KAREN LIZETH POLANÍA HINCAPIÉ

SOIL BACTERIAL COMPOSITION AND DIVERSITY DYNAMICS IN ATLANTIC FOREST AND COFFEE CULTIVATION IN SOUTHEASTERN BRAZIL

LAVRAS - MG
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Prof. Dr. Teotonio Soares de Carvalho
Orientador
Profa. Dra. Fatima Maria de Souza Moreira
Co-orientadora

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DINÂMICA DA DIVERSIDADE E COMPOSIÇÃO BACTERIANA DO SOLO EM MATA ATLÂNTICA E PLANTAÇÕES DE CAFÉ NO SUDESTE DO BRASIL

Dissertação apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ciência do Solo, área de concentração em Biologia, Microbiologia e Processos Biológicos do Solo, para a obtenção do título de Mestre.

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Dr. Marco Aurélio Carbone Carneiro	UFLA
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LAVRAS - MG
2024

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Nelson Rufino

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Nelson Rufino

RESUMO GERAL

A atividade antropogênica no bioma da Mata Atlântica no Brasil tem se intensificado ao longo do tempo, transformando-o principalmente em áreas de cultivo e assentamentos populacionais. O cultivo do café é uma atividade agrícola exercida nesse bioma. No entanto, as implicações dessa atividade na diversidade biológica ainda são pouco conhecidas, especialmente no que diz respeito à dinâmica da comunidade bacteriana do solo. O objetivo deste estudo foi avaliar como a conversão de áreas naturais de Mata Atlântica em plantações de café afeta a composição e a diversidade da comunidade bacteriana do solo. Para isso, foram coletadas amostras de solo por meio de um desenho de transectos em áreas de Mata Atlântica e plantações de café, e as comunidades bacterianas foram avaliadas por meio de uma abordagem metataxonômica. Nossos resultados mostraram que a conversão da Mata Atlântica para o cultivo de café promove a diversidade bacteriana alfa e gama do solo, intimamente relacionada ao aumento do pH do solo. As plantações de café são comumente tratadas com fertilizantes e corretivos (aplicações de calcário), e isso permite uma redução da acidez do solo, promovendo a atividade bacteriana. Uma maior disponibilidade de nutrientes e uma diminuição da acidez do solo foram fatores diferenciadores na composição bacteriana do solo. Nas áreas de Mata Atlântica, a acidez do solo e o Fe provocam mudanças na composição bacteriana, e nas plantações de café a composição bacteriana foi associada a um gradiente de fertilidade. A disponibilidade de P e a textura também foram atributos diferenciadores da estrutura bacteriana do solo entre os usos da terra. A Mata Atlântica apresentou uma composição bacteriana associada à maior disponibilidade de P e ao teor de argila, e as plantações de café, ao maior teor de silte. A conversão da Mata Atlântica em plantações de café promoveu a abundância de alguns filos bacterianos e uma maior proporção de Proteobacteria para Acidobacteria. Por fim, a variação da comunidade bacteriana do solo foi explicada principalmente pelas propriedades do solo.

Palavras-chave: Atividade biológica do solo. Acidez do solo. Disponibilidade de nutrientes. Dinâmica bacteriana do solo. Estrutura bacteriana.

ABSTRACT

Anthropogenic activity in the Atlantic Forest biome in Brazil has been intensified over time, transforming it mainly into cultivation areas and population settlements. Coffee cultivation is an agricultural activity exerted on this biome. However, the implications of this activity on biological diversity are still poorly understood, especially concerning soil bacterial community dynamics. This study aimed to assess how the conversion of natural Atlantic Forest areas to coffee plantations impacts soil bacterial community composition and diversity. For this purpose, soil samples were collected through a transect design in areas of Atlantic Forest and coffee crops, and bacterial communities were assessed by using a metataxonomic approach. Our results showed that the conversion of Atlantic Forest to coffee cultivation promotes soil alpha and gamma bacterial diversity, closely related to increases in soil pH. Coffee plantations are commonly treated with fertilizers and correctives (lime applications), and this last allows a reduction of soil acidity promoting bacterial activity. A greater nutrient availability and a decrease in soil acidity were differentiating factors in soil bacterial composition. In Atlantic Forest areas, soil acidity and Fe drive changes in bacterial composition, and in coffee plantations bacterial composition was associated with a fertility gradient. P availability and texture were also differentiating attributes of soil bacterial structure among land uses. Atlantic Forest had a bacterial composition associated with higher P availability and Clay content and Coffee plantations with a higher Silt content. Conversion of Atlantic Forest to coffee plantations promoted the abundance of some bacterial phyla and a higher Proteobacteria to Acidobacteria ratio. Finally, the variance of the soil bacterial community was mostly explained by soil properties.

Keywords: Soil biological activity. Soil acidity. Nutrient availability. Soil bacterial dynamic. Bacterial structure.

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1 INTRODUCTION

Atlantic Forest has been considered one of the most biologically diverse global biomes. It is estimated that there are about 20 thousand plant species (35% of the species existing in Brazil) and is home to great biodiversity, providing multiple essential ecosystem services for the 145 million Brazilians who live in it (METZGER, 2009; JOLY et al., 2014). This important biome has been constantly threatened by forest degradation, forest area has been reduced to approximately 28% of its original area, initially due to the implementation of sugarcane and later of the coffee cycle, and more recently, due to demographic occupation (METZGER, 2009; COLOMBO; JOLY, 2010; SANTANA; DELGADO; SCHIAVETTI, 2020). Minas Gerais state is one of the main coffee producers in Brazil (responsible for 54.3% of Brazilian coffee production), and Atlantic Forest originally covered 47% of this territory, and currently, only 10.3% remains (2.8 million hectares), with coffee plantation establishment being one of the main drivers of land use change (an estimated cultivated area of 1.25 million hectares) (CONAB, 2020; INPE PRODES, 2020).

Nevertheless, the impact of natural areas transformation into agricultural areas on soil biological properties, and especially on soil bacterial community dynamics, is little understood (CARVALHO et al., 2016). Soil bacterial community fulfills important functions within natural and agricultural ecosystem dynamic, they are essential for plant nutrition and health, as they contribute to nutrient availability by mediating nutrient cycling, participate in processes of organic matter decomposition, xenobiotics degradation, and soil aggregates formation, plant growth promotion, among others necessary for the sustainability of ecosystems (BARDGETT; PUTTEN, 2014; JACOBY et al., 2017).

Bacterial communities are also strongly manipulated by land management practices, so they can form groups based on similar soil conditions and successfully predict specific qualitative values of soil attributes (HERMANS et al., 2020). Therefore, bacterial diversity and composition play an important role in ecosystem assessment so they are commonly used as sensitive indicators to monitor changes in soil quality (ZHANG et al., 2020; DUAN et al., 2022).

Coffee crops are commonly treated with fertilizers and correctives to increase nutrient availability and decrease soil acidity, practices that can modify soil bacterial community diversity and composition (XIONG et al., 2015; ZHAO et al., 2019). Additionally, plant cover homogenization through monoculture implementation could also drive changes in soil bacterial

community dynamics (ARROYO-RODRÍGUEZ et al., 2013; XIONG et al., 2015). A study by Zhao et al. (2018) showed that continuous coffee cultivation decreased soil pH and organic matter, affecting soil bacterial alpha diversity, which was also reduced. Relative abundances of several bacterial phyla including Proteobacteria, Bacteroidetes, and Nitrospira decreased over time and showed positive relationships with coffee plant growth. However, other authors have found contrasting results, reporting that conversion of native areas in agricultural systems based on monocultures increased bacterial alpha diversity, attributed to higher soil pH and nutrient availability (RODRIGUES et al., 2013; TRIVEDI et al., 2016; CARVALHO et al., 2016).

Soil bacterial communities can provide biologically relevant information on the impacts of land use and agricultural practices on soil ecosystems and soil quality because of their direct participation in multiple ecosystem processes and because they are strongly responsive to changes in soil conditions, especially pH, organic compounds, redox, nutrients availability, water, and temperature (HARTMAN et al., 2008; PAZ-FERREIRO; FU, 2016; BÁRCENAS-MORENO; BÅÅTH; ROUSK, 2016; HERMANS et al., 2020). Thus, understanding the dynamics of soil bacterial communities when natural ecosystems are transformed into cultivated areas, and how these may be associated with soil quality is crucial to guide decision-making and improve plant productivity and ecosystem functioning. Therefore, this study aimed to assess how the conversion of natural Atlantic Forest areas to coffee plantations impacts soil bacterial community composition and diversity.

2 THEORETICAL BACKGROUND

2.1 Soil microbial community dynamics in native vegetation and agriculture areas

Agriculture is one of the main anthropogenic activities responsible for the conversion of natural ecosystems into human-modified landscapes, usually leading to native plant cover loss by deforestation processes (GRANADA et al., 2019), which often results in soil properties degradation, erosion, and increased greenhouse gases emissions (CHEN et al., 2019; AHMAD et al., 2020). However, agricultural activity is of great social and economic importance, as it is responsible for feeding the human population (HERRERO et al., 2017). Therefore, there is a constant need for agriculture with less environmental impact, and strategies such as ecological intensification, bioinputs use, and agroecosystems diversification to increase biological

processes in agricultural production are promising alternatives in the construction of sustainable agriculture (TITTONELL, 2014; ISBELL, 2015; SIDDIQUI et al., 2019).

A reduction in plant cover influences the local temperature, luminosity, humidity, litter conditions, nutrient availability, and soil acidity, altering soil microbial community dynamics (CHAUDHARY et al., 2016; DELGADO-BAQUERIZO et al., 2016; GUO et al., 2018; JATOI et al., 2019). For instance, Muñoz-Arenas et al. (2020) detected that the transformation of forest to arable land decreased bacterial diversity by about 45%-75% in alpha diversity. However, a meta-analysis by Trivedi et al. (2016) reported that the conversion of natural areas to agriculture increased significantly alpha bacterial diversity in arid and temperate regions due to an increase in soil pH and higher nutrient availability. Similarly, Carvalho et al. (2016) showed an increased alpha, beta, and gamma diversity when tropical humid forests were converted to mechanized agriculture and pasture. Therefore, the impact of land use on soil bacterial community dynamics could have a wide versatility and should be approached from different points of view.

