Università Politecnica delle Marche
Scuola di Dottorato in Scienze Agrarie, Alimentari ed Ambientali

Effect of slash and burn in Mozambique soils

Ph.D. dissertation of:

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Dominique

Abstract

Slash and burn is an agro-forest system widespread in tropical and subtropical regions and recognized as the main livelihood system in rural areas. The practice consists of a land rotation where a piece of forest is cut to set a new crop field and create charcoal kilns with the cut wood. Due to socio-economic changes, in the last decades the forest fallow period has suffered a contraction, and the scientific community has raised the question of system sustainability. Because of this, the study has dealt with rural areas of the Manica province, central Mozambique, where slash and burn is historically practiced. The survey was carried out in three locations (Vanduzi, Sussundenga, and Macate), where soil profiles were opened under charcoal kilns, crop fields, and forests. These locations were selected for their different time of forest fallow period (≈25, 35, and ≈50 years), considered as the factor able to restore soil fertility. The aim of the study was to evaluate the soil conditions under different land use by determining soil morphology and soil physicochemical properties like pH, particle-size distribution, total organic carbon (TOC), humic carbon (HC), total nitrogen (TN), available phosphorous (available P), water-soluble ions, mineralogy, and Al- and Fe-oxyhydroxides. Results highlighted statistically significant variations among locations for pH, sand, silt, TOC, HC, TN, available P, chloride, nitrate, fluoride, ammonium, mineralogy, and Al- and Fe-oxyhydroxides. On the contrary, few differences in terms of available P, chloride, nitrate, mineralogy, and Fe-oxyhydroxides were detected among land uses within the same location. We ascertained that such differences were mostly due to pedogenic origin rather than the forest fallow length.

In addition to the abiotic components, the bacteria and fungi community was investigated with the aim to assess the influence of the forest fallow length (temporal variation), land use (spatial variation), and the nature of genetic horizons (vertical variation) and of the main soil physicochemical properties (pH, particle-size distribution, easily oxidizable organic carbon, TN, available P, and mineralogical composition) in determining differences on the bacterial and fungal communities. The metataxonomic analysis detected 25 different bacteria operational taxonomic units (OTUs), with a

horizontal and vertical variations of bacteria abundances strongly affected by land use management; in particular, charcoal kilns showed better soil properties and the greatest differences in the microbial community, while crop field and forest were similar. The uncommon application of the pedologic approach for microbial evaluation has allowed us detecting a clear separation in microbiota composition along with the soil profile, with eutrophic bacteria mainly located in the A horizons and oligotrophic bacteria in the Bo horizons. Most of the identified fungi were endophyte or arbuscular mycorrhizal fungi strictly linked to roots and vegetation. Results highlighted differences among locations, few variations among land uses, and great changes between horizons, in relation to the physicochemical soil properties and agronomical management. The fact that the principal variations on the microbiota community were revealed along the profile suggested the inability of a forest fallow shorter than 50 years to improve soil fertility and induce changes in the bacterial and fungal communities.

The overall result of the study indicates that the slash and burn, especially in the last decades, is far to be a sustainable practice and that agronomical practices like mulching, more than the length of the forest fallow period, exert a positive effect on soil fertility expressed as the result of improved chemical and biological properties.

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Chapter 1.

General introduction

The agroforestry system called *slash and burn* is a common livelihood practice widespread in tropical regions all over the world (Mukul and Herbohn, 2016). It has been applied for centuries without substantial changes and consists of cutting, burning, and farming different land plots in rotation (e.g. Riahtam et al., 2015). The scientific community is interested in studying the system to understand how it works and it has been changing through the years. Previously, the fallow period was longer, there was a wide utilization of forest products, and trades were small and local. Nowadays, the field productivity decreases in few years under the minimum threshold necessary to survive, so the land users have to change plot even more frequently (Jakovac et al., 2016). The main weakness of the system is recognized as the short length of fallow period unable to guarantee the recovery of soil fertility (e.g., Gay-des-Combes et al., 2017; Runyan et al., 2012). Since the importance for rural population sustenance, it is crucial to know the system and evaluate negative and positive aspects. As many authors claimed, the effect of the short fallow-period should be analysed join with the type of vegetation, climate, soil characteristics, different techniques of slash and burn, crop associations, use of amendments and fertilizers, etc. (e.g. Brown, 2006; Kilawe et al., 2018; Mertz et al., 2008).

Soil physicochemical properties conditioned by slash and burn system have been widely studied around the world (e.g. Juo and Manu, 1996; Thomaz, 2018; Thomaz et al., 2014), while studies on microbial and fungi communities are scarce (Sall et al., 2006; Sarr et al., 2019; Sul et al., 2013). Microbial diversity and activity are very susceptible to ecosystem variations due to natural factors and/or anthropic activity, but the biotic functionality of the system is still hard to assess and understand (Nannipieri et al., 2017). In detail, bacterial and fungi community are strongly correlated with the nature of the parent material and soil physicochemical properties such as structure, texture, water holding capacity, nutrients availability, and organic matter content (e.g. Lauber et al., 2008;

Sofo et al., 2019; Ulrich and Becker, 2006). Thus, to assess and understand the soil biotic functionality of the slash and burn system, it is mandatory to consider soil physicochemical properties and microbial diversity according to land use (spatial variation), duration of the forest fallow (temporal variation) and, within each soil, the nature of genetic horizons (vertical variation).

1.1 Slash and Burn

Slash and burn is an ancient agricultural practice, also named swidden or itinerant agriculture (Mertz et al., 2009b, 2009a), largely spread in tropical and sub-tropical areas of Asia, Africa, and Latin America (Brady, 1996; van Vliet et al., 2012). In the Amazonian region, paleo-ecologists date back the slash and burn practice to the pre-Columbian population (Arroyo-Kalin, 2012), but also in equatorial areas of Asia and Africa it has been applied for a long time and it occupies an important role in cultural identity (e.g. Brady, 1996; Mertz et al., 2009; van Vliet et al., 2012). The determined characteristic is that the land users slash and burn an afforested area to cultivate it until the production is enough for family sustenance then they shift to another plot repeating the procedure. Often, they use ashes and/or compost to fertilize soil (Gay-des-Combes et al., 2017), and they cut branches to produce and sell charcoal. Through the years, slash and burn system has been changing, and now it is considered no more sustainable (Davidson et al., 2008; Kleinman et al., 1995; Nath et al., 2016). In addition to the turnover reduction (Jarosz, 1993; Rouw, 1995) due to demographic increment (The World Bank; World Statistic; Ickowitz, 2011), with a subsequent rise of food demand, there are political pressures to convert traditional cultivation into cash crops (Wood et al., 2016). The ancient slash and burn presented a long fallow period, better utilization of agroforestry products (Junsongduang et al., 2013), and a better allocation of commodities in local trades. These variations promote soil depletion, loss of habitats (Styger et al., 2007), ongoing deforestation (Dirac Ramohavelo, 2009; Mukul and Herbohn, 2016), reduction of carbon sequestration (Kotto-Same et al., 1997), a gradual decrease in crop yield (Mukul and Herbohn, 2016; Runyan et al., 2012; Styger et al., 2007), and the reduction of forest products like charcoal, medicines, fruits, nuts, and artisanal material (Junsongduang et al., 2013). For the next future, organizations and governments plan to adopt alternatives to the present slash and burn like, for example, the *slash and mulch* system (Félix, 2015), the enhancement of agroforestry products (Nath et al., 2016), and the conversion to cash crops (Temudo and Santos, 2017; Vongvisouk et al., 2014).

1.2 Mozambique

Mozambique, officially the Republic of Mozambique, is a State located in South-East Africa, with an extension of 801,590 km^2 and a coastal line of 2500 km. Mozambique presents two main topographic regions, separated by Zambesi River. The northeast is an extended highland, with a coastal plain stripe originated from coral reef and in deeper Rift Valley Mountain chain; the typical vegetation is miombo woodlands. The southeast is an alluvial plain, covered by savannah and crossed from various rivers, the most important is Limpopo River (Portal do Governo de Moçambique). Mozambique has a tropical climate, with two seasons: a wet monsoon season from October to March, and a dry season from April to September. However, climatic conditions differ along latitude: heavy rainfall in north highlands and coastal zone, and hot temperature and low rainfall in south lowlands. Cyclones and floods are common during the wet season in contrast to droughts during the dry season (Jones et al., 2013; Mafalacusser, 2013). Principal forest ecosystems are miombo (Sitoe, 2004), mopane (Veenendaal et al., 2004), and mangroves (Barbosa et al., 2001). Mozambique economy is based mostly on agriculture, joined with agro-industry, mining industry, fishery, and tourism. Agriculture covers more than one third of GDP, it is a low-input subsistence type based on human work where farmlands are divided for supplying family or tribe necessities using an average surface less than 2 ha. The slash and burn system is widely practiced. Common crops in many smallholdings are cassava, maize/corn, millet, rice and beans, cashew, and mango trees, and in certain regions there are cotton, tobacco, sugar, and tea (FAO, Farming Systems and Poverty). Despite this sector has a relevant economic role in Mozambique, agricultural system has various weaknesses: i) environmental limitations, which includes extreme climatic phenomena and soil conditions; ii) scarce knowledge of agronomic context, with rare fertilizers applications due to their price and consequent adoption of traditional techniques over others more suitable practices to preserve soil fertility like intercropping, use of amendments, mulching, etc.; iii) local trades are limited by the lack of storage facilities and the inadequacy of transport links. In addition, during the last decades, land demand has increased both in urban and rural areas. In certain areas there has been a shift in land use from peasant smallholdings to real estate development and large commercial farms. In these cases, richer owners have the privilege to choose the best land and leave the worst one to poor people. Lands are even more under pressure because of various changes like population growth, urban expansion, and internal migration, all caused by economic and climate-related occurrences (Filipe and Norfolk, 2017).

Chapter 2.

Study areas

The study was carried out in the Manica province, central Mozambique, in three locations of the districts of Vanduzi, Sussundenga, and Macate (Fig. 2.1).

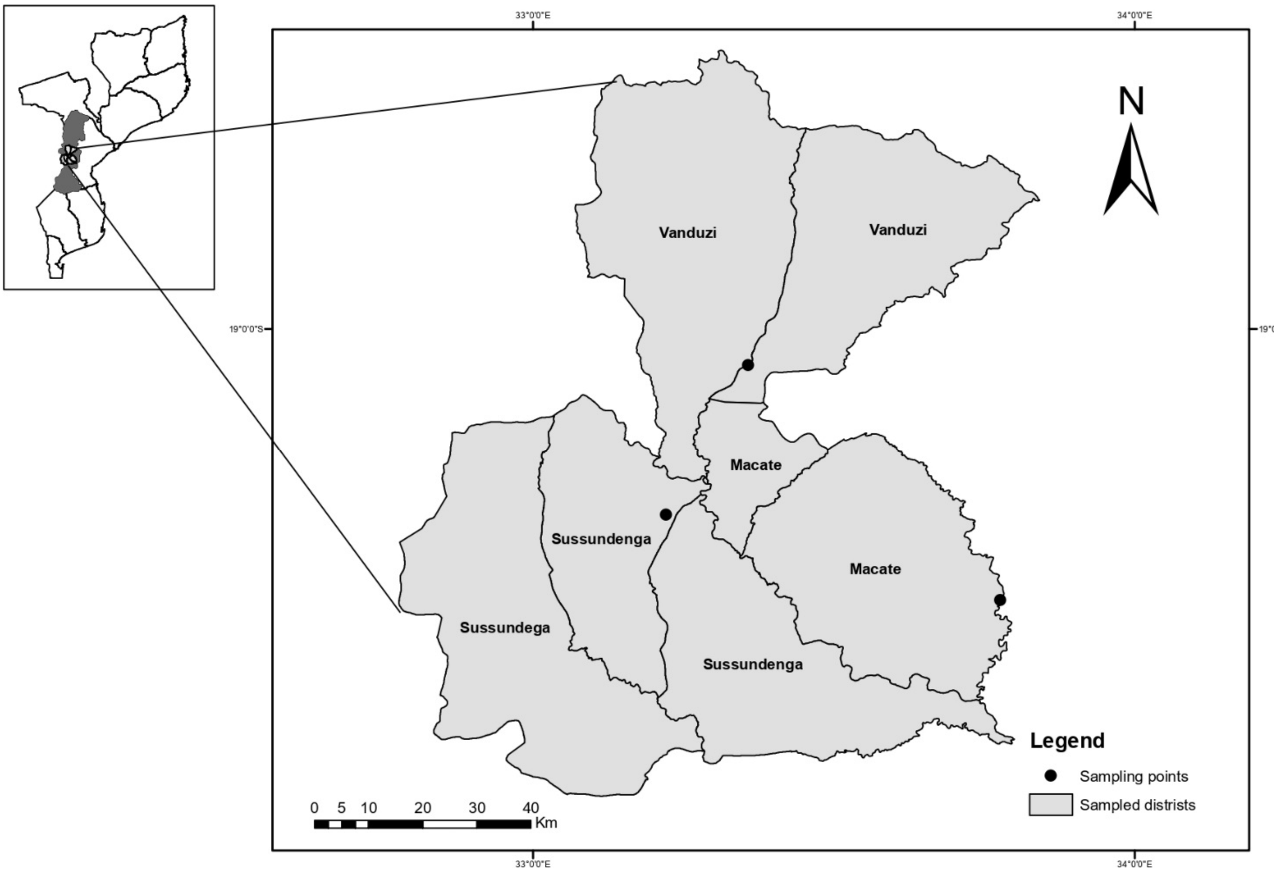

Fig. 2.1 Schematic map of Mozambique and localization of the study sites in the Manica province.

Following the Köppen-Geiger climate classification, locations were included in humid sub-tropical climate, indicating a warm temperate climate with dry season from April to September and hot season from October to March (Belda et al., 2014; Kottek et al., 2006), with frequent storms and cyclones. In the capital city of Manica, the mean annual precipitation is ≈1143 mm and the mean annual air temperature is 21.5°C; the warmest month is February (24.1 °C), and the coldest month is July (17.4 °C) (Climate-Data, 2020). Mozambique economy is principally based on agriculture, with above 4 million farms represented by a low-input subsistence farming based on human work, where farmlands are organized for supplying family necessities (Inquérito Agrícola Integrado, 2015; PEDSA, 2011). The farms are destined to increase following the demography increment registered for the period 2007-2017 in Macate (+1.45% year^{-1}), Vanduzi (+7.56% year^{-1}), and Sussundenga (+2.73% year^{-1}) (City Population, 2020). The main agricultural products in the Manica province are mile, rice, sorghum, and sesame (IAI, 2015), all mostly obtained by the slash and burn practice.

