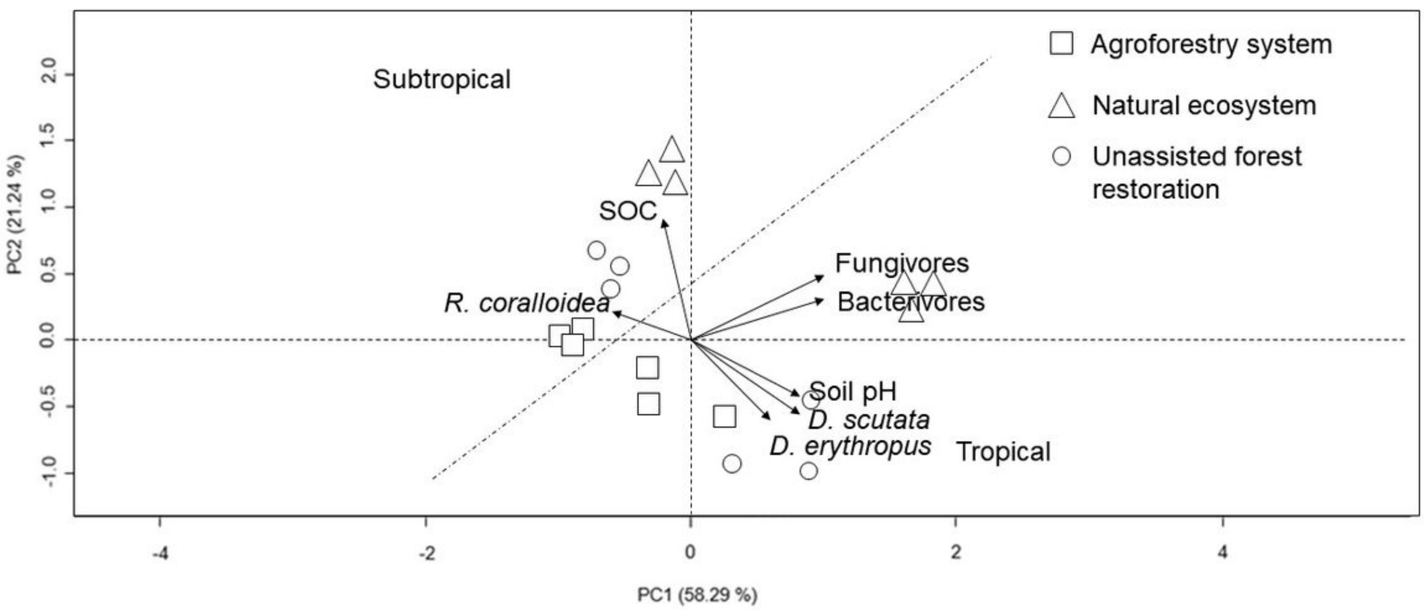

Figure 2

PCA score plot of AMF community and soil nematodes structure here represented by the abundance of AMF species (spores g soil^{-1}), soil nematodes (ind. g soil^{-1}), and soil chemical properties. SOC= soil organic carbon.