As a fundamental energy source, nutrient availability is also a major shaper of soil microbial community by determining the metabolism of microbes, especially carbon- and nitrogen-cycling bacteria (KOYAMA et al., 2014; REN et al., 2018). Soil pH has also been considered as one of the main parameters in determining soil microbial composition and diversity, mainly by mediating soil nutrient availability (ZHALNINA et al., 2015; O'BRIEN et al., 2019). This is especially true for bacterial communities, for which soil pH has been pointed out as the most important predictor of bacterial diversity across multiple biomes (FIERER; BRADFORD; JACKSON, 2007; RODRIGUES et al., 2012; CARVALHO et al., 2016; TRIVEDI et al., 2016). In addition, modifications in soil physicochemical properties induced by amendments and fertilizer applications have been associated with soil microbial composition changes in agricultural soils (LAMMEL et al., 2015; CHEN et al., 2019).

In a study performed by Lan et al. (2017), the conversion from forests to rubber plantations had an impact on bacterial composition, resulting in a soil dominated by Bacillaceae (13,60% for rubber plantations and 4,13%-6,92% for forest areas). Jesus et al. (2009) observed that in different land uses (cropland, pasture, agroforestry, secondary forest, and primary forest), soil bacterial community structure was largely shaped by soil attributes. Community structure changed significantly along gradients of base saturation, Al3+, and pH. Merloti et al. (2019), also explained in a chronosequence study that native forest conversion to agricultural soils (rotation of corn and soybean crops) at different ages (2, 8, and 20 years of conversion) affected bacterial composition. In the most abundant phyla, soils of native forests were mainly

composed of Alphaproteobacteria and Gammaproteobacteria, and agricultural soils were composed of Betaproteobacteria and Deltaproteobacteria, influenced mostly by changes in soil pH, nutrient content, crop rotations, and SOM.

The phyla Proteobacteria and Acidobacteria are commonly observed in several soil bacterial libraries (SPAIN et al., 2009). However, differences have been observed in different land uses concerning their abundance and composition, which have importance in the carbon global cycle, nitrogen, and sulfur (SPAIN et al., 2009; RAMPELOTTO et al., 2013). Carvalho et al. (2016), found that the dominance of Proteobacteria was remarkably reduced in intensive (mechanized) agriculture and pasture systems when compared to undisturbed forest areas, possibly due to the preference of Proteobacteria for labile organic C compounds.

Rampelotto et al. (2013), observed that Acidobacteria were more abundant in natural ecosystems (natural and coniferous forests), with acidic pH (4.0-4.2) and low nutrient levels, confirming the idea that soil pH regulates Acidobacteria abundance, which has the metabolic capacity to adapt to more complex soil environments (SAIT et al., 2006; WARD et al., 2009). Natural area conversions to agriculture could modify the dominance of Acidobacteria due to nutrient availability increase and soil acidity reduction through practices such as liming and fertilization. Acidobacteria is also affected by decreasing labile compounds with plant cover reduction (SOLOMON et al., 2007; NAVARRETE et al., 2013, 2015).

2.2 Chemical and physical properties affect soil bacterial community

Soil dynamics contemplate multiple and complex interactions between the soil-plant-microorganism (DASGUPTA; BRAHMAPRAKASH, 2021). Microorganisms play important roles within biogeochemical cycles and influence biological processes above and below the soil contributing to plant nutrition, soil structure, and fertility. However, soil microbial community composition and diversity are largely influenced by soil properties (XUE et al., 2018; QIANG et al., 2021). Some studies on a local and continental scale have suggested the importance of soil properties as drivers of the structure and diversity of microbial communities. Fierer, Bradford and Jackson (2007) conducted a continental-scale study and demonstrated that microbial activity is mainly controlled by edaphic variables. Soil pH was the major shaper of the soil bacterial community, with bacterial diversity being higher in neutral soils and lower in acidic soils. Likewise, Lan et al. (2017) revealed that the most important factor affecting the bacterial community was soil pH, which explained 70.85% of the total variance, as soil acidity

is considered one of the most influential factors in soil microbial community structuration (FIERER; BRADFORD; JACKSON, 2007; PIETRI; BROOKES, 2009; MENG et al., 2019).

Microbial community composition is highly sensitive to changes in the concentration of nutrients such as nitrogen, phosphorus, and potassium in the soil (ALLISON; MARTINY, 2008). Lan et al. (2017), observed that the availability of plant nutrients in the soil (total N, total P, and total K) explained 43.05% of the total variance of bacterial taxonomic composition. Some bacterial groups also could be associated with certain types of elements when native areas are transformed. For instance, Zhang et al. (2016) observed that the abundance of bacterial groups was mostly correlated with the organic C, total N, available N, and available P contents when forest types of change. Zhao et al. (2019) observed in a study of secondary succession that the relative abundance of Actinobacteria phyla was higher in agricultural areas, becoming predominantly dominated by Proteobacteria after 20 years of succession. This behavior was significantly correlated with SOC, TN, NO3--N, NH4+-N contents, plant coverage, and plant diversity.

Labile compounds derived from soil organic matter (SOM) decomposition could favor specific groups of decomposers due to their different survival strategies. Through decomposition, microorganisms release soil enzymes to obtain C and associate with certain nutrients necessary for their growth and activity (SCHNECKER et al., 2014). For example, some groups of copiotrophic bacteria are predominant in soils with more abundant SOC content and more labile organic compounds, while other groups (oligotrophic taxa) generally grow in soil microhabitats with lower C content and with a predominance of less labile pools (FIERER; BRADFORD; JACKSON, 2007; TIAN et al., 2021). Tian et al. (2017), also found that the dominant bacteria (Proteobacteria, Acidobacteria, and Actinobacteria) were highly responsive to SOC content, with Proteobacteria being the most abundant in soils with higher organic C content, in contrast to Acidobacteria, which were present in areas with low resource availability, indicating that soil organic matter plays an important role in soil biological processes. Likewise, studies suggest that vegetation cover and land use systems are consequently important aspects influencing the structuring of soil microorganisms (THOMSON et al., 2015; LACERDA-JÚNIOR et al., 2019; PLASSART et al., 2019).

Agricultural soils in Brazil are commonly treated with lime and fertilizers because of their lower natural fertility derived from intense weathering processes (BUOL, 2009; REZENDE et al., 2022). These practices modify soil pH and increase nutrient availability, which is expected to stimulate bacterial growth (CARVALHO et al., 2016). Ward et al. (2009)

explained that bacterial phyla such as Acidobacteria, Planctomycetes, and Proteobacteria are more abundant in soils treated with fertilizers and higher soil pH. Therefore, it could be presumed that fertilizer applications and soil pH modifications regulate soil biological processes.

Soil texture (such as loam, sandy loam, or clay) considers the proportions of sand, silt, and clay content of the soil mineral fraction (UPADHYAY; RAGHUBANSHI, 2020). Soil particle structuration affects other soil properties such as bulk density, permeability, and porosity, which regulate water retention, infiltration, and gaseous diffusion while providing moisture and air for microbial growth (MOBILIAN; CRAFT, 2021). Najmuldeen; Mohammad; Amin (2010) studied the influence of soil texture on soil microbial population and showed that clay loam and silty clay loam soils had the highest bacterial populations compared to sandy loam and silty loam. This can be explained by the fact that sandy soils have high permeability and low water-holding capacity compared to soils with higher silt and clay content, creating environments less favorable to bacterial growth (GOMEZ et al., 2002; DELGADO-CABALLERO et al., 2009).

The effect of texture on microbial activity is also related to the storage and stabilization of soil carbon (GÓMEZ-GUERRERO; DOANE, 2018). Clay-textured soils generally store higher amounts of carbon than sandy soils due to fine particles having a higher and more reactive specific surface area (SULMAN et al., 2014). For instance, Carney and Matson (2005), mentioned that fine-textured soils support more microbial biomass than coarse-textured soils. Jana et al., (2010) demonstrated that under similar conditions of moisture and temperature, microbial respiration can be higher in fine-textured soils due to higher water holding capacity and organic substrate content per unit mass of soil. It is estimated that clay loam soil produces ~50% higher CO2 than sandy soil (KOWALENKO et al., 1978; UPADHYAY; RAGHUBANSHI, 2020). Therefore, texture, mineralogy, water retention, porosity, and soil carbon are important in evaluating soil microbial populations' dynamics.

2.3 Bacterial community in bulk soil and rhizosphere zone regulates crop yield

Agriculture yield is a component highly related to soil quality, as more productive systems tend to be more stable from a balance between physical, chemical, and biological soil attributes (PAZ-FERREIRO; FU, 2016; ARAGÃO et al., 2020). Soil microorganisms are essential for the continued productivity of sustainably managed agroecosystems, playing

critical roles related to the resistance and resilience of above-ground plant communities to stress and disturbance (WARDLE, 2006; PUTTEN et al., 2016). Therefore, evaluating soil biological processes in agricultural fields is of fundamental economic and environmental importance.

Microbial drivers on crop yields can be understood by the multiple interactions between soil microbes and plant species (STEFAN et al., 2021). Soil microbial community can enhance plant growth through different mechanisms such as phosphate solubilization, phytohormones production, plant-pathogen inhibition, and nutrient acquisition (GU et al., 2020; SONG et al., 2020). Soil biological attributes also function as indicators of soil quality, which is defined as the ability of the soil to sustain, within natural or ecosystem limits, plant or animal productions while maintaining water and air quality and supporting human well-being (KARLEN et al., 1997). Measuring soil quality through indicators for predicting changes in agroecosystems and guiding decision-making has arisen in the last decades. There is a general agreement that soil biochemical and microbiological attributes complement soil quality estimation than only physicochemical attributes, mainly because they can respond quickly to soil management and alterations (GIANFRED; RUGGIERO, 2006; PAZ-FERREIRO et al., 2016), and this component participates in many soil functions such as organic detritus decayed, biogeochemical cycles, nitrogen biological fixation, and others (GARCÍA-ORENES et al., 2009, 2010, 2012).