2.1 Agro-ecological and vegetation characterizations

The three districts of Vanduzi, Sussundenga, and Macate were selected because strongly devoted to agriculture, in particular to slash and burn system, which is going on since immemorial time. The major litho-tectonic unit of the region is the Mesoproterozoic Southern Irumide Belt (950-1060 Ma) (Chaúque et al., 2019). Our study areas were located above the Mesoproterozoic granitic rocks of the Barue Magmatic Arc, which is made of different types of migmatites and migmatitic gneisses (Wijnhoud, 1997) that formed a continental basement over which the sedimentary cover of the Macossa-Chimoio nappe was deposited. This sedimentary cover mainly consisted of semipelite and metagraywacke paragneisses weakly migmatized that contained quartzite intercalations and biotite, quartz, feldspars (perthitic orthoclase and albite-andesine), garnet, and cordierite (Chaúque et al., 2019). Later, both systems were deformed and metamorphized together (Chaúque et al., 2019), originating the parent materials of our soils. Therefore, the soil parent rock at Vanduzi and Sussundenga was a granitoid rock (possibly gneissic-granite) belonging to the Barue Magmatic Arc (Chaúque et al., 2019; Wijnhoud, 1997), while at Macate it was a migmatitic paragneiss belonging to the supracrustal rocks of the Chimoio group (Chaúque et al., 2019). Based on climatic conditions, soil type, elevation, and farming system, the three districts are in the Agro-Ecological Zone R4, which includes lands between 200 and 1000 m above sea level. Within this Agro-ecological system, we ascertained that forest conditions were poor in terms of number and varieties of trees; however, from farmers oral interview, we learned that in the three areas both biodiversity and tree number were higher some 60-70 years ago. During our surveys, we also ascertained that in some field the remainders of previous charcoal kilns were even more than 20 per hectare and, in some case, charcoal kilns had been installed in the same place as before. As witnessed by the presence of charcoal kiln rests, all the forests surveyed were abandoned fields where a *miombo* biome was re-growing (Montfort et al., 2021). *Miombo* is a local name used to indicate an "open forest" composed by an upper layer of woody vegetation belonging to *Fabaceae* family such as *Brachystegia spiciformis* Benth., *Brachystegia tamarindoides* Benth., and *Julbernardia globiflora* (Benth.) Troupin, with an understorey composed of herbaceous species like *Themeda triandra* Forssk., *Panicum maximum* Jacq., *Hyparrhenia filipendula* (Hochst.) Stapf, and *Andropogon gayanus* Kunth. At Vanduzi there were also some old plants of *Mangifera indica* L., remainders of an abandoned mango orchard. However, since abandonment, a slight exploitation of the reforesting plots was maintained as they represent the source of subsistence goods like timber, poles, firewood, foods, medicines, grazing, leaf litter, and game (Dewees et al., 2010). The fields adjacent the forest areas were cultivated with annual crops typically of slash and burn system like corn, millet, vegetable, and beans.

2.2 The studied slash and burn systems

For each location, soil profiles were opened according to different land use (agricultural field and forest area), all inside a surface of ≈1 ha at 19°04'002" S - 33°21'45" E for Vanduzi, at 19°18'45.328" S - 33°13'21.050" E for Sussundenga, and at 19°41'405" S - 33°51'513" E for Macate (Fig. 2.1). Information about sampling sites were obtained mainly by oral interviews for Vanduzi and Macate, while for Sussundenga information were also retrieved from documents provided by the Research Station at the *Instituto de Investigação Agrária de Moçambique* (IIAM/CZC) of Chimoio. For the aim of the study, it is important to underline that we obtained the following forest fallow chronosequence: 25 years at Vanduzi, 35 years at Sussundenga, and ≈ 50 year at Macate.

- **Vanduzi**

Sampling sites at Vanduzi were selected in a gentle slope (3%), at an altitude of 658 m. Crop field hosted vegetable garden/banana orchard cultivation realized one year before the survey, with no irrigation, fertilization, and machine support. Weeds were represented by invasive species like *Panicum* sp., *Euphorbia* sp., and *Convolvulus arvensis* L.. Forest was ≈25-years old, moderately vigorous with the presence of gaps and renewal, occasionally pastured and burnt with low fire, and used to obtain firewood, timber, and charcoal. Main arboreal species was *Mangifera indica* L., followed by others belonging to *Fabaceae* family. Shrub layer was constituted principally by *Lantana camara* L., *Psidium guajava* L., and *Vangueira infausta* Burch., with an understorey mostly made by *Panicum* sp., *Dichrostachys cinerea* (L.) Wight & Arn., and *Combretum* sp.. The charcoal kiln had been arranged four years before the survey. To resume, at Vanduzi the forest was ≈25-years old, the crop field was 1-year old, and the charcoal kiln was 4-years old.

- **Sussundenga**

Sampling sites at Sussundenga were in an area with gentle slope (2-4%), at an altitude of 649 m. Crop field was created two years before the survey and was cultivated with corn, without irrigation or fertilization, and sowed after the burning of plant residues and a superficial ploughing with cow traction. Yield has roughly amounted to 1.0-1.1 Mg ha^{-1} y^{-1}. A few weeds were represented by *Apocinaceae* sp. and herbaceous plants like *Panicum miliaceum* L. and *Mucuna pruriens* DC.. Documents attested that the Sussundenga forest was 35 years old; it appeared moderately vigorous with presence of gaps and renewal and occasionally used as source of timber. Principal arboreal vegetation was made of *Burkea africana* Hook, with a shrubby layer made of *Annona senegalensis* Pers., *Parinari curatellifolia* Planch. ex Benth., and *Brackenridgea zanguebarica* Oliv.; the ground cover was almost formed by *Cynodon* sp., *Hyparrhenia variables* Stapf, and *Trichilia capitata* Klotzsch. Instead, the charcoal kilns at Sussundenga had been used in the year of survey. Therefore, the areas of Sussundenga where to sample soils were the 35-years old forest, the 2-years old crop field, and the less than 1-year old charcoal kiln.

- **Macate**

Sampling sites at Macate were selected in an area with gentle slope (3%), at an altitude of 555 m. Crop field was created 16 years before the survey and always cultivated with corn (*Zea mays* L.), without irrigation or chemical fertilization. Yield has roughly amounted to 1.1-1.5 Mg ha^{-1} y^{-1}. Crop residues are commonly used for mulching and, only at the end of the 2017 wet season, a controlled crawling fire was applied to reduce weeds of *Mucuna pruriens* DC.. Forest was ≈50 years old, vigorous, without gaps but with renewal. It has been and it is used as a source of timber, firewood, and game. Principal arboreal species were *Albitia versicolor* Welw. Ex Oliv., *Acacia nilotica* (L.) Willd. ex Del., and *Brachystegia microphylla* Harms.; *Psidium guajava* L., *Zanthoxylum* sp., *Senna petersiana* (Bolle) Lock, and *Lantana camara* L. constituted the shrubby layer, while *Cassia* sp., and *Maytenus senegalensis* Lam. (Exell) formed the herbaceous cover. The charcoal kiln was 16-years old, being settled when the forest was cut to arrange the crop field. Synthetically, at Macate the crop field was 16-years old, the forest was ≈50-years old, and the charcoal kiln was 16-years old.

General objectives

The general aim of the study was to assess the impact of the slash and burn system on soil properties and fertility in three locations of central Mozambique (Vanduzi, Sussundenga and Macate) and, in each one, under three different land uses: charcoal kiln, crop field, and forest. To assess if and how the forest fallow duration influences fertility, the locations were selected to have different length of forest fallow, so to obtain the chronosequence: 25 years at Vanduzi, 35 years at Sussundenga, and ≈ 50 year at Macate. To achieve this purpose, we investigated the morphological, physicochemical, mineralogical, and biological soil properties among locations (temporal variation), among land uses (horizontal variation), and between horizons (vertical variation). In doing this, we tested the hypotheses that: 1) higher the length of the forest fallow, higher the recovery of soil fertility; 2) the soils under forest are more fertile than those under crop field; 3) bacteria and fungi communities are affected by spatial, temporal, and vertical physicochemical properties reliant on both soil genesis and soil management.

Chapter 3.

How does slash and burn affect physicochemical soil properties?

3.1 Introduction

The forest fallow is considered one of the main limitations of this agroforest system since it is expected that the soil needs many decades to re-increase fertility after cultivation. As evidence of this, Fachin et al. (2021) studied revegetated soils in Paraná (Brazil) submitted to slash and burn system following a fallow chronosequence from one month to 12-years and found that chemical properties did not directly increase with the forest age and development. All over the world, many authors studied these effects under various point of view by investigating on soil physicochemical properties (e.g. Alegre and Cassel, 1996; Rumpel et al., 2006), plant biodiversity and vegetation dynamics (e.g. De Wilde et al., 2012; Randriamalala et al., 2019), release of greenhouse gases (Davidson et al., 2008; Dhandapani and Evers, 2020), chemical composition of charcoal, and the stable C stocks (Selvalakshmi et al., 2018). For most of these investigations, slash and burn is considered no more sustainable. However, in addition to the shortened forest fallow, other factors should be considered as limiting the sustainability of this practice: extreme climatic conditions, differences in soil parent materials, different applications of agronomic practices, and technical efficiency (e.g. Binam et al., 2004; Brown, 2006; Kleinman et al., 1995; Mertz et al., 2008).

Because of the crucial role covered by slash and burn in many economies of developing countries, we investigated soils of three locations in Mozambique where the slash and burn system has been historically practiced. The locations were selected based on different length of the forest-fallow and of the cultivation period, obtaining a chronosequence of 25, 35 and, 50 years for the forests, and a chronosequence of 1, 2, and 16 years for the crop fields; in each location, both forest and crop field were considered. The aim of this work was to evaluate the impact of the slash and burn system on soil properties and fertility. In particular, we investigated on the morphological, mineralogical, and physicochemical (including extractable Al- and Fe-oxyhydroxides and water-soluble ions) soil properties to assess if and how the length of the forest fallow duration can influence fertility of the revegetating areas. In doing this, we tested the hypotheses that: 1) higher the length of the forest-fallow, higher the recovery of the soil fertility; 2) the soils under forest are more fertile than those under crop field.

3.2 Materials and methods

3.2.1 Soils and soil sampling

In March 2017, in each of the three areas (Fig. 2.1) a geomorphological and soil survey was run to select a representative site for forest, agricultural field, and charcoal kiln. Much effort was made to find, for each area, three sites with similar exposure and slope (Table 3.1). In doing this, several mini-pits and auger holes were opened before choosing the best position where to dig the soil profiles. In the forests, profiles were opened at about 1 m from the trunk of one of the biggest tree of *Brachystegia spiciformis*. In the agricultural fields, profiles were opened in the middle of their extension. The maximum distance among sampling sites was about 30 m at Macate and Sussundenga, while at Vanduzi forest and field sites were at about 700 m. As a replicate, a second field campaign was run in November 2017, opening soil profiles at few metres from the previous ones. As a whole, 12 profiles were samples (3 locations x 2 soil uses x 2 replicates), for a total of 36 horizons collected. The profiles were morphologically described per Schoeneberger et al. (2012) and sampled in large amount (≈4 kg) for each genetic horizon. During the field activities the samples were maintained inside a portable fridge and, once in the laboratory, they were air-dried, sieved at 2 mm to remove the skeletal particles, and maintained at 4°C for maximum of one week before the biochemical analyses.

Table 3.1 General features and morphology of the soils under crop field and forest in the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique. For symbols see legend.

Average data for the period 1982-2012 – Mean annual precipitation: 1036 mm. Mean annual air temperature: 21.2°C; winter (J-J-A) mean air temperature: 16.9°C; spring (S-O-N) mean air temperature: 22.5°C; summer (D-J-F) mean air temperature: 24.1°C; autumn (M-A-M) mean air temperature: 22.5°C.

Horizon[a]	Depth cm	Thickness cm	Boundary[b]	Color[c]	Texture[d]	Rock fragments %, by sight	Structure[e]	Consistence[f]	Roots[g]	Other observations[h]
VANDUZI (37S 19°04'002" S, 033°21'45" E WGS84). Altitude: 658 m; parent rock: granitoid rock (possibly gneissic-granite).										
Crop field. Slope: 3%; Exposure: N-NW. Management: intercropping with different varieties of *Musa paradisiaca* L., M*origa oleifera* Lam., *Sorghum vulgare* Pers.. Vegetation - herbaceous: *Panicum* sp, *Euphorbia* sp., *Convolvulus arvensis* L.. Drainage class: well-drained. Soil: fine, mixed, thermic Typic Eutrotorrox (Soil Survey Staff, 2014).										
Ap	0-40	36-43	C, W	7.5YR 3/4	sl	0	2f gr & f,m,co abk-sbk	m(fr)	3vf, 2f, 1m	CH (<1%), TU (termites)
Bo1	40-55	11-18	C, W	7.5YR 4/6	l	0	3m,co sbk	m(fr)	2f, 1m	FMN, TU (termites)
Bo2	55-100+	-	-	5YR 3/4	l	0	3m,co sbk	m(fr)	1f	FMN, TU (termites)
Forest. Slope: 3%; Exposure: NW. Management: 27 years old spontaneous forest with patches that have been burnt by low fire and occasionally pastured and used to obtain firewood, timber, and charcoal. Vegetation ("open miombo" forest with rests of previous cultivation) – Trees: *Brachystegia spiciformis* Benth., *Brachystegia tamarindoides* Benth., *Julbernardia globiflora* (Benth.) Troupin, *Mangifera indica* L; bushes: *Psidium guajava* L., *Lantana camara* L., *Vangueira infausta* Burch; herbaceous: *Themeda triandra* Forssk., *Panicum maximum* Jacq., *Hyparrhenia filipendula* (Hochst.) Stapf, *Andropogon gayanus* Kunth, *Dichrostachys cinerea* (L.) Wight & Arn., *Combretum* spp.. Drainage class: well-drained. Soil: coarse-loamy, mixed, thermic Typic Eutrotorrox (Soil Survey Staff, 2014).										
A	0-34	30-35	C, W	7.5YR 2.5/3	ls	0	2m,co abk	m(fr)	2vf, 1f	
Bo1	34-47	10-16	D, S	7.5YR 4/3	ls	0	2f,m abk	m(fr)	2vf, 1f,m	Rare CH
Bo2	47-100+	-	-	7.5YR 4/4	sl	0	2f,m abk	m(fr)	2vf 2f, 3m,co	FMN
SUSSUNDEGA (37S 19°18'45.328"S, 33°13'21.050"E WGS84). Altitude: 649 m; parent rock: granitoid rock (possibly gneissic-granite).										
Crop field. Slope: 2 %; Exposure: NE; Management: 2 years old crop field (*Zea mais* L.) Vegetation – Trees: sparse plants of *Apocinaceae* sp.; herbaceous: *Panicum miliaceum* L., *Panicum maximum* Jacq., *Mucuna pruriens* DC. Drainage class: well-drained. Soil: coarse-loamy, mixed, thermic Typic Eutrotorrox (Soil Survey Staff, 2014).										
Ap	0-18	15-19	C, W	7.5YR 2.5/1	ls	0	1 to 2f,m,co sbk-abk	m(fr)	2-3vf,f, 2-3m, 2co	CH (1-2%)
Bo1	18-69	48-52	C, W	7.5YR 4/2	ls	0	2m,co sbk-abk	m(vfr)	2vf, 2f,m	Fine FMN <5%, leopard skin features 15%
Bo2	69-93+	-	-	7.5YR 3/4	ls	0	0sg & 2m sbk	m(fr)	2vf, 2f,m	Rare CH, fine FMN ≈3%, leopard skin features 20-25%, popping
Forest. Slope: 3%; Exposure: NW. Management: 35 years old spontaneous forest with burnt patches, occasionally pastured and used to obtain firewood and timber. Vegetation: "open miombo" forest – Trees: *Brachystegia spiciformis* Benth., *Brachystegia tamarindoides* Benth., *Julbernardia globiflora* (Benth.) Troupin, *Burkea africana* Hook.; bushes: *Annona senegalensis* Pers., *Parinari curatellifolia* Planch. ex Benth., *Brackenridgea zanguebarica* Oliv.; herbaceous: *Cynodon* sp., *Themeda triandra* Forssk., *Panicum maximum* Jacq., *Hyparrhenia filipendula* (Hochst.) Stapf, *Trichilia capitata* Klotzsch., *Andropogon gayanus* Kunth. Drainage class: well-drained. Soil: coarse-loamy, mixed, thermic Typic Eutrotorrox (Soil Survey Staff, 2014).										
Oi	3-0	2-6	C, W	-	-	0	-	-	0	Leaves and twigs, panicum stems

A	0-34	31-36	C, W	7.5YR 3/2	ls	0	2co gr & 2f,m abk-sbk	m(fr)	3vf, 2f, 3m,co	FMN, TU (termites)
Bo1	34-74	36-42	C, W	7.5YR 5/3	ls	0	2m,co abk-sbk	m(fr)	2vf, 1f, 2m, 1co	Rare CH, friable FMN, TU (termites)
Bo2	74-100+	-	-	7.5YR 5/4	ls	0	2f,m abk-sbk	m(fr)	2vf, 1f,m,co	Firm FMN, TU (termites)

MACATE (37S 19°41'405" S, 33°51'513" E WGS84). Altitude: 555 m; parent rock: migmatitic paragneiss.

Crop field. Slope: 3%; Exposure: W. Management: 16 years old crop field in preparation (*Zea mays* L.) Vegetation - herbaceous: *Mucuna pruriens* DC. Drainage class: well-drained.
Soil: coarse-loamy, mixed, thermic Typic Eutrotorrox (Soil Survey Staff, 2014).

Ap	0-22	18-23	C, W	5YR 3/2	sl	0	3f,m,co vc sbk	m(fr), m(fi)	0	CH (<1%), dead roots; QUA
Bo1	22-37	15-19	C, W	2.5YR 3/6	l	0	2f,m sbk	m(fr)	0	Dead roots
Bo2	37-96+	-	-	2.5YR 3/4	sl	0	2f,m abk,	m(fr)	0	Dead roots

Forest. Slope: 3%; Exposure: W. Management: 50 years old spontaneous forest with burnt patches, occasionally pastured and used to obtain firewood and timber and for hunting small animals. Vegetation: "open miombo" forest – Trees: *Brachystegia spiciformis* Benth., *Julbernardia globiflora* (Benth.) Troupin, *Albitia versicolor* Welw. Ex Oliv., *Brachystegia tamarindoides* Benth., *Acacia nilotica* (L.) Willd. ex Del., *Brachystegia microphylla* Harms; bushes: *Psidium guajava* L., *Zanthoxylum* sp., *Senna petersiana* (Bolle) Lock, *Lantana camara* L.; herbaceous: *Cassia* sp., *Themeda triandra* Forssk., *Panicum maximum* Jacq., *Hyparrhenia filipendula* (Hochst.) Stapf, *Andropogon gayanus* Kunth, *Maytenus senegalensis* Lam. (Exell). Drainage class: well-drained.
Soil: coarse-loamy, mixed, thermic Typic Eutrotorrox (Soil Survey Staff, 2014).

Oi	4.5-1.5	1-3	C, W	-	-	-	-	-	0	Leaves and twigs; ants
Oe&Oa	1.5-0	1-2	C, W	-	-	-	-	-	0	Mycelia
A	0-18	15-18	C, W	5YR 3/2	scl	4	3f,m sbk	m(fr), m(fi)	2vf, 1f, 2m,co	QUA
Bo1	18-55	36-39	C, W	2.5YR 3/6	l	1	3f,m sbk	m(fi)	2vf, 1f, 2m,co	Rare CH, strong biological activity, QUA, F3M ≈1%
Bo2	55-91+	-	-	2.5YR 4/6	scl	0	2f,m sbk-abk	m(fr)	2vf, 1f, 2m,co	Mica flakes

[a] horizons' designation according to Schoeneberger et al. (2012).

[b] C=clear, D=diffuse; S=smooth, W=wavy

[c] moist and crushed, according to the Munsell Soil Color Charts.

[d] ls=loamy sand; sl=sandy loam, scl=sandy clay loam, l=loam.

[e] 0=structureless, 1=weak, 2=moderate, 3=strong; f=fine, m=medium, co=coarse, vc=very coarse; abk=angular blocky, sbk=sub-angular blocky.

[f] m(vfr)=very friable with moist soil, m(fr)=friable with moist soil, m(fi)=firm with moist soil.

[g] 0=absent, 1= few, 2=common, 3=many; vf=very fine, f=fine, m=medium, co=coarse.

[h] CH=charcoal fragments; QUA= quartz fragments; F3M= masses of oxidized iron Fe^{+3}; FMN= iron-manganese nodules; TU= tunnels/tubular pores produced by ants/termites.

3.2.2 Soil analyses

The mineralogical assemblage was evaluated by X-ray diffractometry on manually compressed powdered samples by using a Philips PW 1830, which produced a Fe-filtered Co Kα1 radiation, operating at 35 kV and 25 mA. The identification of the minerals was done based on their characteristic peaks (Brindley and Brown, 1980; Dixon and Schulze, 2002). A semi-quantitative assessment of the mineralogical assemblage was obtained by estimating the area of the primary peaks by multiplying the peak height by its width at half-height.

The particle-size distribution was determined by the pipette method (Day, 1965) after dissolution of organic cements by NaClO at pH 9 (Lavkulich and Wiens, 1970). Sand fraction (2-0.05 mm) was separated by wet sieving, while silt was separated by clay after sedimentation in column at 19-20°C air temperature. The pH was determined potentiometrically in water at a 1:2.5 solid:liquid ratio, using a combined glass-calomel electrode immersed into the suspension. The content of total organic C (TOC) was estimated by K-dichromate digestion, heating the suspension at 180 °C for 30 min (Allison, 1960), and the humic C (HC) was determined by Walkley-Black titration method (Nelson and Sommers, 1996). The total nitrogen (TN) was determined by Kjeldahl method and the potentially plant available phosphorous (P) was estimated according to Olsen et al. (1954).

The amounts of Al and Fe forming pedogenic oxyhydroxides were estimated by extraction with dithionite-citrate-bicarbonate (DCB) treatment (Jackson, 1958), using 30 ml of mixed solution plus 1 g of Na-dithionite to treat 2 g of sample; the extraction was repeated two times and then washed. The total extract was filtered with an ashless Whatman 42 filter paper, and the Al and Fe in solution were determined by Optical Emission Spectrometer – Optima 8300.

Soluble ions were extracted by distilled water at a 1:10 solid:liquid ratio. After gentle stirring for 1 min, the suspension was left to rest for few minutes and the supernatant was filtered with an ashless Whatman 42 filter paper. On the solutions, the concentration of anions (chloride, sulphate, nitrate, phosphate, fluoride, nitrite, bromide, acetate, oxalate, and formate) and cations (calcium, magnesium, potassium, sodium, ammonium, and lithium) was determined by a Dionex ICS-900 Ion System Chromatograph, equipped with IonPac AS23 column for anions and IonPac CS12 column for cations and using a 0.5 M Na-bicarbonate solution as eluent. The concentration of bicarbonate ions was obtained from the difference between the summation of cations and the summation of anions, expressed in μeq kg-1. For each soil sample, two extractions were obtained from separate specimens.

3.2.3 Statistical treatment of the data

For each horizon, a single determination was performed for mineralogy, particle-size distribution, pH, TOC, HC, TN, available P, and total extractable Fe and Al. Instead, for the soluble cations and anions, two extractions were obtained for each sample, and the two values averaged to obtain more reliable results. R program (1.3.1093) was used for statistical analysis. By ANOVA we assessed that the results obtained by the two sampling campaigns did not differ (Table S3.1, S3.2, S3.3, and S3.4, $P > 0.05$). Because of this, the samples of the two campaigns were considered as replicates, and weighted average for the thickness of each horizon joined with standard deviation were calculated. Then, ANOVA was applied to enhance significant differences in soil properties among crop fields and forests from the three locations, and between crop field and forest within each location. To apply the ANOVA, data were tested for normality and homoscedasticity. The improvement of the assumption to normality and homoscedasticity was verified on residuals by the Shapiro-Wilk statistical test (stats R package) and by Levene's test (car R package), both at 5% of significance level (Table S3.5, S3.6, S3.7, S3.8, and S3.9, $P > 0.05$). When data were not normally distributed, the logarithmic transformation was selected by the maximum likelihood procedure devised by Box and Cox (Meloun et al., 2005). If the transformed data were normally distributed, a post-hoc Tukey's Honest Significant Difference (HSD) test with $P \leq 0.05$ was used to compare the means. When normality was not respected, the Kruskal-Wallis test was applied. In case of heteroscedasticity, the Welch one-way ANOVA test was performed. ANOVA tests were deemed significant when $P \leq 0.05$.

3.3 Results

3.3.1 Morphological and physical properties

In all locations (Vanduzi, Sussundenga, and Macate), the soils belonged to the order of Oxisols per Soil Survey Staff (2015) or Ferralsols per IUSS (2015) due the presence of A (umbric) and Bo (oxic) horizons (Soil Survey Staff, 2014) (Table 3.1). In general, A and Bo horizons showed red-yellowish colour and a good degree of aggregation made of blocks generally coarser in the A than in the Bo horizons. Such good state of aggregation, the coarse texture (from loamy sand to sandy loam), and the absence of redoximorphic features indicated these soils as well-drained and, consequently, with low water-holding capacity (Agrawal, 1991; Suzuki et al., 2007). Roots were rather abundant, from very fine to coarse in size, in the A and Bo horizons under forest, while under crop fields root density and size decreased along the profile to disappear in the cultivated soil of Macate. The A horizons under crop fields always showed a charcoal content of <1%, while under forest only rare charcoal fragments were found in the subsurface horizons. Two of the three afforested areas presented O horizons, identified as Oi at Sussundenga and as Oi and Oe&Oa at Macate. Only under crop field at Vanduzi and under forest at Sussundenga, soil tunnelling with termites was found.

In all the soils mineralogical composition was dominated by quartz, with the highest contents at Sussundenga (90-95%) and the lowest at Macate (67-79%). A major variability in mineralogical composition was observed in the Macate soils, where plagioclases and kaolinite were present in higher quantities than in the Vanduzi and Sussundenga soils. Vanduzi showed the highest content of 2:1 clay minerals under crop field and the lowest content of kaolinite under both land uses. Within each location, the only difference was observed at Macate, where a slightly higher content of 2:1 clay minerals were found in the soil under forest than in that under crop field (Table 3.2).

Table 3.2 Mineralogical assemblage (semi-quantitative estimation) of the A and Bo horizons of the soils under crop field and forest in the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique. Numbers in parentheses are the standard deviations (n=2). For each column within land use and location, mean values with different letters significantly differ for $P < 0.05$.

	Horizons	Quartz		Plagioclases*		Orthoclase		Micas*		2:1 clay minerals		Kaolinite	
		%											
		Vanduzi											
Crop field	Ap	89(1)		6(10)		-		-		4(2)		-	
	Bo1	83(7)	bA	8(7)	aA	-	-	-	-	9(6)	aA	-	cA
	Bo2	80(14)		11(7)		-		-		7(7)		-	
Forest	A	88(11)		5(7)		1(1)		-		6(3)		-	
	Bo1	80(21)	**ab**A	8(9)	**a**A	1(1)		-	**-**	10(13)	**a**A	1(1)	**c**A
	Bo2	76(21)		8(6)		1(1)		-		12(13)		3(1)	
		Sussundenga											
Crop field	Ap	95(4)		-		-		-		1(1)		4(2)	
	Bo1	94(4)	aA	-	bA	-	-	-	-	1(1)	bA	5(2)	bA
	Bo2	94(0)		1(1)		-		-		1(1)		4(2)	
Forest	A	91(5)		4(5)		-		-		1(1)		4(2)	
	Bo1	90(7)	**a**A	5(7)	**a**A	-	-	-	**-**	1(1)	**a**A	4(2)	**b**A
	Bo2	93(4)		3(4)		-		-		1(1)		4(2)	
		Macate											
Crop field	Ap	79(14)		10(7)		-		-		1(1)		9(7)	
	Bo1	74(14)	cA	10(7)	aA	-	-	1(1)	-	1(1)	bB	14(7)	aA
	Bo2	74(14)		12(11)		-		1(1)		1(1)		12(4)	
Forest	A	78(6)		2(1)		-		1(1)		4(2)		15(7)	
	Bo1	70(7)	**b**A	6(6)	**a**A	-	-	1(1)	-	4(2)	**a**A	20(7)	**a**A
	Bo2	67(4)		7(4)		-		1(1)		6(6)		19(0)	

* Plagioclases are mainly of albitic composition; Micas are mainly represented by muscovite; 2:1 clay minerals are mainly represented by vermiculite.
Lowercase normal letters = comparison between crop field soils of the three locations.
Lowercase bold letters = comparison between forest soils of the three locations.
Capital letters = comparison between soils under crop field and forest within each location.

In all the soils, the particle-size distribution revealed a predominance of sand, followed by clay and silt. Both crop field and forest soils displayed the highest content of sand at Sussundenga, while the lowest was at Macate (Fig. 3.1A). The forest soil at Macate showed the highest abundance of silt in comparison to the forest soils of Vanduzi and Sussundenga (Fig. 3.1B). No difference was observed between crop field and forest within each location (Fig. 3.1A, B, C).