Microbial biomass, microbial respiration, soil enzymatic activities, N mineralization, and bacteria and fungi proportion, are some of the biological indicators more commonly used for soil quality assessment (SHAO et al., 2008). Nevertheless, in studies advanced in microbial taxonomic identification, soil microbial composition is also considered a soil quality indicator. Plassart et al. (2019) found that soil bacterial composition at the genus level serves as a bioindicator for different land uses associated with soil attributes and geographical distance. These authors detected that arable, grass, and forestry soils with lower quality were associated with Pseudolabrys, Azospira, Elusimicrobium, Pelobacter, Xanthomonas genus; and soils conformed mainly by forest and better soil quality were associated with Blastochloris, Halophaga, Steroidobacter, Gaiella, Bacillus genus, suggesting that land use is a major driver of soil biodiversity (CONSTANCIAS et al., 2015).

Efforts to quantify soil quality are increasing throughout the world and several physical and chemical indicators have been identified (KARLEN; STOTT 1994). However, it is very closely linked to soil biological properties (SINGH; SHARMA, 2020). Most of the indicators are governed by rhizosphere either directly or indirectly. Soil rhizosphere is a

microenvironment contrastingly different from non-rhizosphere soil, and its high microbial activity leads to better cycling and availability of nutrients and improves chemical soil quality indicators (BHADURI et al., 2015). Therefore, soil bacterial diversity and composition belonging to rhizosphere zone could be a biological indicator more sensitive to the alterations caused by agricultural activity, allowing more accurate prediction of changes and guiding the management within the farms.

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SEGUNDA PARTE

ARTIGO 1

CHANGES IN SOIL BACTERIAL DIVERSITY ASSOCIATED WITH THE CONVERSION OF ATLANTIC FOREST TO COFFEE PLANTATIONS IN SOUTHEASTERN BRAZIL

ABSTRACT

In Brazil, the conversion of Atlantic Forest biome into agricultural systems has been highly intensified, with coffee cultivation being one of the main drivers of land use change. However, the impact that the conversion of native areas to agriculture has on soil bacterial dynamics is still poorly understood. Therefore, the objective of this study was to assess how the conversion of natural Atlantic Forest areas to coffee plantations impacts soil bacterial diversity and composition. For this, soil samples were collected along 200 m transects in both land uses (Atlantic Forest and Coffee plantations). The soil bacterial community was evaluated using a metataxonomic approach by sequencing the 16s SSU rRNA gene (V3-V4 region). The resulting sequences were clustered into operational taxonomic units (OTU) at a 97% similarity threshold. Our results showed that conversion of Atlantic Forest to coffee cultivation increased alpha (when q = 0, q = 1 and Faith's Phylogenetic diversity) and gamma (when q = 0 and q = 1) bacterial diversity, which was closely related to an increase in soil pH promoted through management practices such as liming, which is often carried out in these agricultural systems. Acidity and nutrient availability were important shapers of soil bacterial communities. Atlantic Forest had a different bacterial composition, driven by higher exchangeable acidity, exchangeable Al, Al saturation and Fe; and bacterial community composition in coffee plantations was influenced by a fertility gradient (increased pH and higher Ca, Mg, K, P contents). In addition, we found that Atlantic Forest areas can be naturally more fertile and change their bacterial composition. Bacterial composition in Atlantic Forest was also influenced by higher silt content and in coffee plantations by higher P availability and clay content. Bacterial phyla such as Chloroflexi, Firmicutes, Gemmatimonadetes and Planctomycetes were more abundant in the coffee plantations because some of these bacterial groups are favored in soils with reduced acidity. Verrucomicrobia was more abundant in Atlantic Forest because it is easily adapted to more acidic soils. Proteobacteria to Acidobacteria ratio was higher in coffee plantations indicating that this land use has coprotrophic environments. Finally, through the variance partitioning analysis was detected that soil properties explained most of the variance of the soil bacterial community.

Keywords: Land use change, sequencing, soil acidity, liming, nutrient availability.

1 INTRODUCTION

Tropical forests are constantly threatened by vegetation cover removal. For instance, Atlantic Forest formerly occupied about 13% of the Brazilian territory and has now been reduced to 28% of its original area (SANTANA; DELGADO; SCHIAVETTI, 2020; ROSA et al., 2021), despite being one of the 25 main global biodiversity hotspots, supporting 44% of

vascular plants and 35% of vertebrates species (PINTO et al., 2006; RAMOS; NUVOLONI; LOPES, 2022). Currently, an increasing fraction of global biodiversity lives in forest patches embedded in areas dominated by agricultural land (GIBSON et al., 2011; ARROYO-RODRÍGUEZ et al., 2013).

Atlantic Forest was initially transformed by the establishment of crops such as sugar cane and coffee, and later by human settlements, as it is estimated that 70% of the Brazilian population lives in this territory (PINTO; VOIVODIC, 2021; MARQUES; GRELLE, 2021). In Minas Gerais state, Atlantic Forest originally covered 49% of the state's total land area; in 2018, only 10.2% of the original forest cover remained (2.829.026 ha) (BATISTA et al., 2021). Much of this area has been transformed into coffee plantations (1.25 million hectares), making it the largest coffee producer in Brazil with approximately 50% of the country's share of coffee production, and 74% of the total income produced by agricultural activities in Minas Gerais comes from coffee (CONAB, 2020).

However, the impact of the conversion of natural areas to farmland on soil biological activity, and in particular on soil bacterial community, is poorly understood, despite the important role played by these microorganisms in ecosystem maintenance and especially in agricultural production systems (BARDGETT; PUTTEN, 2014). Soil bacteria mediate biogeochemical cycles, controlling soil organic matter decomposition and nutrients cycling such as carbon (C), nitrogen (N), sulfur (S), and phosphorus (P) (FALKOWSKI; FENCHEL; DELONG, 2008; QI et al., 2022). In addition, numerous bacteria promote plant growth and productivity, turning bacterial community structure into an essential indicator of soil health and ecosystem sustainability (HAYAT et al., 2010; XUE et al., 2017). Nevertheless, since soil represents a highly dynamic and complex environment, soil bacterial communities inhabiting this ecosystem can be influenced and altered by many biotic and abiotic factors (KAISER et al., 2016; QI et al., 2022).

Coffee cultivation in Brazil commonly relies on synthetic fertilizers (potassium, nitrogen, phosphorus) and correctives (lime is the most usual Ca and Mg source), which increase nutrient availability and reduce soil acidity to sustain high coffee yields (FENILLI et al., 2008; FERNANDES et al., 2020). These practices could also modify the soil microbial structure and stimulate bacterial growth (BIRKHOFER et al., 2008; CARVALHO et al., 2016). Several studies have shown that fertilizer use increases microbial diversity and biomass, and modifies soil bacterial composition (EILERS et al., 2012; KUMAR et al., 2017; DINCĂ et al., 2022). Li et al. (2014), found that fertilizer use modified soil bacterial structure, increasing

Proteobacteria and Actinobacteria abundance, while Acidobacteria abundance decreased. On the other hand, monoculture establishment could homogenize organic residue inputs into the soil and reduce the diversity of microhabitats and organic compounds, thus reducing soil bacteria diversity (WARDLE, 2006; GUO et al., 2018).

In this context, understanding differences in soil bacterial diversity and composition between natural areas and coffee crops is important to assess the environmental impact of this important agricultural activity and guide the sustainable management of coffee production systems in the Atlantic Forest biome. Therefore, the objective of this study was to compare soil microbial diversity and composition associated with Atlantic Forest areas and coffee crops in southeastern Brazil. We hypothesize that: 1) Atlantic Forest systems have a soil bacterial community more diverse than coffee cultivation areas; 2) coffee cultivation changes soil bacterial communities in relation to natural areas; 3) Soil bacterial community composition can be partially explained by soil physicochemical attributes changes associated with forest conversion to coffee fields; and (4) soil Proteobacteria to Acidobacteria ratio will be higher in Atlantic Forest areas than in coffee crop areas.

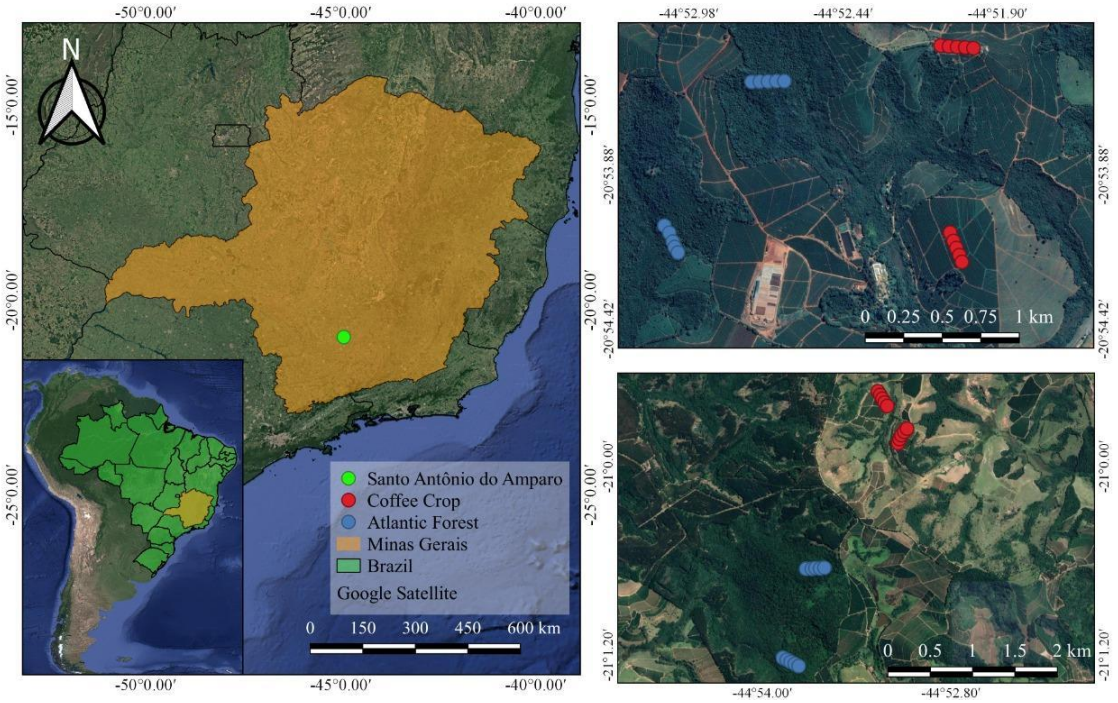
2 MATERIALS AND METHODS

2.1 Study area

This study was conducted in southeastern Brazil, state of Minas Gerais, specifically in the municipality of Santo Antônio do Amparo (Figure 1). The geographical coordinates of this municipality are 20°56′47″S 44°55′8″W, with an altitude of 1013 AMSL. According to Koppen's climate classification, this region is classified as Cwa: Monsoon-influenced humid subtropical climate. Additionally, it presents an average temperature varying from 12 to 28 ºC, relative humidity of 71 %, and annual average precipitation of 1167 mm (MINDAT, 2024).