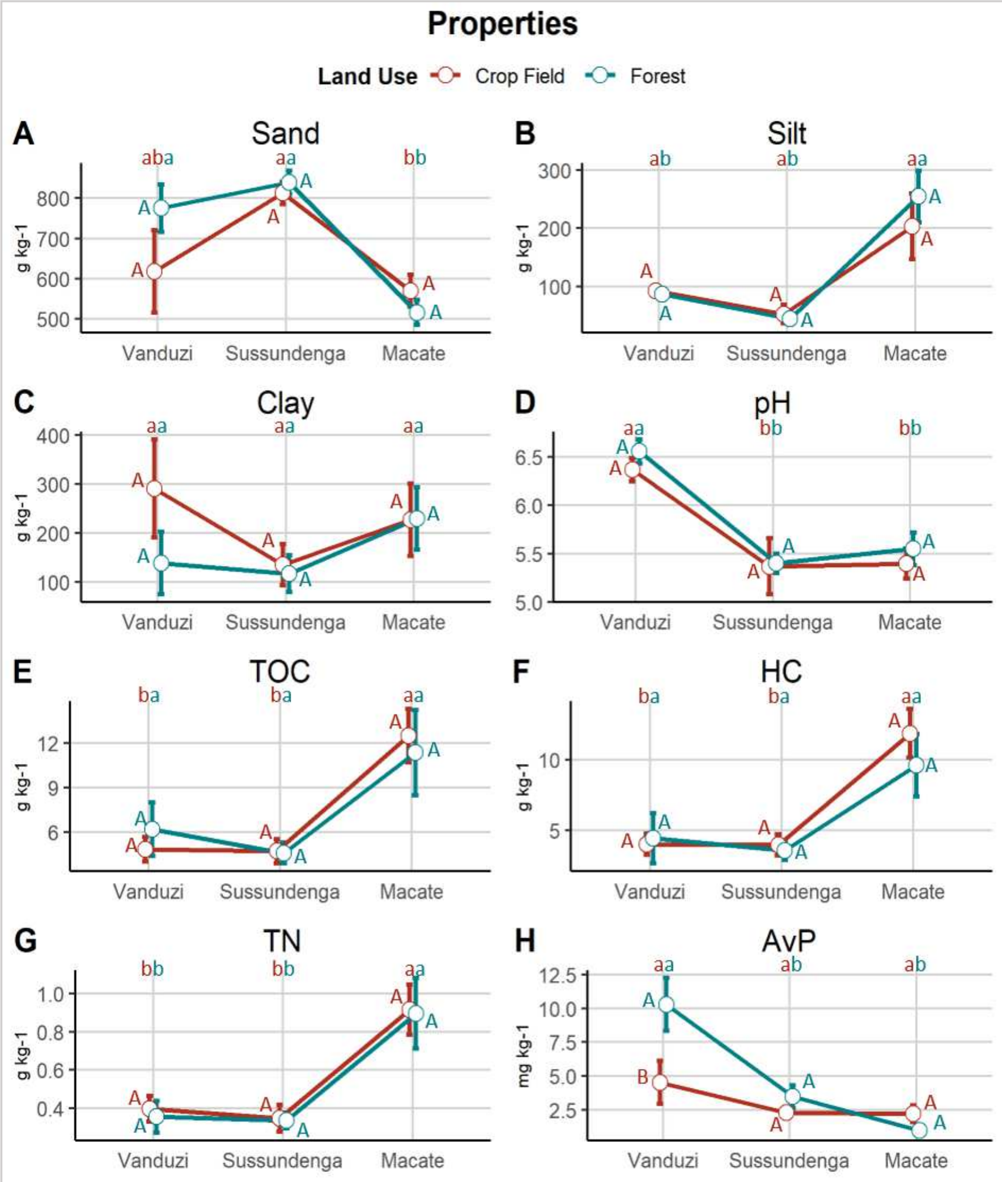

Fig. 3.1 Physicochemical properties for the soils under crop field and forest in the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique. Error bars represent the standard deviation (n=2). For each parameter, mean values with different letters significantly differ for P < 0.05, specifically:

i) red lowercase letter (crop field) and blue lowercase letter (forest) point out differences among the three locations;

ii) red capital letter (crop field) and blue capital letters (forest) point out differences within each location.

3.3.2 Chemical properties, including extractable (pedogenic) Al and Fe

The soils of Vanduzi were the least acidic, with values ranging from 6.3 to 6.8 (Fig. 3.1D). As expected, the contents of TOC, HC, and total N were low on absolute values, but resulted higher in the crop field soils of Macate than in those of Vanduzi and Sussundenga (Fig. 3.1E, F). Thus, while among forest soils no significant difference was observed for TOC and HC, the total N displayed the highest concentrations in both crop field and forest soils of Macate (Fig. 3.1G). The available P content was always very low, with the highest content in the forest soil of Vanduzi, where it was also higher than in the crop field (Fig. 3.1H).

In all the soils, the total extractable Al ranged from 1.1 to 7.1 g kg^{-1}, while Fe varied from 3.3 to 40.4 g kg^{-1} (Table 3.3). The soils of Macate displayed the highest concentrations of extractable Al and Fe in both crop field and forest soils. Only at Macate the forest soil showed a concentration of extractable Fe higher than that of the crop field soil (Table 3.3).

Table 3.3 Mean values of extractable (pedogenic) Al and Fe from the A and Bo horizons of the soils under crop field and forest in the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique. Numbers in parentheses are the standard deviations (n=2). For each column within land use and location, mean values with different letters significantly differ for $P < 0.05$.

Horizons		Al		Fe	
		g kg^{-1}			
		Vanduzi			
Crop field	Ap	3.6(3.5)		18.3(20.0)	
	Bo1	4.6(4.8)	Aab	22.0(24.8)	Aab
	Bo2	6.2(4.2)		28.0(22.9)	
Forest	A	1.4(0.7)		6.3(3.8)	
	Bo1	1.2(0.9)	A**b**	6.8(5.9)	A**b**
	Bo2	3.4(2.3)		18.2(14.6)	
		Sussundenga			
Crop field	Ap	1.7(0.2)		6.7(0.6)	
	Bo1	1.1(0.2)	Ab	3.3(1.1)	Ab
	Bo2	1.1(0.3)		3.7(1.8)	
Forest	A	1.5(0.1)		5.2(0.7)	
	Bo1	1.5(0.1)	A**b**	5.0(1.5)	A**b**
	Bo2	1.6(0.2)		5.7(0.1)	
		Macate			
Crop field	Ap	5.4(0.1)		24.5(3.3)	
	Bo1	6.5(4.9)	Aa	30.2(0.5)	Ba
	Bo2	6.3(1.5)		29.8(10.0)	
Forest	A	5.8(1.0)		32.0(6.5)	
	Bo1	7.1(1.1)	A**a**	40.4(1.6)	A**a**
	Bo2	6.9(1.3)		39.4(3.2)	

Lowercase normal letters = comparison between crop field soils of the three locations.
Lowercase bold letters = comparison between forest soils of the three locations.
Capital letters = comparison between soils under crop field and forest within each location.

3.3.3 Water-soluble anions and cations

Among the ions considered (Appendixes 3.1 and 3.2), formate and lithium were always below the detection limits, while bromide was detected in very small amount (1 µeq kg^{-1}) only in one horizon (Appendix 3.1). Significant differences for anions were detected only for chloride, fluoride, and nitrate, and only for ammonium among the cations (Fig. 3.2). Chloride concentration was similar in all the soils under crop field, while those under forest showed the highest value at Macate and the lowest at Sussundenga. Chloride also differed between land uses in the soils of Vanduzi, with higher concentrations in the crop field than in the forest (Fig. 3.2A). Nitrate concentration was the highest in the soils of Macate, while the lowest was observed under crop field of Sussundenga and forest of Vanduzi (Fig. 3.2B). Fluoride was the highest in the soils of Vanduzi and Macate, with no significant difference between land uses (Fig. 3.2C). Finally, ammonium was higher in the soils of Macate than in those of Vanduzi and Sussundenga (Fig. 3.2D).

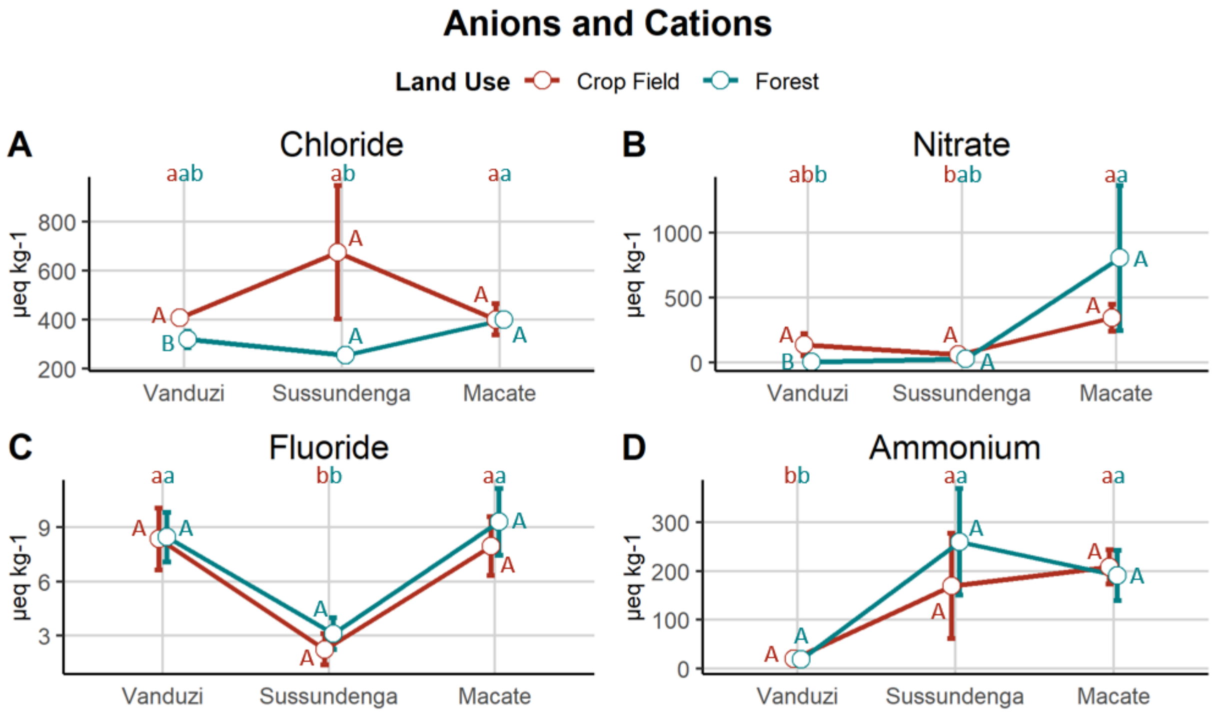

Fig. 3.2 Water extractable chloride, nitrate, fluoride, and ammonium in the soils under crop field under crop field and forest in the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique. Error bars represent the standard deviation (n=2). For each parameter, mean values with different letters significantly differ for $P < 0.05$; specifically:

i) red lowercase letter (crop field) and blue lowercase letter (forest) point out differences among the three locations;

ii) red capital letter (crop field) and blue capital letters (forest) point out differences within each location.

3.4 Discussion

3.4.1 Impact of the forest-fallow length on soil properties and fertility

Morphological and physical properties

The predominant reddish color of the soils and their abundance of quartz and sand separate underlined the strong weathering processes faced by the studied soils, where the more easily weatherable minerals in the upper soil meter have been removed by alteration. Similar results for the soils of the area have been reported by Sá et al. (1972) and FAO (1982) and attributed to the process of lateritization responsible for the development of Oxisols (Van Wambeke et al., 1983). This process

is also responsible for the formation of a good soil structure because of the progressive increment of Al- and Fe-oxyhydroxides that act as cementing agents (Igwe et al., 2009; Krause et al., 2020). The small mineralogical variability among locations betrayed the different parent material from which the soils have developed. In fact, the lowest quartz and the highest kaolinite contents in the soils of Macate were probably due to the parent rock of this site, a migmatitic paragneiss, which is a lithology generally richer of fine-grained clastic sediments than the granitoid rocks of the other two sites. Crystalline rocks like granites and gneisses may contain intercalations of sedimentary silty or clayey beds (Gray et al., 2016), and this could be the explanation of the different particle-size distributions of our soils. The occurrence of tunnelling in the crop field soil of Vanduzi and in the forest soil of Sussundenga was ascribed to attempts of termites to colonize these soils; as a matter of fact, no termites nest was observed in the hectare of surface under study, nor in the close surroundings.
Therefore, the small morphological and physical differences among locations appeared related to geology rather than to the duration of the forest-fallow or of the cultivation period.

Chemical properties, including extractable (pedogenic) Al and Fe

The relatively high pH values in the Vanduzi soils were ascribed to the higher presence of 2:1 clay minerals (mainly vermiculite), which offer a buffering capacity much higher than all the other minerals present (Abate and Masini, 2005; Abollino et al., 2008; Malandrino et al., 2006). Because of this, the distinct parent material and related mineralogical assemblage appear to be the main responsible for the different soil pH values. TOC and HC values were present in very low amount, in line with the values reported by Rafael Alves et al. (2019) for Mozambican soils. However, while both TOC and HC contents were similar in the forest soils, they were relatively higher in the crop field soil of Macate. These results suggest that,

i) in this environment, a 50-years forest-fallow is not able to enrich the forest soil of organic matter. Studying the *miombo* characteristics after slash and burn disturbance, Montfort et al. (2021) found that organic carbon stock in the upper 30 cm soil was similar in 20 and 25 years old *miombo* and in mature woodland due to the rapid vegetation regeneration, and that disturbances typical of slash and burn (biomass removal, fire, and soil tillage) can decline this content. Moreover, a study conducted by Williams et al. (2008) in arid Mozambican *miombo* reported no identifiable changes in soil organic C content between woodlands of 2 and 20 years of re-growth and an older abandoned woodland, and attributed the absence of differences to the extremely slow additions of organic matter to the soil; and that,

ii) for the higher TOC and HC contents in cultivated soils of Macate, unexpectedly it occurred for the soil cultivated for the longest time (16 years) compared to the soils of Vanduzi and Sussundenga (1 and 2 years, respectively). The reason of this was ascribed to the fact that, after the beginning of cultivation, the farmer has always practiced mulching in between and after crops, with only a controlled crawling fire applied to reduce weeds. It is possible that mulching of crop residues combined with the absence of fire have increased the organic matter content and reduced erosion so to maintain a soil fertility that has supported the crops for all the cultivated years. This practice resulted ineffective for the available phosphorous, whose generalized low values were attributed to the selective adsorption of phosphates on the abundant Fe- or Al-oxyhydroxides (Parfitt, 1989; Rafael Alves et al., 2020) and to the lack of fertilizations. However, high contents of extractable Al and Fe have also a positive aspect, being the Al- and Fe-oxyhydroxides particularly involved in the stabilization of organic matter via the formation of complexes (Six et al., 2000; Totsche et al., 2018; Zhao et al., 2017).

The soils of Macate also showed the highest total N content. Trees in the forest of Macate were vigorous and many belonged to *Fabaceae* family, plants that are well known for establishing symbiotic associations with N_2-fixing bacteria (e.g. De Boer and Kowalchuk, 2001; Franche et al., 2009). Also the forests at Sussundenga and Vanduzi hosted leguminous plants, but they were less vigorous and subjected to frequent stresses due to fires for hunting purposes or disturbances to obtain firewood, timber, and charcoal. Being the forest of Macate older and less stressed, as demonstrated by the presence of a rather well-expressed litter (Oi and Oe&Oa horizons), than those of Vanduzi and Sussundenga, the relatively higher soil N content was ascribed to the presence of leguminous trees that enriched the soil because of 50 years of undisturbed plant-microbial association. For the crop field soil, even though cultivated for 16 years, the soil contained a relatively high total N content probably because of the continuous mulching (Dong et al., 2018; Fang et al., 2011) and the almost absence of fires; in fact, N is an extremely volatile element that can be easily lost during the vegetation burning (Da Silva Neto et al., 2019).

In well-drained soils with acidic pH, low cation exchange capacity, and quartz dominated mineralogy like those here studied, fertility is extremely low (Eshett et al., 1989), and a proper soil management including absence of fire and soil mulching is crucial to guarantee a minimum level of organic matter and nutrients stock able to support biomass production (Bahr et al., 2014; Temudo and Santos, 2017).

Soluble anions and cations

Well-drained and acid soils like ours are easily leached out of the most soluble ions (Juo and Manu, 1996), so it appeared reasonable that the water-extracted anions and cations assumed concentrations of μeq kg^{-1} as order of magnitude. Although in low concentrations, significant differences were observed for chloride, fluoride, nitrate, and ammonium. Chloride was detected in higher contents in the forest soil of Macate in comparison to those in Vanduzi and Sussundenga. Among the several sources of chloride listed by Geilfus (2019), notwithstanding the long distance between our study sites and the Mozambique sea channel, we cannot exclude the contribute due to airborne sea salts, especially at Vanduzi, where the angular coefficient of the Cl/Na relationship of the soil extract was similar to that of the sea water (Keene et al., 1986) (Fig. S3.1). Differences in fluoride content can be due to natural and anthropogenic sources (Ali et al., 2016; Mikkonen et al., 2018; Wang et al., 2019). Parent material is considered the most common source of fluoride, which is present in minerals like fluorites, apatites, and micas, which form granite and igneous rocks, but also in topaz, which is commonly associated with silicic igneous rocks, and cryolite, which comprises pegmatitic rocks (e.g.

Battaleb-Looie et al., 2012; Mikkonen et al., 2018). In our soils, F^- was detected at highest concentrations under crop field and forest at Vanduzi and Macate, namely in soil with different parent rock; because of this, the geogenic sources of F^- was considered irrelevant in determining the differences. Consequently, as largely reported in the literature (e.g. Choubisa and Choubisa, 2016; Feng et al., 2002; Fu et al., 2019), the relatively higher F^- content in the soils of Vanduzi and Macate was ascribed to windblown materials coming from the surrounding mining activities devoted to the extraction and transformation of copper, nickel, gold, silver, iron, and bauxite, which are absent in a radius of at least 30 km at Sussundenga (Lehto and Gonçalves, 2008; MIREME, 2021). In the Macate soils, where there was the highest content of total N, also nitrates (NO_3^-) and NH_4^+ were relatively abundant, possibly because of mulching. In fact, Yaşar Korkanç and Şahin (2021) demonstrated that soil mulching with various organic materials reduced NO_3^- and NH_4^+ losses through water runoff when compared to uncovered plots, and for an environment where rainstorms and cyclones are frequent, mulching could make the difference. In the Sussundenga soils, where no use of fertilizer has been never made, only NH_4^+ showed the highest concentrations possibly because of the ongoing mineralization of tree roots after the recent (one year) slash and burn (Béliveau et al., 2015; Juo and Manu, 1996; Vitousek, 1981). In addition, ammonium is the direct product during biomass burning (Knicker, 2007), and the recent slash and burn could have contributed to the ammonium release.
Therefore, concentrations in anions and cations were mainly ascribed to the arrival of windblown materials for Cl- and F-, and to the soil management for NO3- and NH4+, with no relation with the different length of the forest-fallow period.

3.4.2 Contrasting forest and crop field within location

Morphological and physical properties

In each location, cultivated and forest soils were similar, with only a slightly content of 2:1 clay minerals in the forest than in the crop filed soil at Macate. Agronomical practices actuated in slash and burn management might increase minerals weathering because of tillage, temperature fluctuations, and direct rainfall (Lemenih et al., 2005). Further, forest vegetation is more efficient in controlling soil erosion and runoff than crop fields, especially when the understorey is thick and made of shrubs and herbaceous vegetation (Thomaz, 2013; Cerdà and Doerr, 2005). However, it seems unrealistic that these differences have been produced in only 16 years of cultivation for a depth of ≈1 m. Most probably this was a site-specific difference inherited from the parent material and that was maintained between in the two soils.

Chemical properties, including extractable (pedogenic) Al and Fe

Significant differences in chemical properties were highlighted only for available P in the soils of Vanduzi. The slight P deficiency in the crop fields was probably exacerbated due to plant absorption and erosion processes (Da Silva Neto et al., 2019), even though the crop field was settled only one year before the soil sampling. In Oxisols, the richness of Fe-oxyhydroxides promote a strong insolubilization of phosphates (Lü et al., 2017; Markovic et al., 2019), and the plant absorption in absence of fertilization can rapidly decline available P (Shen et al., 2011). Considering the scarce chemical differences between cultivated and forest soils within locations, it appeared that the effect of reforestation on the re-acquiring of soil fertility was irrelevant.

Soluble anions and cations

Only at Vanduzi the soil under crop field appeared enriched of Cl^- and NO_3^- with respect to the forest soil. In general, possible vectors of Cl^- and NO_3^- are fertilizations, irrigation water, and/or other human activities (e.g., Geilfus, 2019; Martinez Uribe et al., 2020; Oberhelman and Peterson, 2020). In our case, fertilization can be totally excluded, while a manual irrigation is practiced taking advantage of the water of a near stream that, in the previous five km, crosses an area devoted to industrial poultry production, an urban district at 4 km NW from the city of Chimoio, and a nearby industrial area. Geilfus (2019) mentioned as possible source of Cl^- animal wastes like cattle manure, pig slurries, and chicken or pigeon manures. Instead, in addition to fertilizers, sewage systems and manure are considered as possible NO_3^- sources (Jin et al., 2018; Torres-Martínez et al., 2021; Wakida and Lerner, 2005). Because of this, we think that the relatively high content of Cl^- and NO_3^- in the soil under crop field of Vanduzi may derive from the irrigation water collected in the near stream. As a further support of this,

Therefore, also for cations and anions distribution, soil management rather than the length of the fallow period appeared to exert some effect.

3.5 Conclusions

The present study evaluated various soil properties in sites undergone to slash and burn practice with different time of forest-fallow period to evaluate the impact of the system on the agricultural and ecological soil functions and to verify if a higher length of forest-fallow had positive effects in soil recovery. Starting with the premise that these acidic soils undergone slash and burn practice showed poor and very poor conditions, the main changes were underlined among locations, while within the location soils at Macate differed for 2:1 clay minerals and extractable Fe-oxyhydroxides, and at Vanduzi for Available P, chloride and nitrate. Morphological and physicochemical variations were mostly ascribed to differences in the parent material and soil management rather than the length of the fallow period. As predictable, anions and cations concentrations in well-drained soils were scarce, although in some cases external sources have contributed to determining differences. To resume, afforested soils did not show better soil properties than those under cultivation, furthermore, the recovery of soil appeared not proportional to the length of the fallow period, at least for a maximum length of 50 years. It is therefore beneficial adopted agronomical practices aimed at providing a stable sink of organic nutrients to the soil.

Chapter 4.

Bacterial metataxonomic diversity under different land use

4.1 Introduction

Soils subjected to slash and burn practice have been widely studied for their variable physicochemical properties and fertility levels (Juo and Manu, 1996; Thomaz et al., 2014; Thomaz, 2018), whereas their microbial communities have been scarcely investigated (Sall et al., 2006; Sarr et al., 2019; Sul et al., 2013). Microbial diversity and activity are very susceptible to ecosystem variations due to natural factors and/or anthropic activity, but the biotic functionality of the system is still hard to assess and understand (Nannipieri et al., 2017). In detail, bacterial community diversity is strongly correlated with the nature of the parent material and soil physicochemical properties such as structure, texture, water holding capacity, nutrients availability, and organic matter content (Ulrich and Becker, 2006; Lauber et al., 2008; Sofo et al., 2019). Thus, to assess and understand the soil biotic functionality of the slash and burn system, it is mandatory to consider soil physicochemical properties and microbial diversity according to land use (spatial variation), duration of the forest fallow (temporal variation) and, within each soil, the nature of genetic horizons (vertical variation).

Based on these premises, we hypothesised in our research that notwithstanding centuries of slash and burn that could have homogenized all the system, bacterial community can differentiate horizontally (location and land use) or vertically (horizons). Therefore, the aims of the study were i) to evaluate the bacterial diversity through a metataxonomic approach in soils subjected to slash and burn, and ii) to investigate the effect of spatial, temporal, and vertical variations in selecting bacterial populations as due to the main soil physicochemical properties. For testing this, we selected three locations of central Mozambique submitted to slash and burn where soil samples were collected under charcoal kiln, agricultural field, and forest (spatial variations). The locations were selected on the base of the forests age, so to obtain a chronosequence driven by the duration of the forest fallow (temporal variation). Furthermore, as a novel and almost unique approach, soil samples were collected by genetic horizons (vertical variation).

4.2 Materials and methods

4.2.1 Soils and soil sampling

In March 2017, in each of the above-mentioned area (Fig. 2.1) a geomorphological and soil survey was run to select the sampling sites. At each area we selected a rather flat area (plateau) with gentle slope (2-4%). In all cases, each soil was characterized by two master horizons: a brownish A horizon (umbric) and a reddish Bo (oxic) horizon (Table S4.1). In each area, for any land use (charcoal kiln, agricultural field, and forest) we selected two representative sites with similar micro-topography and, for the forest, vegetation. Since Oxisols are very weathered soils and the mean temperature of the area slightly differ among seasons, to evaluate eventual differences in terms of bacterial community along the year, we chose to run two sampling campaigns following the most different agricultural seasons: crop end in March 2017 (Autumn) and field preparation for seeding in November 2017 (Spring). In the charcoal kilns the profiles were opened in the middle of their extension, while those in the agricultural fields were opened at ≈25 m from the border with forest. In this latter, profiles were opened at ≈1 m from the trunk of one of the biggest tree of *Brachystegia spiciformis*. The maximum distance among sampling sites was about 30 m at Macate and Sussundenga, while at Vanduzi forest and field sites were about 700 m distant. For each sampling campaign, the position where to dig the soil profiles was selected after opening several manual mini-pits and auger holes. Once excavated, each profile was described according to Schoeneberger et al. (2012) and sampled by genetic horizons (A and Bo). A large amount of sample (about 4 kg) was collected from each horizon. The number of profiles excavated was 9 (3 land uses x 3 locations) in March and 9 in November, for a total of 18 profiles and 36 horizon samples.

Samples were collected in sterilized polyethylene bags and stored at ≈4 °C inside a portable fridge during the field operations. Once in the laboratory, the samples were air-dried and then passed through a sieve (2 mm mesh) to remove the skeletal particles and coarse vegetal residues.

4.2.2 Soil analyses

The pH was determined potentiometrically in H_2O after one night of solid:liquid contact, using a combined glass-calomel electrode immersed into the suspension (1:2.5 solid:liquid ratio). Particle-size distribution was determined after dissolution of organic cements by NaClO at pH 9 (Lavkulich and Wiens, 1970). Sand (2-0.05 mm) was recovered by wet sieving, while silt was separated from clay by sedimentation maintaining the columns at 19-20°C. The amount of easily oxidizable organic carbon (EOOC) was estimated by the Walkley-Black method by K-dichromate digestion without heating (Nelson and Sommers, 1996). The total nitrogen (N) content was determined by the semi-micro Kjeldahl method and potentially plant-available phosphorous (P) was determined according to Olsen et al. (1954). The mineralogical assemblage was assessed by X-ray diffractometry on manually compressed powdered samples by using a Philips PW 1830 diffractometer (Fe-filtered Co $K\alpha 1$ radiation, 35 kV and 25 mA). Minerals were identified on the basis of their characteristic peaks (Brindley and Brown, 1980; Dixon and Schulze, 2002), while a semi-quantitative mineralogical composition was obtained by estimating the area of the diagnostic peaks by multiplying the peak height by its width at half-height.

4.2.3 Microbial DNA extraction and sequencing

Total microbial DNA was extracted from 100 mg of each soil sample using the E.Z.N.A. DNA-based analysis was preferred to mRNA analysis because in complex matrices like soil, RNA can be rapidly degraded by RNAases, with a consequent less reliability of the soil microbial composition (Nannipieri et al., 2020). Soil DNA Kit (Omega Bio-Tek, Inc., Georgia, USA) following the manufacturer's instruction. The extracted DNA was quantified by using the Qubit dsHS kit (Thermo Fisher, Milan, Italy) and standardized at 25 ng μL^{-1}. One μl of each DNA suspension was used as template for PCR amplification by using primers 16SR and 16SF spanning the V3-V4 region of the 16S rRNA gene following the procedure described by Klindworth et al. (2013), and a negative control was included in the PCR reactions by replacing the DNA solution with water. The PCR amplicons were purified and sequenced according to the Illumina metagenomic pipeline instructions. The sequencing was performed with a MiSeq Illumina instrument (Illumina) with V3 chemistry, generating 250 bp paired-end reads according to the manufacturer's instructions. To prevent preferential sequencing of the smaller amplicons, the amplicons were cleaned using the Agencourt AMPure kit (Beckman coulter, Brea, USA) according to the manufacturer's instructions; subsequently, DNA concentrations of the amplicons were determined using the Quant-iT PicoGreen dsDNA kit (Invitrogen Life Technology) following the manufacturer's instructions. In order to ensure the absence of primer dimers and to assay the purity, the quality of generated amplicon libraries was evaluated by a Bioanalyzer 2100 (Agilent, Palo Alto, CA, USA) using the High Sensitivity DNA Kit (Agilent). Following the quantitation, cleaned amplicons had been mixed and combined in equimolar ratios. Pair-end sequencing using the Illumina MiSeq system (Illumina, San Diego, USA) had been carried out at the Sequencing Platforms of the Fondazione Edmund Mach (FEM, San Michele a/Adige, Italy).

4.2.4 Bioinformatics analysis

After sequencing, raw reads were merged with FLASH software (Magoc and Salzberg, 2011) and analyzed with QIIME 1.9.0 software (Caporaso et al., 2010); the detailed pipeline was described by Ferrocino et al. (2017). The USEARCH version 11 software (Edgar et al., 2011) was adopted for chimera filtering, against the 16S reference databases. Centroid sequences of each operational taxonomic unit (OTU) cluster (at 97% of similarity) by using UCLUST (Edgar, 2010) were mapped against Greengenes 16S rRNA gene database by means of the RDP Classifier, with a minimum confidence score of 0.80 (Wang et al., 2007).