The experimental areas were selected to represent two land uses typical of this region. The study site is located within the Atlantic Forest biome. Due to the conversion of native areas to agricultural fields over time, a large proportion of the landscape is composed of coffee fields, with only small fragments of native vegetation remaining, usually surrounded by agricultural sites and pastures. Coffee cultivation is managed under conventional agriculture, including heavy use of mineral fertilizers, chemical weed control, fully mechanized harvesting, and reduced vegetative cover between crop rows.

Figure 1 - The geographic location of the study site, in Minas Gerais state, Brazil. Red and blue points indicate soil samples collected in the transect.



The selected study areas have similar altitudes. Soil type is classified as *Latossolo Vermelho-Amarelo* according to the Brazilian classification system and *Oxisol* according to the USDA classification system. These soils are characterized by undulating to strongly undulating relief, medium to low natural fertility, being naturally acidic, with a high level of aluminum saturation, low base saturation, and low phosphorus availability (BARUQUI; NAIME, 2006; FAORO et al., 2010). The selected coffee plantations were characterized by having a clay texture (Clay > 35%) and Atlantic Forest areas presented a medium texture (they have a more uniform distribution among clay and sand particles).

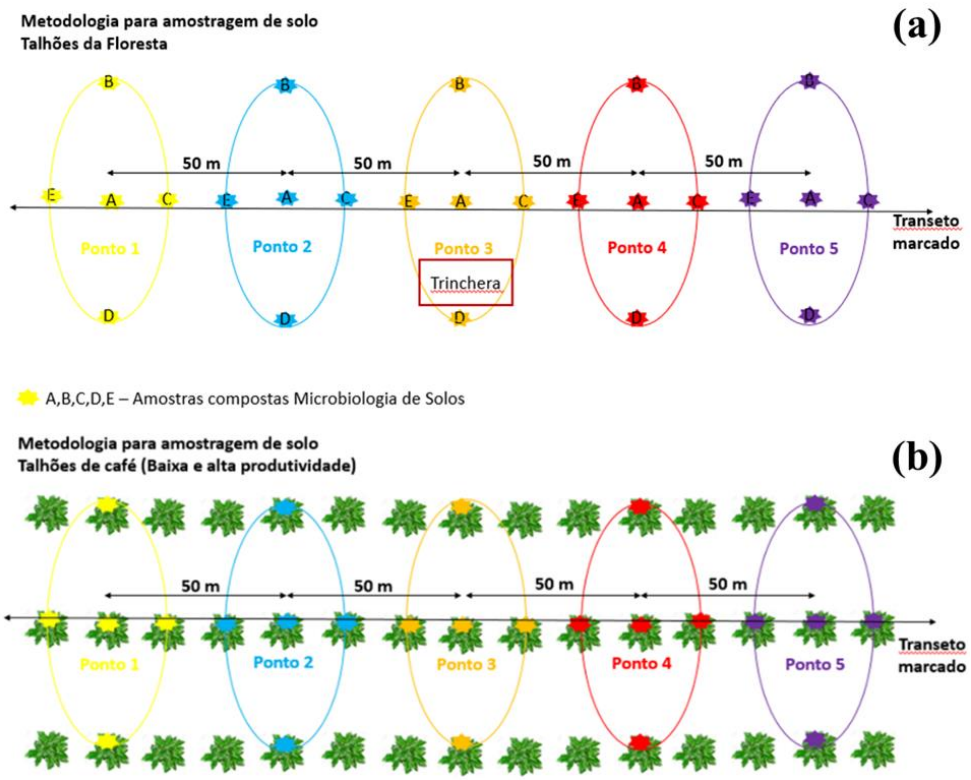
2.2 Soil sampling

Soil samples were collected at the beginning of the dry season along 200 m transects. Each transect was composed of 5 sampling points spaced 50 m apart. In Atlantic Forest and coffee cultivation, 4 transects were selected for each land use system (Figure 1). For Atlantic Forest, at the sampling points, five soil subsamples were collected at the depth of 0-10cm along a circle with a radius of about 2 m centered in the sampling point. Soil subsamples were carefully homogenized to obtain a composite sample (Figure 2a). In the coffee plantations, four

coffee fields, two of Catuaí and two of Catuaí 62 cultivars, were selected. At each sampling point, a subsample was collected from the projection of the coffee plant canopy of the tree directly on the sampling point. Other four subsamples were taken following the same approach for the other four neighboring plants as shown in Figure 2b.

A 20g portion from each soil sample was placed in sterile bags, immediately stored on ice (0 °C) in the field, and then permanently stored in the laboratory at -20 °C until subsequent DNA extraction. Another aliquot of about 500g was used for soil texture and fertility analysis.

Figure 2 - Soil sampling design on the transect. (a) Forest sampling; (b) Coffee sampling.



2.3 Soil physical and chemical analyses

Soil physical and chemical attributes were analyzed to relate them to bacterial community structure. Soil pH was measured in soil suspension and H_2O (1:2.5); phosphorus (P), potassium (K), and soil micronutrients such as zinc (Zn), manganese (Mn), copper (Cu), and Iron (Fe) were extracted by double acid solution (Mehlich I) (MEHLICH, 1953); Boron (B) was extracted by a pressurized hot water method (WEBB; HANKS; JOLLEY, 2006); calcium (Ca), magnesium (Mg), and aluminum (Al) extracted by 1 mol L^{-1} KCl (McLEAN et

al., 1958); potential acidity (H + Al) by the SMP extractant (SHOEMAKER; McLEAN; PRATT, 1961); remaining phosphorus (Prem) was evaluated as described by Alvarez et al. (2000); cation exchange capacity at pH 7.0 (T) by KCl solution 1M and determined by titration with NaOH 0.01M; base saturation index (V) and aluminum saturation (m) were calculated; sulfur (S), extracted by monocalcium phosphate in acetic acid (HOEFT; WALSH; KEENEY, 1973); and texture, by the Bouyoucos method (BOUYOUCOS, 1951).

2.4 DNA extraction, PCR amplification and sequencing

The PowerSoil DNA Isolation Kit (MoBIO Laboratories Inc.) was used for DNA extraction. A 0.25g portion of soil from each sample was weighed and added to PowerBead tubes for the homogenization and cell lysis procedure in a Mobio PowerLyzer bench equipment. All subsequent steps were performed according to the manufacturer's instructions.

For characterizing the bacterial community, a metataxonomic approach was used. Primers 515F-806R targeting the hypervariable V3 region of the 16s SSU rRNA were used as described by Caporaso et al. 2012. Primer barcoding was used to allow multiplexing of samples and decrease sequencing costs (PARADA; NEEDHAM; FUHRMAN, 2016; QUINCE et al., 2011). PCRs were performed by amplifying samples in triplicate in volumes of 25 µL. Triplicate PCR reactions for each sample were pooled in a single volume (75 µL), without combining amplicons from different samples. Amplicons were run on agarose gel expecting a size of ~290 bp. Amplicons were cleaned with MagSi-NGSPREP Plus beads (Magtivio) and quantified using the Qubit 4.0 (Thermo Fisher Scientific, Waltham, MA, USA) and the Qubit dsDNA HS Assay Kit. An equal amount of amplicon from each sample was combined into a single sterile tube and used for the sequencing library preparation. The template library was prepared with the One Touch 2 System with the Ion PGM™ Template Hi-Q OT2 400 Kit. The amplified library was sequenced using the Ion PGM™ Hi-Q Sequencing 400 Kit within a 318™ Chip v2.

2.5 Sequences processing

The QIIME2 tool (BOLYEN et al., 2019) was used for sequencing processing using a docker image (quay.io/qiime2/core:2023.5) to ensure reproducibility of the analysis. All the steps for sequence processing were performed using a bash script available in the Git repository

associated with this manuscript (see section 2.8). Briefly, sequences were demultiplexed and quality filtered using the default parameters. Then, DADA2 was used to remove the first 35 nucleotides from each sequence (for removing primers), denoise and deduplicate sequences, and to truncate the resulting sequences at a length of 215bp, a length at which base call was reliable, as indicated by Phred scores above 25. Then sequences were taxonomically classified using a classifier (gg-13-8-99-515-806-nb-classifier) based on the GreenGenes database (DeSANTIS et al., 2006). Finally, the sequences were de novo clustered into operational taxonomic units (OTUs) at 97% similarity for subsequent analysis using vsearch (ROGNES et al., 2016).

2.6 Diversity and community analyses

The true diversity index (Hill's number) was used to measure alpha, beta, and gamma diversity. These indexes are widely used in ecological studies due to their intuitive capacity to interpret the concept of diversity (HILL, 1973; JOST, 2006). In addition to those, Faith's phylogenetic diversity index was also used (FAITH, 1992).

Given the sampling scheme used in this study, each transect was considered a metacommunity, encompassing the five individual communities from each sampling point. Therefore, we estimated the alpha diversity as the mean of the diversity metrics (Hill's number and Faith's phylogenetic diversity) along the five points in each transect. The gamma diversity was calculated by applying these metrics for the transect as a whole, representing the overall diversity of the metacommunity. Finally, the beta diversity was calculated using the multiplicative decomposition discussed by Jost (2007) by dividing the gamma diversity by the alpha diversity, therefore measuring how heterogeneous the communities are within the metacommunity.

The resulting diversity indexes were analyzed using linear mixed effects models with land use as fixed effects and transect identity as random effects, accounting for the expected dependency between sampling points belonging to the same transect.