Centroids sequence were manually blasted to check the taxonomic identification. To avoid biases due to the different sequencing depths, OTU tables generated through QIIME was rarefied at the lowest number of reads and showed the highest taxonomy resolution that was reached. The data generated by sequencing were deposited in the NCBI Sequence Read Archive (SRA) and are available under the Bioprojects Accession Number-PRJNA550507 for replicate 1 and PRJNA631872 (biosamples accession number from SAMN14895357 to SAMN14895411) for replicate 2.

4.2.5 Statistical treatment of the data

R program (1.3.1093) was used for statistical analysis. By ANOVA we assessed that the results obtained from the analyses of samples collected in the two sampling campaigns in terms of physicochemical properties (pH, particle-size distribution, EOOC, total N, and available P) did not differ (Table S4.2, $P > 0.05$). Because of this, the samples collected in the two sampling campaigns were considered as replicates and ANOVA was run to test significative differences for sampling locations (Vanduzi, Sussundenga, and Macate), land uses (charcoal kiln, crop field, and forest), and horizons (A and Bo) (Table S4.3, $P > 0.05$). To apply the ANOVA, we previously verified the normal distribution of the data and, then, the equal variances. The improvement of the assumption to normality and homoscedasticity was verified on residuals by the Shapiro-Wilk statistical test (stats R package) and by Levene's test (car R package), both at 5% of significance level. When data were non-normally distributed, each numerical variable was transformed by the Box-Cox procedure (Meloun et al., 2005). If the transformed data were normally distributed, a post-hoc Tukey's Honest Significant Difference (HSD) test with $P \leq 0.05$ was used to compare the means. When normality was not respected, the Kruskal-Wallis test was applied to assess if the differences were significant. In case of heteroscedasticity, the Welch one-way ANOVA test was performed. ANOVA tests were deemed significant when $P \leq 0.05$. In case of heteroscedasticity and non-normality, we run the Friedman test (rstatix package) combined with Kendall's W to measure the Friedman test effect size and pairwise Wilcoxon signed-rank tests. The arithmetic means and relative standard deviations for physicochemical properties (Tables 4.1, 4.2, and 4.3) and OTUs were calculated for sampling locations (n=12), total land use (n=12), land use of each area (n=4), total horizons (n=18), and horizon of each site (n=6). Non-parametric pairwise Wilcoxon tests were used when appropriate to determine the significant differences of OTU abundance and alpha diversity. Spearman correlation analysis was performed through the *psyc* package and plotted by using the function *corrplot* of R. The P values were adjusted for multiple testing using the Benjamini-Hochberg procedure, which assesses the false discovery rate (FDR).

Table 4.1 Mean values of physicochemical properties for the three study sites from Manica province, central Mozambique. Numbers in parentheses are the standard deviations (n=12). For each column, mean values with different letters significantly differ for $P < 0.05$.

Location	pH[1]	Particle-size distribution			EOOC*[2]	Total N[1]	Available P[3]	Main mineralogical composition**
		Sand[2]	Silt[3]	Clay[1]				
		g kg^{-1}			g kg^{-1}		mg kg^{-1}	
Vanduzi	6.6(0.5) a	748(168) a	87(18) b	165(163) a	5.2(3.4) b	0.4(0.2) b	12(8) a	Q(84), CM(7), P(9)
Sussundenga	6.0(0.8) ab	759(136) a	50(30) c	191(143) a	5.7(3.0) b	0.5(0.2) b	6(5) b	Q(93), CM(6), P(1)
Macate	5.8(0.7) b	598(85) b	215(94) a	187(147) a	13.5(5.1) a	1.1(0.4) a	4(3) b	Q(76), CM(15), P(9)

* EOOC=easily oxidizable organic carbon.
**In parentheses the percentage content of each mineral (semi-quantitative estimation). Q=quartz, CM=clay minerals, P=plagioclases.
[1] Kruskall-Wallis test ($P < 0.05$).
[2] One-way ANOVA test ($P < 0.05$).
[3] Friedman test ($P < 0.05$).

Table 4.2 Mean values of physicochemical properties for A+Bo horizons for each land use and for the three study locations from Manica province, central Mozambique. Numbers in parentheses are the standard deviations. For each column within land use and location, mean values with different letters significantly differ for $P < 0.05$.

Land use	pH	Particle-size distribution			EOOC	Total N	Available P	Main mineralogical composition*
		Sand	Silt	Clay				
		g kg^{-1}			g kg^{-1}		mg kg^{-1}	
Land use **								
Charcoal kiln	6.8(0.8)[1] a	723(151)[2] a	119(77)[1] a	157(154)[1] a	9.2(6.4)[2] a	0.7(0.4)[1] a	11(9)[3] a	Q(86), CM(7), P(7)
Crop Field	5.8(0.6)[1] b	674(169)[2] a	110(69)[1] a	215(172)[1] a	8.0(5.1)[2] a	0.6(0.4)[1] a	4(3)[3] b	Q(86), CM(8), (6)
Forest	5.9(0.5)[1] b	708(153)[2] a	122(82)[1] a	170(138)[1] a	7.1(5.0)[2] a	0.6(0.4)[1] a	7(5)[3] a	Q(82), CM(12), P(6)
Vanduzi ***								
Charcoal kiln	7.2(0.5)[1] a	841(67)[1] a	77(17)[1] a	82(78)[1] a	5.3(2.7)[1] a	0.4(0.2)[1] a	18(9)[1] a	Q(89), CM(2), P(9)
Crop Field	6.3(0.3)[1] b	641(239)[1] a	98(16)[1] a	261(233)[1] a	4.7(2.6)[1] a	0.4(0.2)[1] a	5(5)[1] a	Q(84), CM(7), P(9)
Forest	6.5(0.2)[1] b	764(121)[1] a	86(18)[1] a	150(126)[1] a	5.5(5.2)[1] a	0.4(0.2)[1] a	12(5)[1] a	Q(80), CM(12), P(8)
Sussundenga ***								
Charcoal kiln	6.8(0.9)[1] a	674(215)[1] a	66(8)[2] a	260(223)[4] a	5.9(4.2)[1] a	0.6(0.3)[1] a	8(9)[1] a	Q(93), CM(7)
Crop Field	5.7(0.7)[1] ab	786(63)[1] a	49(42)[2] a	164(100)[4] a	6.4(2.9)[1] a	0.5(0.2)[1] a	4(2)[1] a	Q(95), CM(5)
Forest	5.5(0.2)[1] b	817(48)[1] a	34(28)[2] a	149(75)[4] a	4.8(2.2)[1] a	0.4(0.2)[1] a	5(3)[1] a	Q(92), CM(4), P(4)
Macate ***								
Charcoal kiln	6.4(0.9)[1] a	656(74)[1] a	215(58)[1] a	130(91)[1] a	16.3(4.6)[1] a	1.2(0.3)[1] a	8(3)[1] a	Q(76), CM(11), P(12), M(1)
Crop Field	5.4(0.5)[1] a	596(85)[1] a	183(115)[1] a	220(195)[1] a	13.0(5.3)[1] a	1.0(0.4)[1] a	2(2)[1] b	Q(78), CM(12), P(10)
Forest	5.6(0.4)[1] a	543(72)[1] a	246(115)[1] a	211(161)[1] a	11.2(5.1)[1] a	1.0(0.5)[1] a	3(3)[1] ab	Q(75), CM(20), P(5)

* In parentheses the percentage content of each mineral (semi-quantitative estimation). Q=quartz, CM=clay minerals, P=plagioclases, M=micas.
** Standard deviation, n = 12.
*** Standard deviation, n = 4.
[1] One-way ANOVA test ($P < 0.05$).
[2] Kruskall-Wallis test ($P < 0.05$).
[3] Friedman test ($P < 0.05$).
[4] Welch one-way ANOVA test ($P < 0.05$).

Table 4.3 Mean values of physicochemical properties for A and Bo horizons of each study locations and for the A and Bo horizons for each land use. Manica province, central Mozambique. Numbers in parentheses are the standard deviations. For each column within land use and location, mean values with different letters significantly differ for $P < 0.05$.

Horizons	pH	Particle-size distribution			EOOC	Total N	Available P	Main mineralogical composition*
		Sand	Silt	Clay				
		$g\ kg^{-1}$			$g\ kg^{-1}$		$mg\ kg^{-1}$	
Horizons **								
A	6.4(0.8)[1] a	765(124)[1] a	126(78)[1] a	109(93)[1] b	11.2(5.0)[1] a	0.9(0.4)[1] a	10(7)[1] a	Q(88), CM(8), P(4)
Bo	5.9(0.7)[1] b	639(150)[1] a	108(104)[1] a	253(158)[1] a	5.0(3.9)[1] b	0.5(0.3)[1] b	4(5)[1] b	Q(80), CM(12), P(8)
Vanduzi ***								
A	6.7(0.6)[1] a	803(131)[1] a	92(17)[1] a	105(122)[1] a	8.0(2.2)[1] a	0.5(0.1)[1] a	16(8)[1] a	Q(90), CM(4), P(6)
Bo	6.5(0.4)[1] a	694(194)[1] a	82(19)[1] a	224(188)[1] a	2.4(1.0)[1] b	0.3(0.1)[1] b	8(7)[1] a	Q(79), CM(10), P(11)
Sussundenga ***								
A	6.4(0.9)[1] a	848(44)[1] a	64(34)[1] a	88(69)[2] b	8.3(1.4)[1] a	0.7(0.2)[1] a	9(6)[1] a	Q(94), CM(5), P(1)
Bo	5.6(0.6)[1] a	670(140)[1] b	36(19)[1] a	294(122)[2] a	3.0(1.2)[1] b	0.3(0.1)[1] b	2(0)[1] b	Q(92), CM(7), P(1)
Macate ***								
A	6.1(0.8)[1] a	644(75)[1] a	223(44)[3] a	134(92)[1] a	17.4(3.2)[1] a	1.4(0.2)[1] a	6(4)[1] a	Q(81), CM(12), P(6), M(1)
Bo	5.5(0.5)[1] a	552(72)[1] b	207(132)[3] a	241(179)[1] a	9.6(3.2)[1] b	0.8(0.2)[1] b	3(2)[1] a	Q(72), CM(17), P(11)
Charcoal kilns ***								
A	7.2(0.7)[1] a	801(96)[1] a	121(63)[1] a	77(64)[1] a	12.4(6.1)[1] a	0.9(0.4)[1] a	16(6)[1] a	Q(89), CM(5), P(6)
Bo	6.4(0.7)[1] b	646(163)[1] a	117(96)[1] a	237(180)[1] a	6.0(5.3)[1] a	0.5(0.4)[1] a	7(7)[1] a	Q(83), CM(9), P(8)
Crop fields ***								
A	6.0(0.6)[1] a	728(145)[1] a	129(74)[1] a	143(127)[1] a	10.9(5.1)[1] a	0.8(0.4)[1] a	6(4)[1] a	Q(89), CM(7), P(4)
Bo	5.6(0.6)[1] a	621(170)[1] a	92(101)[1] a	287(191)[1] a	5.1(3.1)[1] b	0.5(0.2)[1] a	2(1)[1] b	Q(81), CM(10), P(9)
Forests ***								
A	6.0(0.5)[1] a	766(138)[1] a	128(106)[1] a	107(82)[1] a	10.4(4.3)[1] a	0.9(0.4)[1] a	9(6)[1] a	Q(87), CM(9), P(4)
Bo	5.7(0.6)[1] a	650(143)[1] a	116(130)[1] a	234(119)[1] a	3.9(3.4)[1] b	0.4(0.3)[1] b	4(3)[1] a	Q(77), CM(16), P(7)

* In parentheses the percentage content of each mineral (semi-quantitative estimation). Q=quartz, CM=clay minerals, P=plagioclases, M=micas.
** Standard deviation, n = 18.
*** Standard deviation, n = 6.
[1] One-way ANOVA test ($P < 0.05$).
[2] Kruskall-Wallis test ($P < 0.05$).
[3] Welch one-way ANOVA ($P < 0.05$).

4.3 Results

4.3.1 Soil morphology

In all locations (Sussundenga, Vanduzi, and Macate), the soils were Oxisols due the presence of diagnostic Bo horizons (Soil Survey Staff, 2014) (Table S4.1). The A horizons under charcoal kiln showed a charcoal content always higher than 30%, to become ≈1% in the crop fields and to be absent under forests. The Bo horizons showed a reddish colour and, especially at Vanduzi, they displayed a relatively high content of Fe-Mn-oxides (≈5%). In general, both A and Bo horizons presented a good degree of aggregation, with the presence of sub-angular and angular blocks generally coarser in the A than in the Bo horizons (Table S4.1). The good state of aggregation, the coarse texture (from loamy sand to sandy loam), and the absence of any redoximorphic feature indicated these soils are well-drained and, consequently, with low water-holding capacity (Agrawal, 1991; Suzuki et al., 2007).

4.3.2 Microbiota diversity

The relative abundances of bacterial taxa were examined at phylum rank to determine whether there were differences at the scale of location, land use, or horizon (Fig. 4.1). In total, 25 different phyla were detected that reached approximately 96.5% of the bacterial pool, being Actinobacteria (22%), Proteobacteria (19%), Chloroflexi (17%), Firmicutes (15%), Planctomycetes (10%), Acidobacteria (5%), Verrucomicrobia (3%), Nitrosphirae (2%), and AD3 (1%) the most representative by considering the average relative abundance for all samples. Regarding the minor OTUs fraction, we observed that Bacteroidetes, Gemmatimonadetes, Armatimonadetes, Cyanobacteria, Gal15, Chlamydiae, TM7, OD1, and Crenarchaeota (relative abundance between 0.1-1%) represented about 3.4% of the total bacterial community. At Vanduzi and Macate, for the alpha diversity value we observed the highest number of OTUs and a higher richness (Chao1 and Shannon index) in the A horizons than in the Bo horizons (data not shown, $FDR < 0.05$), while no difference was observed among the land uses. Conversely, at Sussundenga, the alpha diversity value showed no difference between forest and crop field, which displayed a higher number of OTUs and a higher richness than the charcoal kiln (data not shown, $FDR < 0.05$); no difference was observed between the horizons.

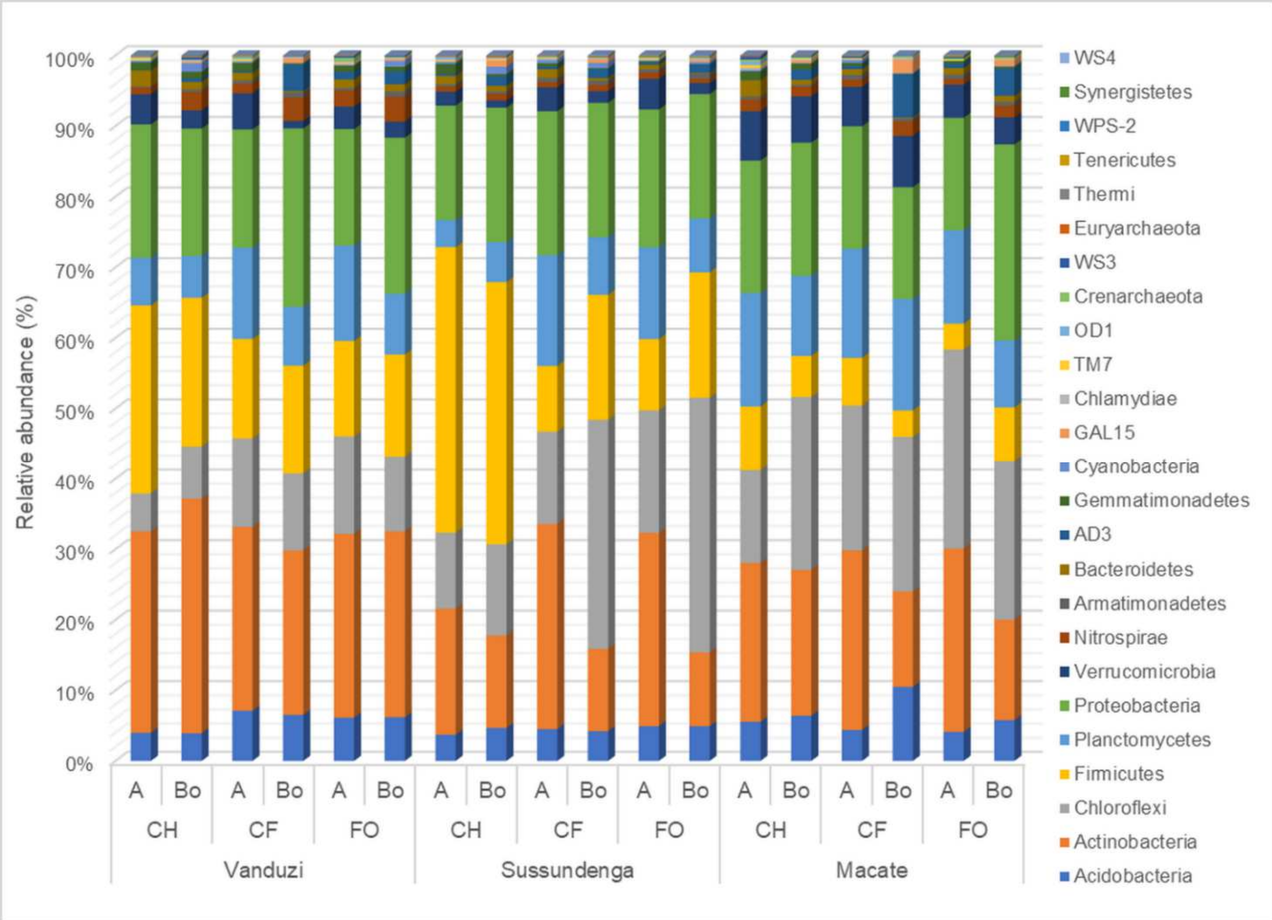

Fig. 4.1 Phyla relative abundance (%) in the A and Bo horizons of soils under charcoal kiln (CH), crop field (CF), and forest (FO) at Vanduzi, Sussundenga, and Macate. Manica province, Central Mozambique.

4.3.3 Location effect

The soils from Vanduzi showed the highest pH and the highest content of available P, while EOOC and total N were the greatest at Macate (Table 4.1). Particle-size distribution was always dominated by the sand fraction and mineralogically by quartz, with minor contents of clay minerals and plagioclases. Regarding OTUs association, Vanduzi displayed the highest abundance of Actinobacteria, Firmicutes, Nitrospirae, and WS3, Sussundenga the highest for Firmicutes, Cyanobacteria and WS4, while Macate showed the highest presence of Chloroflexi, Planctomycetes, Verrucomicrobia, and WS3 (Fig. S4.1, FDR < 0.05).

Distributions at a lower taxonomical rank were presented in Fig. 4.2 (FDR < 0.05) and the highest abundances found were summarized in Appendix 4.1.

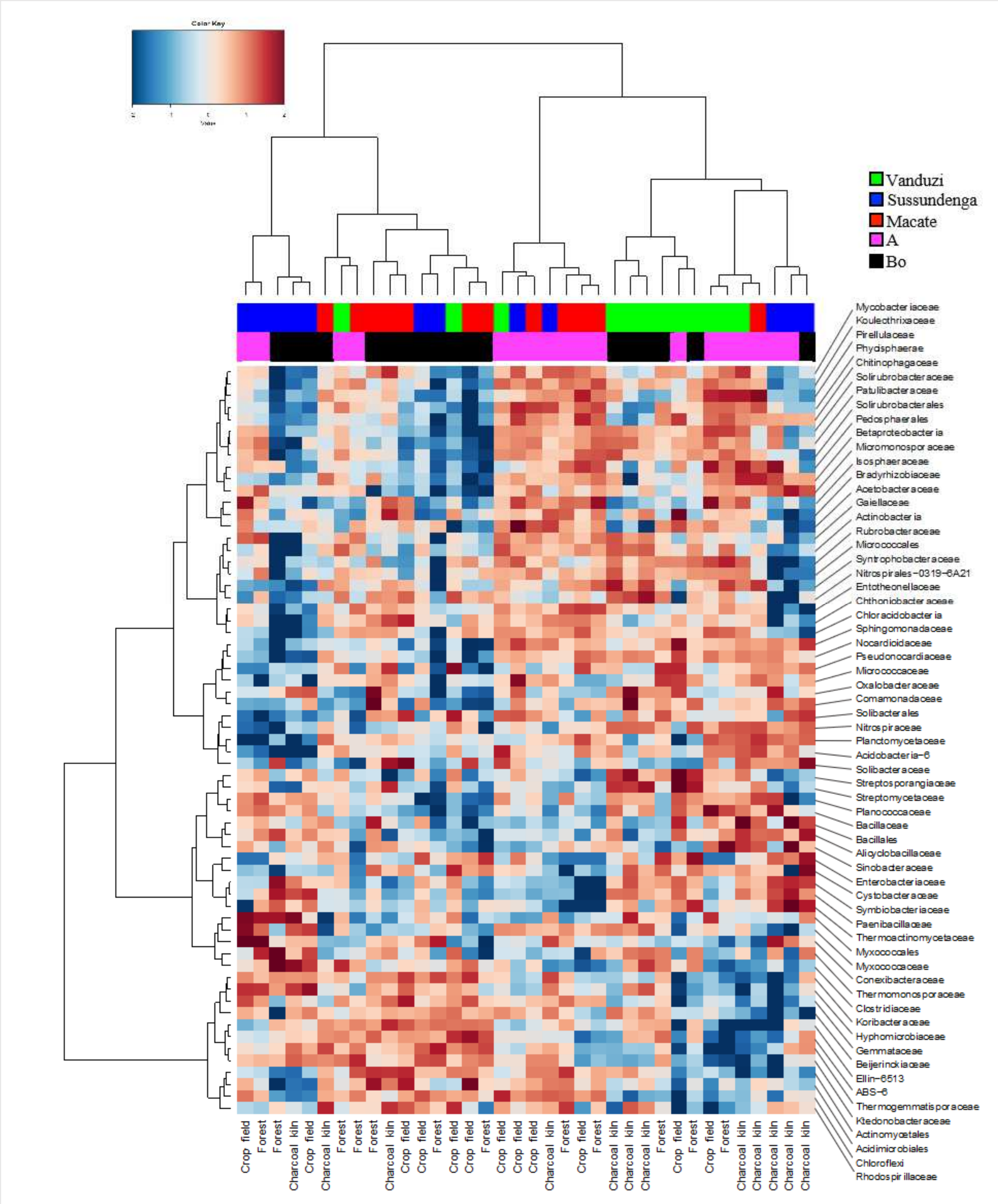

Fig. 4.2 Average-linkage clustering of soil samples based on OTUs relative abundance at the highest taxonomical rank, for A and Bo horizons, different land use, and locations. Manica province, central Mozambique. The colour scale represents the OTUs abundance denoted as Z-score, with brown indicating high abundance and blue indicating low abundance.

The results of bacteria diversity at phylum rank among locations were schematically synthesized in Fig. 4.3.

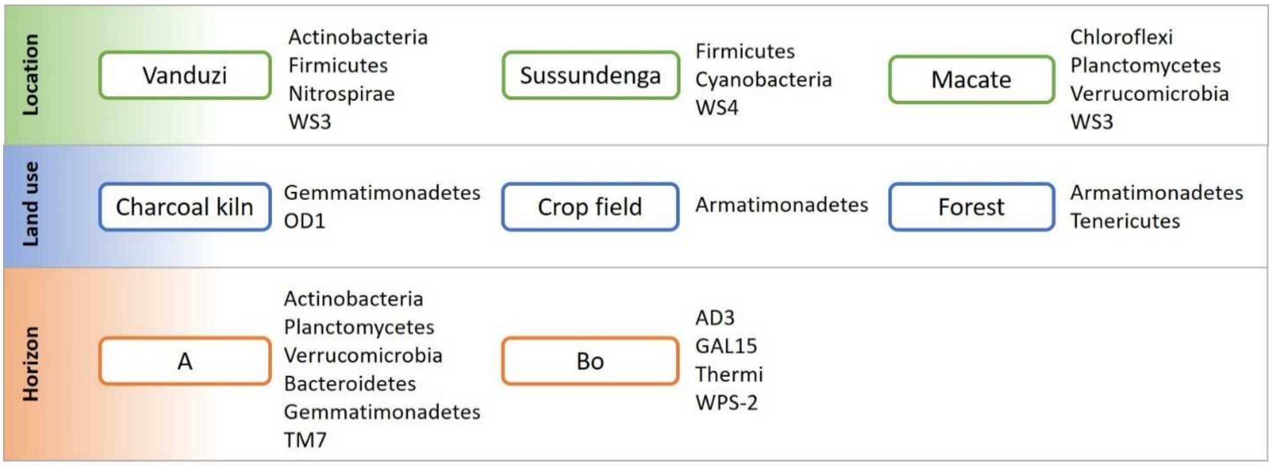

Fig. 4.3 Graph showing the statistically most abundant OTUs in soils at phylum rank according to location, land use, and horizon. Manica province, central Mozambique. Abundances significantly differ at FDR ≤ 0.05.

4.3.4 Land use effect

The soils under charcoal kiln had the highest pH, while both charcoal kilns and forests displayed the largest available P content (Table 4.2). In all land uses, sand was the most represented separate and the mineralogy was dominated by quartz. In the different locations, the highest pH values were observed for the charcoal kilns of Vanduzi and Sussundenga (Table 4.2). The largest available P content occurred at Vanduzi for charcoal kilns, while at Sussundenga and Macate there was a scarce dotation of this nutrient (Table 4.2). Charcoal kilns showed the highest abundance of Gemmatimonadetes and OD1 and the lowest abundance of Armatimonadetes and Tenericutes. An opposite trend was observed for the same bacteria in soils under crop field and forest (Fig. S4.2, FDR < 0.05). Looking at each location, soils under charcoal kiln at Vanduzi abounded in Firmicutes, while at Sussundenga soils under charcoal kiln showed the lowest abundance of Planctomycetes (Fig. S4.3, FDR < 0.05). At Macate, under charcoal kiln the soils showed the lowest abundance of Armatimonadetes while, soils under forest showed the lowest abundance of Chlamydiae (Fig. S4.3, FDR < 0.05).

At low taxonomical rank, differences of bacterial distribution were displayed in Fig. 4.2 (FDR < 0.05), and briefly reported in Appendix 4.1, while differences at phylum level among land uses, and among land uses within location were synthetized in Figs.4.3 and 4.4, respectively.

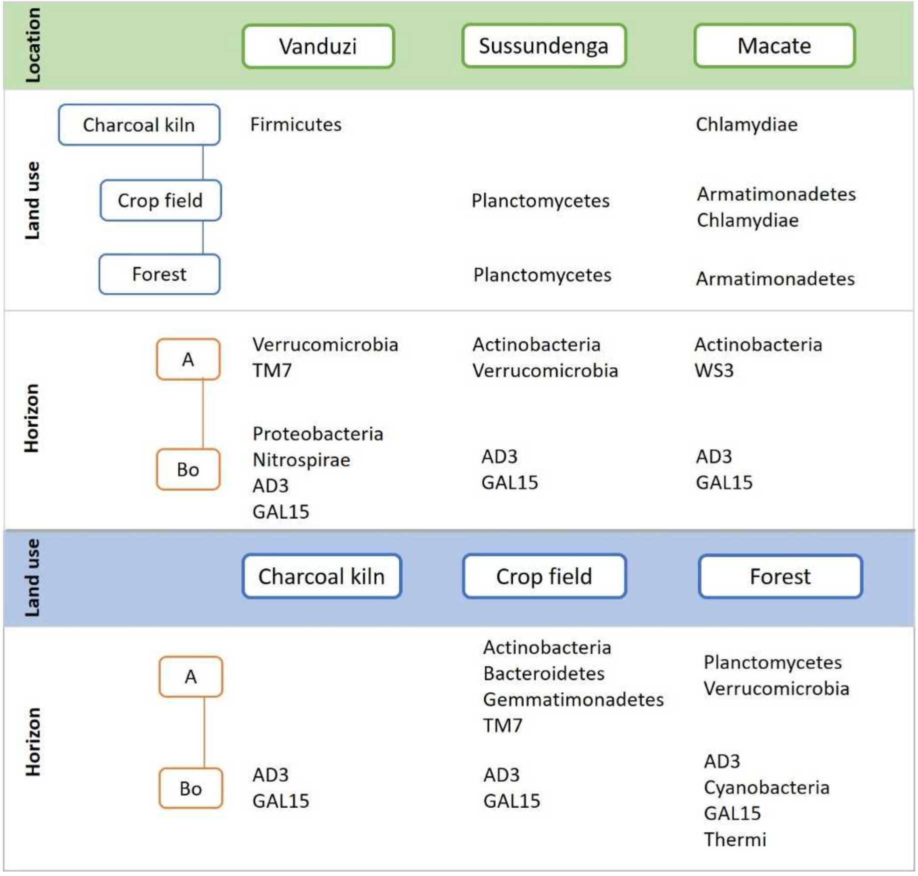

Fig. 4.3 Graph showing the statistically most abundant OTUs in soils at phylum rank between land uses and horizons within locations, and between horizons within land uses. Manica province, central Mozambique. Abundances significantly differ at FDR ≤ 0.05.

4.3.5 Horizon effect

The pH and the contents of EOOC, total N, and available P were higher in the A compared with the Bo horizons, while, as expected for Oxisols, the clay content was much larger in the Bo than in the A horizons (Table 4.3, $P < 0.05$). In all the locations, EOOC and total N were the highest in the A horizons. At Sussundenga and Macate the sand content was the highest in the A horizon, while the clay abounded in the Bo horizon. Only at Sussundenga the available P abounded in the A horizons (Table 4.3, $P < 0.05$). Mineralogical assemblage was similar in all situations, with quartz as the most abundant mineral, always higher in the A than in the Bo horizons, while clay minerals were always higher in the Bo than in the A horizons (Table 4.3). With respect to soil use, in the charcoal kilns only the pH values were higher in the A than in the Bo horizons. In the crop fields, EOOC and available P showed the highest contents in the A horizons, while in the forests EOOC and total N were the largest in the A horizons.