2.7 Community composition analysis

To investigate how soil, land use and their interrelationship shape bacterial communities we conducted a redundancy analysis (RDA) on a Hellinger-transformed OTU table using the

Vegan 2.6 in R 4.3, as described in de Carvalho et al. (2016). The significance of the RDA was assessed using restricted permutations because of the nested nature of the sampling points within each transect. To circumvent the high degree of correlation between soil variables, the explanatory matrix of soil variables was prepared by conducting a principal component analysis on the original variables and extracting the first three components, which accounted for 78% of the variation in the original data. Then, a backward selection procedure was used to remove those variables with non-significant contribution in the RDA (LEGENDRE, 2018). A variation partitioning procedure was used to disentangle the effects of land use, soil variables and their shared effects using the varpart procedure in Vegan. Finally, to visualize the contribution of the original soil variables on the RDA plot, we projected the original variables using the envfit procedure from Vegan.

2.8 Data availability

To ensure reproducibility of our results, all data and scripts used to generate the results presented here are publicly available in the form of a Git repository: https://github.com/teodecarvalho/SAABacterialCommunity.git.

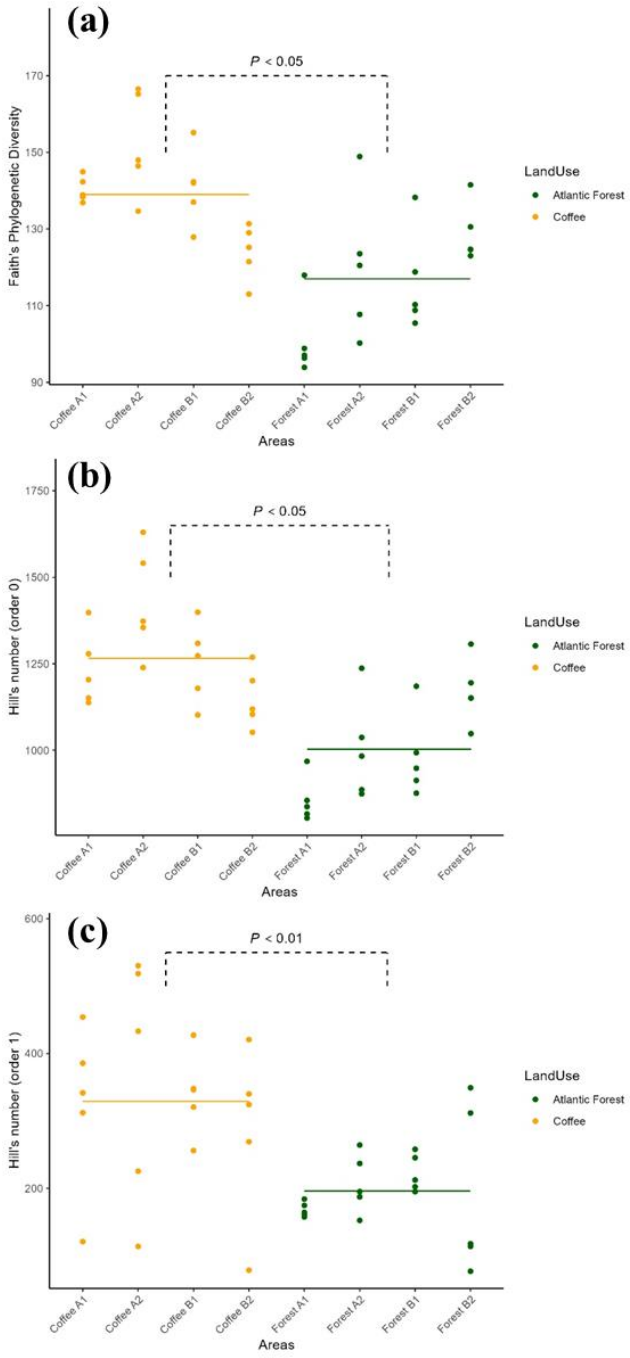
The raw sequences from this study and their associated metadata are available in the Sequence Read Archive database from NCBI under the BioProject with accession PRJNA1011846.

3 RESULTS

3.1 Soil bacterial diversity related to land use change

Bacterial and phylogenetic alpha diversity was generally higher in all coffee cultivation systems than in Atlantic Forest systems (Figure 3). The Faith's phylogenetic diversity in coffee cultivation areas was significantly ($p < 0.05$) greater compared to Atlantic Forest areas (Figure 3a). Another metric of diversity, Hill's number, had similar behavior, both when all OTUs ($q = 0$) and "typical" OTUs ($q = 1$) were considered, with coffee farming systems presenting consistently more diverse bacterial communities than Atlantic Forest systems (Figure 3bc).

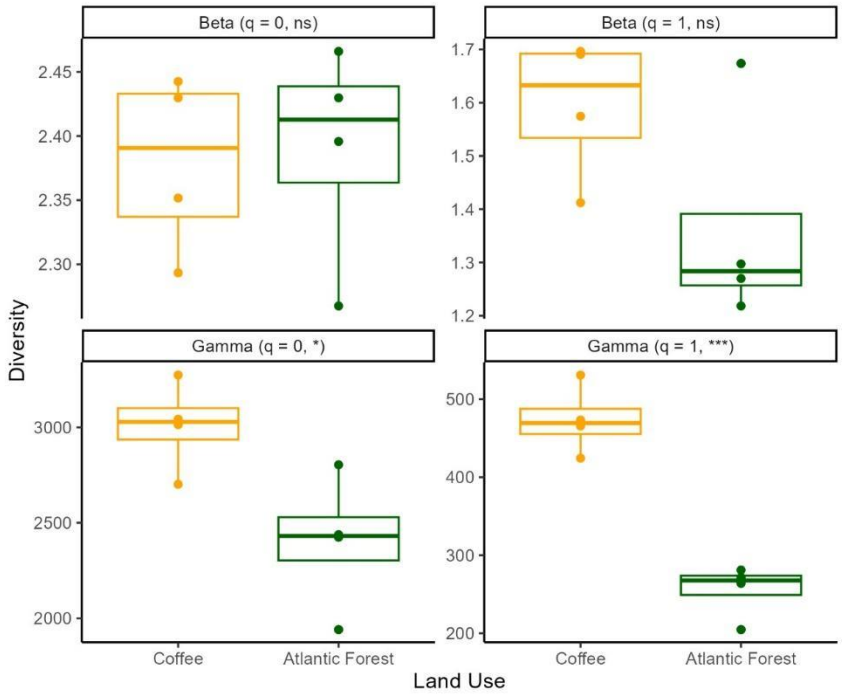
Figure 3 - Soil bacterial alpha diversity based on Hill's numbers and phylogenetic diversity. (a) Faith's phylogenetic diversity; (b) Hill's number of order 0 (q = 0, Richness); (c) Hill's number of order 1 (q = 1, typical" OTUs). Yellow and green lines indicate the mean for each land use system (Coffee, n = 20; Atlantic Forest, n = 20). Significant at $P \leq 0.05$; Significant at $P \leq 0.01$



On the other hand, beta diversity, a measure of community heterogeneity, did not differ among land uses for both all OTUs (q = 0) and for "typical" OTUs (q = 1) (Figure 4). However, gamma diversity presented a similar behavior to previous alpha diversity metrics, with coffee

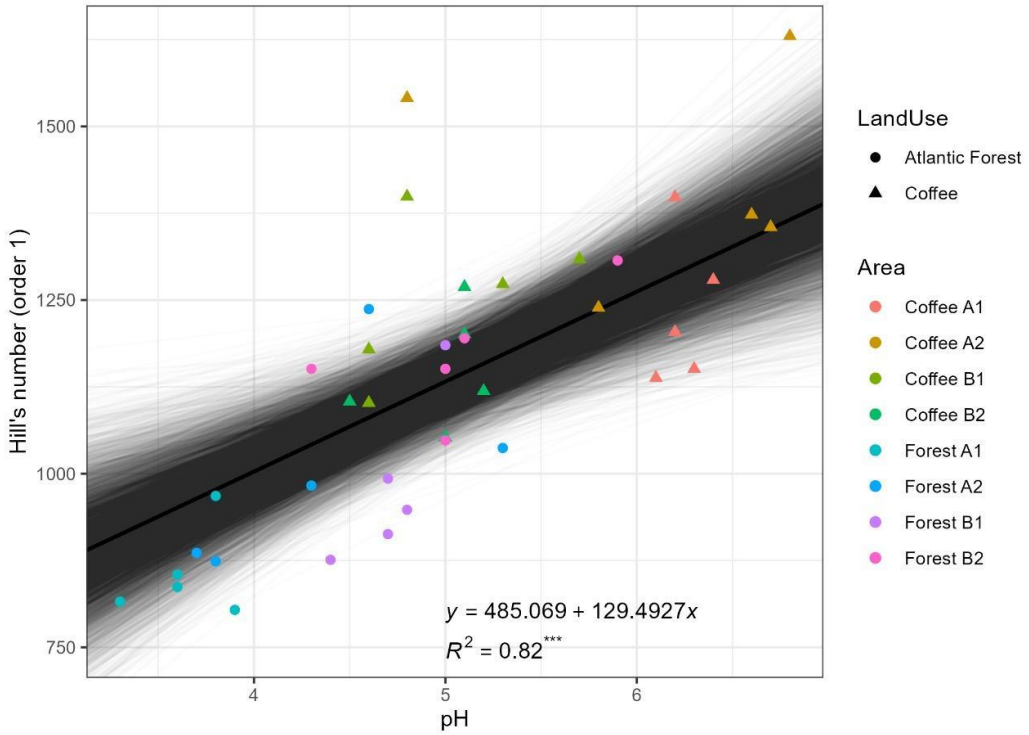
cultivation systems being significantly more diverse than Atlantic Forest areas ($p \leq 0.05$ for $q = 0$; $p \leq 0.001$ for $q = 1$).

Figure 4 - Beta and Gamma diversity for all OTUs (q = 0), and "typical OTUs (q = 1). The box plots indicate data distribution (Coffee, n = 20; Atlantic Forest, n = 20). Yellow and green lines in bold indicate the mean for each land use system. * Significant at $p \leq 0.05$; ** Significant at $p \leq 0.01$; *** Significant at $p \leq 0.001$; ns, no significant.



Bacterial alpha diversity (Hill's number when q = 0) was strongly related to soil pH for the evaluated land use systems (Figure 5). A positive association was detected between the variables, indicating that areas with higher pH had a greater bacterial diversity. This result is closely linked with the observed higher alpha diversity in coffee systems because these cultivated soils showed higher pH values (i.e. they are placed at the right end of the pH gradient), where higher diversity was expected based on the observed relation between soil pH and alpha diversity.

Figure 5 - Model relating alpha diversity (typical OTUs, equivalent to Hill's number when q = 1) and soil pH for each transect. The fitted values for each model are represented as the black line and their standard errors are indicated by the shaded area.



3.2 Soil bacterial composition related to land use change

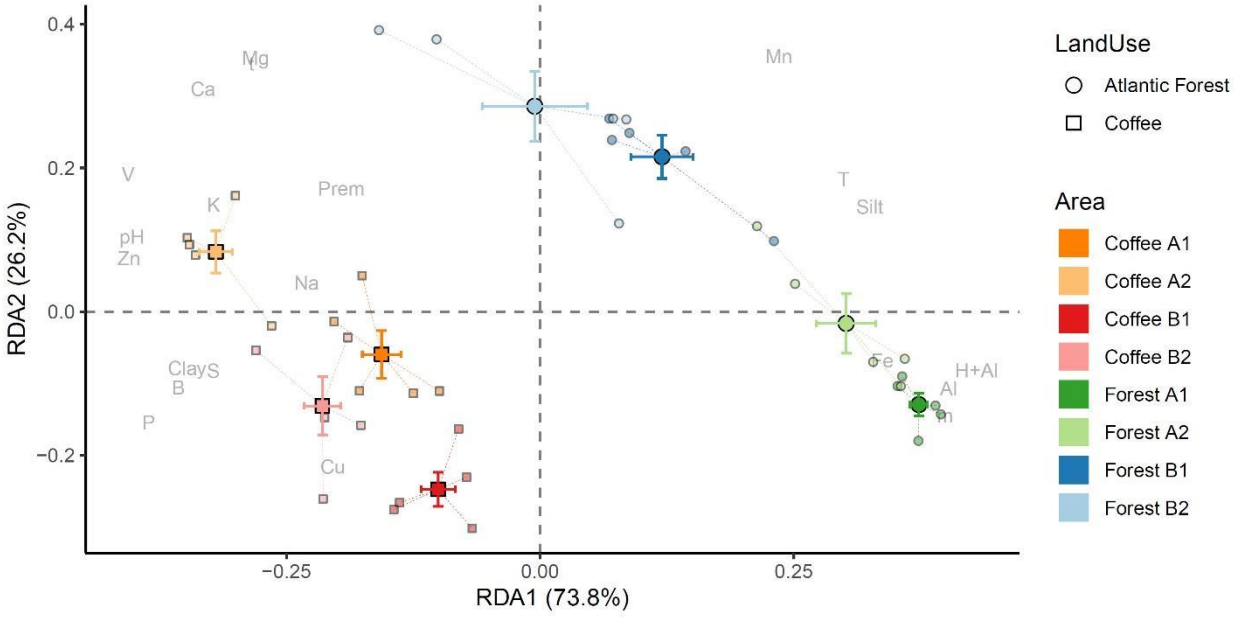
Soil bacterial community composition was clearly distinct among land uses and this was also related to changes in soil properties, as indicated by the redundancy analysis. The ordination of soil bacterial community composition constrained by land use and soil properties evidenced a clear fertility gradient, associating Atlantic Forest areas (Forest A1 and A2) with soil indicators such as Fe, Al, m, and H+Al, and Coffee areas with indicators such as pH, K, V, P, Prem, Ca, Mg, among others (Figure 6). Therefore, Coffee and Atlantic Forest areas were significantly separated from each other, indicating that areas destined for Atlantic Forest have a different bacterial composition than those destined for Coffee use (Figure 6). Soil land use separation within the RDA was also influenced by soil indicators, with Coffee areas having a higher P and Clay content, and Atlantic Forest areas having a higher Silt content.

On the other hand, although a clear land use separation was observed, a quite differentiated separation was also detected between Atlantic Forest areas composed of Forest A1 and Forest A2 in relation to Forest B1 and Forest B2 areas (Figure 6). Furthermore, the distance between these areas could be compared with the distance observed between land uses

(Coffee and Atlantic Forest), indicating a considerable variability in their bacterial community composition that is not explained by land use only. Additionally, the ordination of Forest B1 and Forest B2 areas follows the fertility gradient observed in redundancy analysis, indicating that they have high natural fertility in the soil surface layer evaluated (0-10 cm).

Another interesting finding in this RDA was that, although Coffee A1 and Coffee A2 plots are geographically closer to each other than to Coffee B1 and Coffee B2 plots, Coffee A1 and Coffee B2 areas have more similar bacterial communities relative to each other than to their respective neighbors (Figure 6), evidencing the soil management influence on bacterial composition.

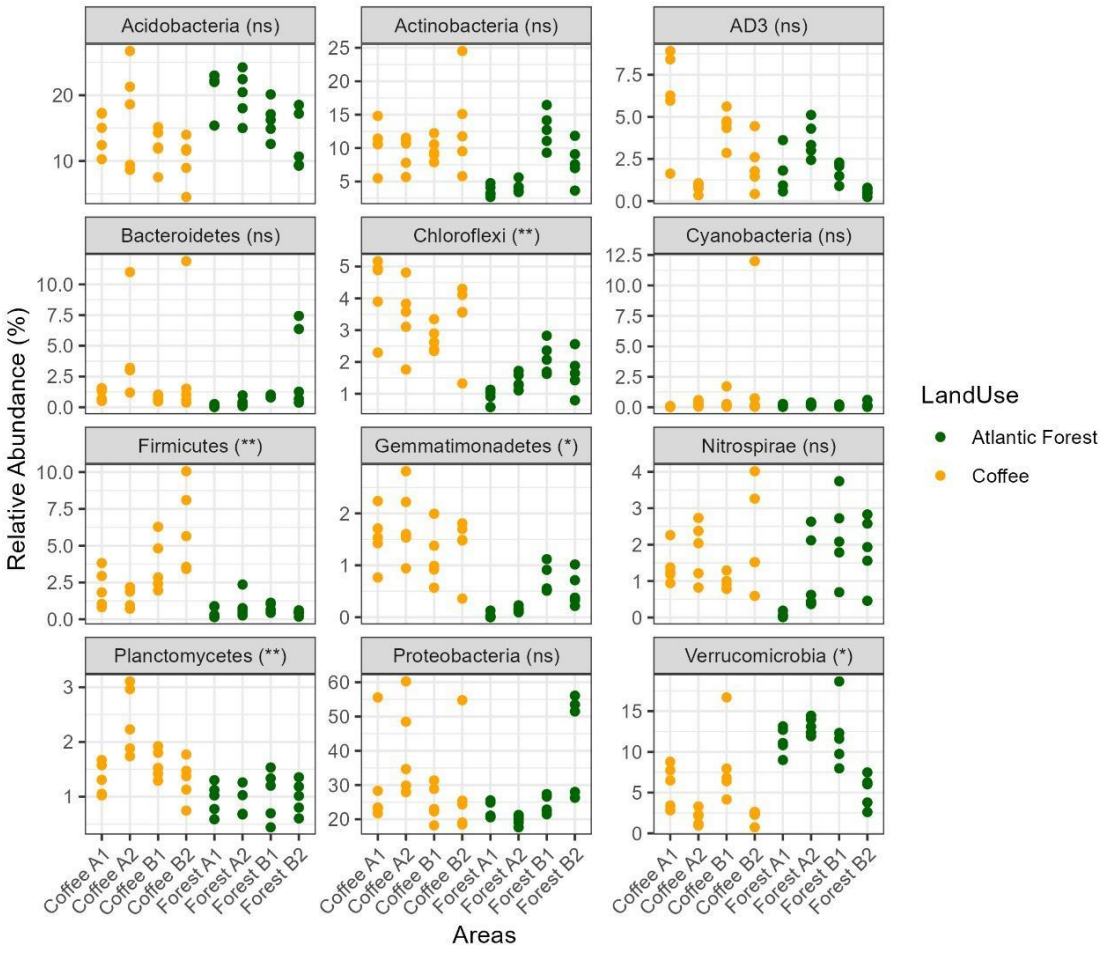
Figure 6 - Redundancy analysis of the effect of the land use on soil bacteria composition in southeastern Brazil. The circle symbol indicates areas of Atlantic Forest (containing Forest A1, Forest A2, Forest B1, and Forest B2) and the square symbol indicates areas of coffee (containing Coffee A1, Coffee A2, Coffee B1, and Coffee B2). Larger circle or square symbols represent the mean in the transect. Smaller circle or square symbols represent the results of each sample in the transect. Error bars indicate the standard error. The percentages indicated on both axes represent the fraction of the community variation explained by land use (33% of the total variation) that is represented by the respective axis. V, base saturation; m, aluminum saturation; T, potential cation exchange capacity; Prem, remaining phosphorus.



Variance partitioning using soil properties and land use as explanatory matrices in RDA indicated that both matrices together explain 33% of the total variation in bacterial community composition.

Figure 7 compares the soil bacteria relative abundance of the twelve most abundant phyla for both Coffee and Atlantic Forest systems. Generally, bacteria relative abundance did not differ significantly for most bacterial phyla, except for the phyla Chloroflexi, Firmicutes, and Planctomycetes, which were significantly ($p \leq 0.01$) more abundant in coffee cultivation systems; or Gemmatimonadetes and Verrucomicrobia, which had a higher bacteria relative abundance in Coffee areas (significant at $p \leq 0.05$) when compared to Atlantic Forest areas.

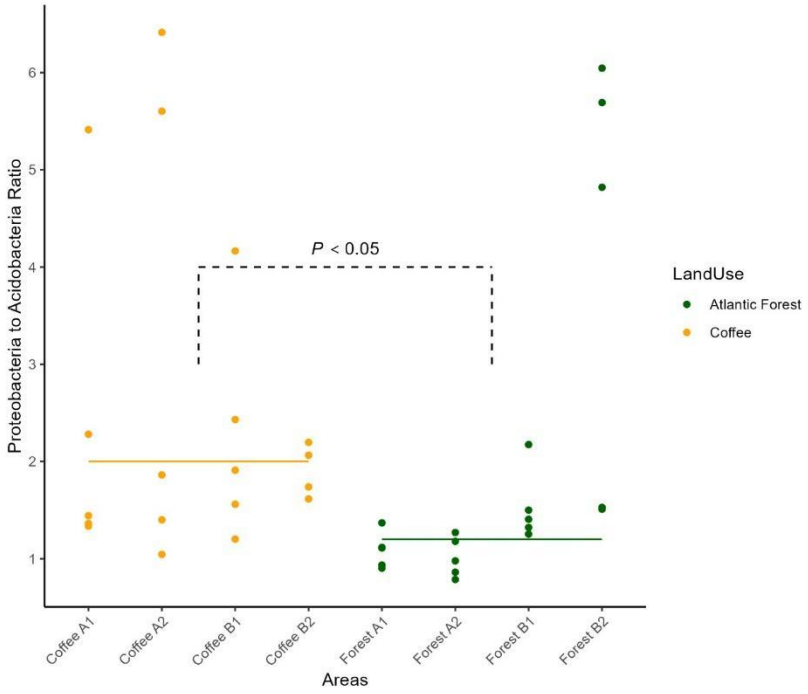
Figure 7 - Relative abundance of the most abundant bacterial phyla in Atlantic Forest (Green point) and Coffee cultivation (Yellow point) systems. * Significant at $P \leq 0.05$; ** Significant at $P \leq 0.01$; *** Significant at $P \leq 0.001$; ns, no significant.



Although the relative abundance of Proteobacteria and Acidobacteria was not statistically significant between land uses (Coffee and Atlantic Forest) (Figure 7),

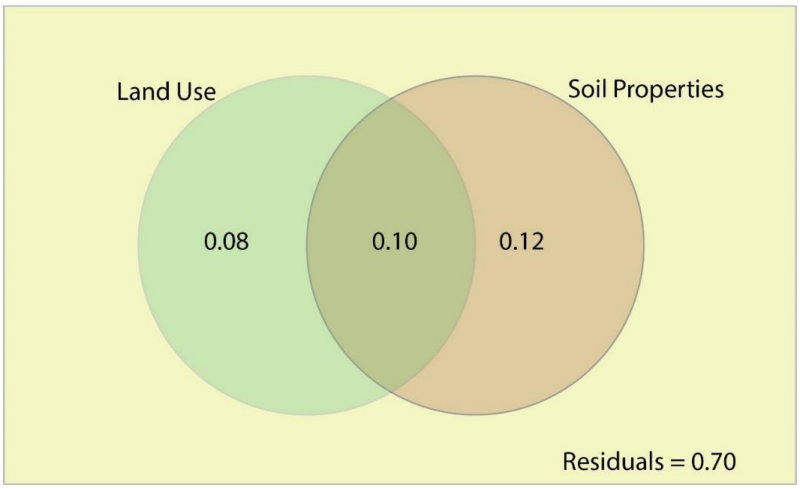
Proteobacteria to Acidobacteria ratio was significantly higher ($p<0.05$) in coffee cultivation than in Atlantic Forest systems (Figure 8).

Figure 8 - Proteobacteria to Acidobacteria ratio in Coffee cultivation (Yellow point) and Atlantic Forest (Green point) systems. Yellow and green lines indicate the mean for each land use system (Coffee, n = 20; Atlantic Forest, n = 20). Significant at $P \leq 0.05$.



The variance of the soil bacterial community was partitioned to distinguish combined and individual effects of land use and soil properties as drivers of bacterial communities (Figure 9). Only 30% of bacterial community variance was explained by both explanatory matrices (land use and soil properties) together. From those, 8% was explained only by land use, and 12% was only related to soil properties. Another 10% was associated with the interrelationships between land use and soil properties.

Figure 9 - Variance partitioning of the soil bacterial community explained by the effect of land use and soil properties. In this analysis, 70% of the variance was not explained (residuals) and 30% was explained by the combined effect of land use and soil properties.



4 DISCUSSION

4.1 Soil bacterial diversity related to land use change

Understanding the mechanisms that affect or modify soil properties and microbial communities when natural systems are converted to agricultural systems has become extremely important for understanding the consequences that land use changes have on soil health (SALA et al., 2000; TRIVEDI et al., 2016). Microbial diversity has been proposed as a sensitive indicator to monitor changes in soil quality (NIELSEN; WINDING, 2002; SCHLOTER et al., 2018; ZHANG et al., 2020). It is considered that more diverse microbial communities are more reliable and exhibit greater stability of ecosystem functions (OSBURN et al., 2023), and that loss of microbial diversity can affect key ecosystem functions with possible consequences for plant productivity (CHEN et al., 2019, 2020). However, the results shown here suggest that soil bacterial diversity in Atlantic Forest areas should be interpreted with caution because most of the diversity components (alpha and gamma diversity) were higher in coffee cultivation systems (Figures 3 and 4).

Several studies have reported higher alpha bacterial diversity when natural areas are converted to agricultural systems in tropical, arid, semi-arid and temperate regions (TRIVEDI et al., 2016; DUBE et al., 2019; MASON et al., 2023; MISHRA et al., 2023). Carvalho et al. (2016) reported higher alpha, beta and gamma diversity in areas of intensive use such as

mechanized agriculture and pastures (for all OTUs and typical OTUs), compared to natural and little intervened areas, in tropical rainforests in Brazilian Amazon. The close relationship between alpha bacterial diversity and soil pH (Figure 5) could explain the mechanism by which conversion from Atlantic Forest to coffee cultivation increases the soil bacteria diversity. Soil pH is a key driver of bacterial diversity and community composition (FIERER; BRADFORD; JACKSON, 2007; WU et al., 2017; WANG et al., 2019; MUNEER et al., 2022), and a significant reduction in soil acidity can directly affect bacterial community diversity and composition (ROUSK et al., 2010; CHO; KIM; LEE, 2016; BAI et al., 2023).

Tropical soils belonging to Atlantic Forest biome are characterized by being naturally acidic, with a high level of aluminum saturation (>50%), low base saturation, low available P and low natural fertility (FAORO et al., 2010; CUNHA; FONTES; LANI, 2019). These conditions become limiting for development and agricultural crop production (VAN RAIJ, 1991; CARVALHO et al., 2016; ENESI et al., 2023). However, Atlantic Forest soils show good physical properties, making them suitable for cropland through practices such as liming and fertilizer application, presenting great yields in coffee crops (FONTANA et al., 2023). In coffee production areas in Brazil, lime is incorporated before planting (commonly up to 0.4 m depth) and other applications are usually made in high doses (several tons per hectare) on soil surface (BARBOSA et al., 2020; MELO et al., 2022; MATIELLO et al., 2020).

A variety of studies have addressed liming effects on soil bacterial community and established that this practice can significantly increase soil bacterial diversity as a consequence of increasing soil pH (HUANG et al., 2018; CHA et al., 2021). Most bacterial taxa have a relatively narrow growth tolerance range, as bacterial activity can be reduced by up to 50% between environments where pH differs by 1.5 units (FERNÁNDEZ-CALVIÑO; BÅÅÅTH, 2010; ROUSK et al., 2010). Bacteria that show reductions in their activity present limitations in their maintenance system, so their growth can be quickly overtaken by other bacteria that are not affected by changes in pH, leading to changes in bacterial community structure (CHA et al., 2021).

Research conducted to date has shown that soil pH can indirectly influence the availability of toxic elements. A decrease in pH is accompanied by processes of minerals dissolution and hydrous oxides of Fe, Mn and Al, on which heavy metal ions can also be adsorbed (VEGA et al., 2004; BORCH et al., 2010; ZENG et al., 2011). This results in a lack of access to other important plant nutrients (which become insoluble at low pH) (BORDA; SPARKS, 2008), and reduced biological activity of bacteria that is associated with inhibited

transformations of nitrogenous compounds and decreased fertility of arable land (WANG et al., 2006; KICIŃSKA; POMYKAŁA; IZQUIERDO-DIAZ, 2021). In contrast, increasing pH promotes the formation of organometallic complexes that, if stable enough, can remove toxic elements from soil solution (THALASSINOS et al., 2023). Apart from that, toxic elements bioavailability may be decreased due to the formation of inorganic complexes, mainly with phosphates and carbonates, which are usually very insoluble (OLANIRAN; BALGOBIND; PILLAY, 2013).

While our results regarding alpha diversity are aligned with those found by other authors when conversion from native ecosystems to agriculture is studied in tropical soils, the fact that we find no differences in beta diversity among land uses and higher gamma diversity in coffee farming systems (Figure 4) challenges the hypothesis of biotic homogenization, which posits an increase in community similarity of soil bacteria over time or space in anthropic systems (RODRIGUES et al., 2013; MEYER et al., 2019; WANG et al., 2022). For instance, Rodrigues et al. (2013) detected a biotic homogenization of bacterial communities through a reduction in beta diversity in response to conversion from tropical forest to pasture. These authors established heterogeneous spatial distances (from 0.1 m to 10 km) and showed that bacterial communities were more similar with increasing spatial distances at small and large scales. Goss-Souza et al. (2017) reported similar results with conversion from Atlantic Forest to pasture. However, they did not observe significant reductions in bacterial beta diversity when Atlantic Forest areas were associated with no-till agricultural systems. It was also reported that biotic homogenization drives endemic bacteria loss from natural ecosystems, resulting in a net diversity loss, so it was suggested that microbial diversity loss through homogenization in space should be considered to assess land use change impact (RODRIGUES et al., 2013; TRIVEDI et al., 2016).

Higher gamma bacterial diversity in coffee cultivation could be explained by the high soil pH levels in these agricultural areas (Figure 5). Carvalho et al. (2016) were the first to attribute higher bacterial beta and gamma diversity to soil pH heterogeneity when natural ecosystems are converted to agricultural use areas and pastures. They argued that soil pH is a dominant predictor of bacterial diversity, dissociating the relationship that greater plant diversity in native areas drives soil bacterial diversity and that reducing acidity through practices such as liming in agricultural areas provides environments suitable for growth and increased soil bacterial diversity.

4.2 Soil bacterial composition related to land use change

In the community analysis, we found evidence that variations in soil bacterial community composition can be partially explained by soil physicochemical indicators, supporting one of the hypotheses put forward in our study. Bacterial community composition in Atlantic Forest areas was driven by higher soil acidity and was differentiated from coffee cultivation systems through a fertility gradient, especially attributed to an increase in soil pH, nutrient content, and soil texture (Figure 6).

Soil acidity is a key regulator in shaping soil bacterial community structure, due to the narrow pH range for optimal bacterial growth (SHANG et al., 2021; YU et al., 2021). For instance, Wang et al. (2022) reported that bacterial community composition present in more acidic soils (pH 4 to 5) was differentiated from those present in less acidic soils (pH 5 to 6 and pH 6 to 7). Likewise, repeated inorganic fertilizer application could be a selective force in shaping soil bacterial structure and functionality because it leads to long-lasting modifications of soil chemical properties and increased nutrient availability (CRUZ et al., 2009; DINCĂ et al., 2022; ZHANG et al., 2022). Some authors have found that mixed N, P, and K fertilization promotes bacterial growth and modifies soil bacterial composition (CRUZ et al., 2009; XIA et al., 2020; WONGKIEW et al., 2022).

Soil bacterial composition among land use systems was also driven by soil properties such as P, clay, and silt. A differentiated bacterial composition was detected by a higher P and clay content in coffee crops and a higher silt content in Atlantic Forest areas (Figure 6). Soil particle structure affects other soil properties such as bulk density, porosity, and permeability, which can provide moisture and air within the soil profile and create a favorable environment for bacterial growth (MOBILIAN; CRAFT, 2021). Najmuldeen; Mohammad; Amin (2010) studied the influence of soil texture on microbial population, and they showed higher bacterial populations in clay loam and silty clay loam soils compared to sandy loam and silty loam. This may be explained by the fact that coarser-textured soils have higher permeability and lower water-holding capacity compared to fine-textured soils, hindering bacterial establishment (GOMEZ et al., 2002; DELGADO-CABALLERO et al., 2009).

P content correlates significantly to soil bacterial community in agricultural soils. P is a dominant regulator of bacterial structure because most microorganisms require P for ribosomal RNA synthesis according to the growth rate hypothesis, synthesis of ATP, nucleic acids, and phospholipids among many other essential biomolecules (YU et al., 2021). Therefore,

management practices such as phosphate fertilization in agricultural areas could influence soil bacteria occurrence. This was demonstrated by Cheng et al. (2020) who studied the influence of phosphate fertilizers on bacterial communities with different P application rates (60 and 120 kg/ha) in cultivated soils and found that available P was a dominant contributor to changes in bacterial community composition.

We observed that soil bacterial community composition in Atlantic Forest areas also varies remarkably as a function of natural fertility gradients in the soil (Figure 6). However, from the data we have available, it is hard to distinguish how much of those differences in soil bacterial communities are a result of different pedogenetic processes (e.g. differences in soil parent material, relief) or the influence of the distinct plant communities found on each of those native areas. The vegetation can directly influence bacterial communities due to differences in root exudates composition and abundance, litter deposition, among others, and indirectly through changes in soil fertility and structure. For instance, a greater litter accumulation on the soil surface may result in higher nutrient availability due to organic matter mineralization (e.g. Ca, Mg, P, K, and S) (ROSS; MATSCHONAT; SKYLLBERG, 2008; MARTINS et al., 2015). Lopes et al. (2015) found that Atlantic Forest areas with higher organic C, Ca, Mg and K contents also have higher organic residue depositions and a low C/N ratio since these conditions allow accelerated mineralization and litterfall turnover. In addition, Atlantic Forest may have accelerated organic matter mineralization due to high temperatures, humidity, and precipitation (BARROSO et al., 2018).

Sequencing analysis revealed that among the most abundant bacterial groups, Acidobacteria, Proteobacteria, Actinobacteria, Bacteroidetes, Gemmatimonadetes, Firmicutes, Chloroflexi, Planctomycetes and Verrucomicrobia were present (Figure 7). These groups are dominant in tropical forest soils, which agrees with the results of previous studies (FAORO et al., 2010; TRIPATHI et al., 2016; WEI et al., 2018). However, bacterial phyla such as Gemmatimonadetes, Firmicutes, Chloroflexi and Planctomycetes were significantly more abundant in coffee cultivation areas. In contrast, Verrucomicrobia was the only bacterial phyla with a higher relative abundance in Atlantic Forest areas. Gemmatimonadetes bacteria have a cosmopolitan distribution in terrestrial systems due to the wide versatility of their metabolism, which makes them persistent and important members of soil communities (DeBRUYN et al., 2011). Nevertheless, it has been reported that agricultural soils (crops and pastures) are enriched with Gemmatimonadetes compared to forest soils, associated with the fact that

Gemmatimonadetes growth is favored in soils with pH close to neutral than in acid soils (LAUBER et al., 2008, 2009; DeBRUYN et al., 2011).

Firmicutes phyla stands out due to its preference for environments rich in nutrients and involved in labile organic compounds degradation, so it is commonly more abundant in agricultural soils (SADET-BOURGETEAU et al., 2022). Rodrigues et al. (2013) and Montecchia et al. (2015) found a proportional increase in Firmicutes abundance with land-use conversion (Forest to pasture and Forest to agricultural soils, respectively). They reported that these trends may also be explained by the fact that members of this phyla may have advantages in grazing and agricultural systems, where soil surface temperatures vary abruptly during the day. Different studies revealed that Chloroflexi members are more abundant in agricultural use areas, attributed to their preference for environments where C and N are highly available, and to their wide adaptability to soil temperature variation (FULLERTON; MOYER, 2016; WEI et al., 2018; MERLOTI et al., 2022). In addition, increases in soil pH by lime application in coffee cultivation could also explain a higher Chloroflexi abundance. Some studies reported increased relative abundances of Chloroflexi under liming treatments, as it has been suggested that this bacterial group could use $CaCO_3$ as a calcium or carbon source for growth (BARTON et al., 2014; GUO et al., 2019; LI et al., 2021).

Verrucomicrobia is a bacterial taxon with oligotrophic characteristics, and its abundance is reduced in soils with optimal fertility (GALANTINI; ROSELL, 2006; CARBONETTO et al. 2014; NAVARRETE et al., 2015b). Our results agree with other studies that confirm a correlation between Verrucomicrobia abundance patterns and conditions of limited nutrient availability (NAVARRETE et al., 2015ab). NAVARRETE et al. (2015a) showed that verrucomicrobial community structures of tropical forest soils were related to Mn, Cu and Fe contents, and potential acidity (H + Al). They demonstrated that Verrucomicrobia is a bacterial phylum adapted to low substrate concentrations in soil, where fertility is naturally low and is maintained through nutrient cycling of topsoil and under high moisture conditions (NOLL et al., 2005). Huang et al. (2012) and Mendes et al. (2015) reported a decrease in Verrucomicrobia abundance following increases in available nitrogen, phosphorus, and potassium in agricultural soils than in natural forest soils. Our findings on Verrucomicrobia abundance corroborate previous findings that higher Verrucomicrobia community abundance is associated with soils containing lower P and K contents and higher potential acidity (H + Al), Mn and Fe. Other studies have also shown that the relative abundance of Planctomycetes is directed by soil pH,

as this group is mainly found in soils with pH ranging between 5.5 and 6.5 (GOSS-SOUZA et al., 2019; MERLOTI et al., 2022).

Although Proteobacteria and Acidobacteria phyla evidenced no difference in relative abundance, Proteobacteria to Acidobacteria ratio was calculated (Figure 8). It has been suggested as a microbial indicator using the principle that these groups broadly represent copiotrophic and oligotrophic life strategies (respectively), that is, lower Proteobacteria to Acidobacteria ratios would be indicative of oligotrophic environments, while higher ratios would be observed in copiotrophic conditions (SMIT et al., 2001; HARTMAN et al., 2008; KIELAK et al., 2016). Contrary to the initial hypothesis, a higher Proteobacteria to Acidobacteria ratio was observed in coffee cultivation areas, confirming that these agricultural systems present copiotrophic conditions.

Coffee trees support a high density of fine shallow roots, below the canopy projection, where soil samples were collected (depth 0-10 cm). The fine roots stimulate nutrient decomposition and release from C sources present in the soil, creating a carbon accumulation zone that enriches microbial activity in the rhizosphere zone (KRAVCHENKO et al., 2019; MARTINS et al., 2021; BIRT et al., 2022). Roots also release a large amount of labile organic compounds through rhizodeposition processes that can select a higher proportion of copiotrophic bacteria (DENNIS; MILLER; HIRSCH, 2010; FEUDIS et al., 2017). Our results are also in agreement with other studies that showed that forest soils and soils with poor fertility are considered oligotrophic environments and agricultural soils with optimal fertility as coprotrophic environments due to increased nutrient availability and seasonal presence of crop residues (GALANTINI; ROSELL, 2006; CARBONETTO et al. 2014; NAVARRETE et al. 2015b).

5 CONCLUSIONS

In conclusion, our study found that conversion from Atlantic Forest to coffee cultivation increased alpha and gamma bacterial diversity, challenging the biotic homogenization hypothesis. The effect of land use on bacterial diversity was strongly coupled with its effect on soil pH, with cultivated systems presenting higher pH values and bacterial diversity than soils under natural vegetation, highlighting the importance of this attribute as the main driver of bacterial diversity. Notable changes in bacterial composition were driven by higher nutrient availability in coffee cultivation areas and high acidity in Atlantic Forest areas. However,

Atlantic Forest areas have strong natural fertility gradients, resulting in remarkable differences in bacterial community composition. Land use change (Atlantic Forest to coffee cultivation) also affects the relative abundance of bacteria, with notable increases in bacterial phyla such as Chloroflexi, Firmicutes, Gemmatimonadetes, and Planctomycetes. Finally, a higher Proteobacteria to Acidobacteria ratio was found in coffee crops, suggesting that this land use favors copiotrophic bacterial communities.

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