By comparing the OTUs composition, Actinobacteria, Planctomycetes, Verrucomicrobia, Bacteroidetes, Gemmatimonadetes, and TM7 were the most abundant in the A horizons, whereas the Bo horizons displayed the highest abundance of AD3, GAL15, Thermi, and WPS−2 (Fig. S4.4, FDR < 0.05). At Vanduzi, Verrucomicrobia and TM7 were found to be the most abundant bacteria in the A horizons, while Proteobacteria, Nitrospirae, AD3, and GAL15 were mainly associated with the Bo horizons (Fig. S4.5, FDR < 0.05). At Sussundenga, Actinobacteria and Verrucomicrobia were predominant in the A horizons, while AD3 and GAL15 abounded in the Bo horizons (Fig. S4.6, FDR < 0.05). At Macate, Actinobacteria and WS3 abounded in the A horizons, while AD3 and GAL 15 predominated in the Bo horizons (Fig. S4.7, FDR < 0.05). Considering soil horizons under different land use, the Bo horizons under charcoal kiln was dominated by AD3 and GAL15 (Fig. S4.8, FDR < 0.05). The A horizons under crop field were characterized by Actinobacteria, Bacteroidetes, Gemmatimonadetes, and TM7, while the Bo horizons were dominated by AD3 and GAL15 (Fig. S4.9, FDR < 0.05). Under forest, the A horizons showed the highest abundance of Planctomycetes and Verrucomicrobia, while the Bo horizons showed the predominance of AD3, Cyanobacteria, GAL15, and Thermi (Fig. S4.10, FDR < 0.05).

At lower taxonomical rank, differences were displayed in Fig. 4.2 (FDR < 0.05) and details about the highest abundances within locations were summarized in Appendix 4.2. The bacteria diversity at phylum rank between A and Bo horizons, and between horizons within location was synthetized in Figs. 4.3 and 4.4, respectively.

4.3.6 Correlation between microbiota and physicochemical properties

By plotting the correlation between OTUs of the most represented phyla and the soil physicochemical properties (Fig. S4.11, FDR < 0.05), we observed that the presence of Actinobacteria was positively associated with available P, while Chloroflexi was directly associated with clay and inversely with sand, available P, and pH. Firmicutes were positively associated with pH and sand but inversely correlated with total N. Planctomycetes was negatively associated with pH and, together with Verrucomicrobia, they were positively correlated with EOOC, total N, and silt. Armatimonadetes and AD3 resulted negatively correlated with available P and sand, but positively correlated with clay. Bacteroidetes, Gemmatimonadetes, and TM7 were directly associated with pH and available P. GAL15 displayed the highest negative correlation with pH, EOOC, available P, and sand, and were observed to be positively correlated with clay, while OD1 displayed the opposite correlations (FDR < 0.05).

4.4 Discussion

4.4.1 Different forest fallow period effect (temporal variation)

The three locations differed in microbial community abundances for several taxa. In detail, Actinobacteria phylum (among which *Rubrobacteraceae*, *Streptomycetaceae*, and *Streptosporangiaceae* were the most abundant families and *Micrococcales* the most abundant order) was the dominant in the soils at Vanduzi. Actinobacteria phylum has been widely reported for soils under various environmental conditions, including extreme environments like Antarctica and Sahara (e.g., Saker et al., 2015; Tytgat et al., 2016), and this is probably the reason this phylum is one of the most abundant in the soils here studied. Araujo et al., (2020) have found some Actinobacteria taxa abounded in soils near to neutral pH, including *Rubrobacter* genus belonging to *Rubrobacteraceae* family. Instead, Koyama et al., (2014) reported a reduction of Actinobateria in soils enriched with N, while Prada Salcedo et al., (2014) studied the ability of some Actinobacteria strains to solubilize both tricalcium phosphate and Al-phosphate in acid soils, making P available in solution. Our correlation plot (Fig. S4.11) showed that Actinobacteria was positively correlated with the available P but, as in the case of Vanduzi, also with the highest pH values and the lowest total N contents. At Vanduzi there was also the highest presence of Nitrospirae, specifically of the *Nitrospirales* order. Vipindas et al., (2020) described Nitrospirae as chemolithoautotrophic bacteria, mainly involved in N mineralization, in particular in the oxidation of nitrite to nitrate. In fact, Wang et al., (2018) reported that the nitrate addition to soil resulted in the decline of Nitrospirae and of the nitrification activity. In addition, Zhou et al., (2015) associated a high presence of Nitrospirae to soils with neutral pH and not fertilization with N and P. It is therefore conceivable that bacteria of the Nitrospirae group abound in scarcely fertile soils where they play an important role to produce nitrate by nitrite oxidation. Sussundenga soils were characterized by the dominance of Cyanobacteria and WS4. Cyanobacteria abounded in the Sussundenga soils, where there was the largest quartz content, but they were scarce at Macate, where quartz was in the lowest quantity. The fact that the different distribution in quartz may influence Cyanobacteria abundances was ascribed to the adaptation of these bacteria to arid conditions (Lacap-Bugler et al., 2017), which are well-expressed at the grain surface of quartz, one of the less hydrophilic silicates in soil because of its lack of isomorphic substitutions (Tarasevich et al., 2002). At Macate, soils showed the highest presence of Chloroflexi, Verrucomicrobia (among which the family *Chthoniobacteraceae*) and Planctomycetes (among which the family *Gemmataceae*). Various studies have reported that Chloroflexi are involved in the organic matter decomposition and, consequently in the C and N cycling (e.g., Hug et al., 2013; Ibrahim et al., 2020). Chloroflexi abounded at Macate, where there were the highest amounts of EOOC and total N, even though this correlation was not statistically significant. Instead, at Macate, Verrucomicrobia were positively correlated with the contents of EOOC, total N, and silt, and the correlations were statistically significant. Similar results were reported by Buckley and Schmidt, 2001), who found a positive correlation between Verrucomicrobia and soil organic carbon, total N, and soil moisture. Also, Planctomycetes are directly correlated with EOOC, total N and silt, but inversely with pH. Zhao et al., (2018) also observed a significant correlation between soil organic carbon and Planctomycetes abundance. Firmicutes, represented in large amount by *Paenibacillaceae* and *Bacillaceae* families, abounded at Vanduzi and Sussundenga and showed a positive correlation with pH and sand content, but negative with total N. Vos et al. (2011) described *Paenibacillaceae* as mesophilic and termophilic, but also as neutrophilic and alkaliphilic bacteria. Since the soils at Vanduzi and Sussundenga displayed all these physicochemical conditions, with pH values closed to neutrality and the prevalence of sand particles that favour high temperatures transmission at depth in case of heat flow (Abu-Hamdeh and Reeder, 2000), we supposed that Firmicutes proliferated in these soils because of these soil properties.

4.4.2 Land use effect (horizontal variation)

As expected, charcoal kilns represented a unique ecosystem, with peculiar microbial community if compared to crop field and forest as, for example, a higher abundance of OD1 and Gemmatimonadetes. Following the report of (Coomes and Miltner, 2017), who also found Gemmatimonadetes in soils under charcoal kiln, and the correlations reported in Fig. S4.11, we ascribed the presence of these bacteria in our charcoal kiln soils to the relatively large content of available P and relatively high pH values. A similar distribution is reported for OD1, which were largely abundant in charcoal kiln soils and resulted positively correlated with pH, available P, and sand, but negatively with clay (Fig. S4.11). Since pH showed the most significative variations between charcoal kiln soils and crop field/forest soils, we suggest OD1 bacteria are mainly influenced by soil reaction rather than the other correlated properties. On the contrary, Armatimonadetes were more abundant in crop field and forest soils than charcoal kilns and showed a positive correlation with clay but a negative correlation with available P and sand. These results suggested a predilection of Armatimonadetes for soils scarce in available P; moreover, Tytgat et al. (2016) identified Armatimonadetes as negatively associated with pH but positively associated with moisture. As in the case of our soils under charcoal kiln (Table 4.2), the available P was always the highest probably for the large presence of charcoal, which commonly supplies soluble P to soil (Rafael Alves et al., 2020), and in charcoal kiln moisture could be negatively influenced by heating. Tenericutes mainly abounded in forest soil, without significant correlation to physicochemical properties. Lanc et al., (2013) reported that Tenericutes were particularly abundant in soils from Brazilian semi-arid forests during the rainy season. Although more investigation on this phylum is needed, we suppose Tenericutes proliferation is favoured by the presence of relatively high soil organic matter content and moisture, conditions that occurred in our forest soils (Scott and Kleb, 1996).

A few microbial differences among land uses were restricted to some locations. For example, at Vanduzi, Firmicutes abounded in the charcoal kiln area possibly because of the high pH values due to the alkalinising effect of ash and biochar (Fidel et al., 2017) and to the sand content, which favour penetration of high temperatures in soil during charcoal production. As a support of this, Firmicutes belonging to the *Bacillales* order abound in soils after wildfire and burning treatments (Smith et al., 2008; Sul et al., 2013), while bacteria of the *Bacillaceae* family include spore-forming species able to resist to extremely high temperature (Battistuzzi and Hedges, 2009; Galperin, 2015). At Sussundenga, Planctomycetes showed the lowest abundance in charcoal kiln area. Yang et al., (2020) and Jenkins et al., (2017) observed a decrease of Planctomycetes when soil pH increased following fire or biochar addition. As a demonstration of this, Navarrete et al., (2015) reported of a higher abundance of Planctomycetes in forest soils with low pH. Our results agreed with the above-mentioned studies, being the soil pH at Sussundenga the highest in charcoal kiln and the relation between Planctomycetes and pH negative (Fig. S4.11). At Macate, differences were detected for Armatimonadetes, the least abundant phylum in charcoal kiln soils, and Chlamydiae, the least abundant in forest soils. We ascribed Chlamydiae distribution to the behaviour of some Chlamydiae bacteria as pathogens of arthropods (Horn et al., 2004; Wagner and Horn, 2006), including soil isopods like woodlouse (Collingro et al., 2020). Specifically, soil isopods are Chlamydiae's soil dwelling that generally feed of decaying organic matter (Saska, 2008) including corn litter (Johnson et al., 2012), which was the major remainders of cultivation in the Macate fields.

4.4.3 Horizon effect (vertical variation)

The horizon effect has marked a clear separation of the physicochemical properties and microbiota. The higher abundance of Actinobacteria in the A than in the Bo horizons appeared correlated with the highest contents of available P, EOOC, and total N at Macate and Sussundenga and in the crop fields. Although Actinobacteria have been associated to soils with low organic carbon content (Fu et al., 2019; Sul et al., 2013), other studies demonstrated their optimum growth substrate is represented by soils rich in organic matter and N, with neutral pH, good soil aeration, and moderate temperature (e.g., Dai et al., 2018; Liu et al., 2017; Tang et al., 2016), conditions that mainly attained in the A horizons (Table 4.3). In the soils at Vanduzi, Proteobacteria were the most abundant in the Bo horizons. Proteobacteria have been described as copiotrophic bacteria that are involved in carbon, nitrogen, and sulphur cycles (Mendes et al., 2015), which abound in moderately affected by agronomical practices and fertile soils (Dai et al., 2018; Mendes et al., 2015; Yin et al., 2010). If this requirements not fully agreed with the soil conditions at Vanduzi, it is also true that some Proteobacteria are able to catalyse the Fe-oxidation reactions (Hedrich et al., 2011) and the Bo horizons of these soils are particularly rich of Fe-Mn nodules (≈5%), which could be the soil property favouring bacteria of this phylum. Planctomycetes (among which the *Phycisphaerae* family) abounded in the A horizons under forest, probably because some species belonging to this phylum is involved in carbon and N turnover (Fuerst and Sagulenko, 2011). Like Planctomycetes, Verrucomicrobia (in detail *Chthoniobacteraceae* family and *Pedosphaerales* order) were more diffused in the A than in the Bo horizons especially at Vanduzi and Sussundenga, and under forest. In our case, Verrucomicrobia were largely present concomitant with the highest quantities of EOOC, total N, and available P. At this regard, Sangwan et al. (2004) and O'Brien et al. (2016) recognized *Chthoniobacteraceae* as utilizers of saccharides from plant biomass or engaged in symbiosis with soil nematodes. Instead, *Pedosphaerales* were found by Bach et al. (2018) to abound in large macroaggregates rather than in microaggregates. Thus, the large abundance of Verrucomicrobia in the A horizons was ascribed to their relatively higher organic matter content, which fairly includes sugars, and the generalized coarser structure.

Bacteroidetes (among which the *Chitinophagaceae* family), Gemmatimonadetes, and TM7 abounded in the A horizons, particularly of the crop fields, and were positively correlated with pH values and available P (Fig. S4.11). As reported by Wolińska et al. (2017), Bacteroidetes are involved in the organic matter cycle and, joined with Gemmatimonadetes, they have been found associated with the degradation of complex organic polymers (Chaudhry et al., 2012). In particular, *Chitinophagaceae* mainly colonize the rhizosphere rather than the bulk soil (Madhaiyan et al., 2015) and have been found to be positively correlated with the C:N ratio (Dennis et al., 2019). Furthermore, Zhou et al. (2015) reported of positive correlations between TM7 and the contents of total N, nitrates, ammonium, and soil organic matter. All this considering, the abundance of Bacteroidetes, Gemmatimonadetes, and TM7 in the A horizon was ascribed to a predilection for complex organic substrates with an incipient decaying of organic matter.

AD3 and GAL15 were more abundant in the Bo than in the A horizons. Looking at the correlation plot (Fig. S4.11), AD3 was directly correlated with clay and inversely correlated with available P and sand. This distribution was probably due to the general properties of Oxisols, which showed an increase of acidity and clay with increasing depth. As a support to this, Mesa et al. (2017) found abundant AD3 in biofilms and sediments of acid mine drainage. Also GAL15 resulted to be directly correlated with clay and inversely correlated with available P and sand, but also with pH and EOOC. Since the members of these taxa seemed to prefer oligotrophic habitats (e.g., Li et al., 2020; Liu et al., 2020), it is conceivable they diffuse in the Bo horizons rather than in the A horizons. Also the phyla Thermi and WPS-2 abounded in the Bo horizons. Since Thermi were found in hypolithic communities of Taklimakan Desert in China (Lacap-Bugler et al., 2017) and WPS-2 were more abundant in unfertilized soils and in oil palm plantation than in primary and regenerating forests

(Wood et al., 2017), we assumed the members of these phyla prefer oligotrophic soil conditions, and consequently mainly inhabit the Bo horizons.

Only at Vanduzi, Proteobacteria and Nitrospirae showed a large abundance in the Bo horizons, with no significant correlation with the soil physicochemical properties (Fig. S4.11). Similar conditions were found by Hedrich et al., (2011), who ascribed to Proteobacteria a high grade of adaptation and the peculiarity of some species to survive with iron-oxidizing forms in presence of oxygen and preferably with neutral to acid pH. The diffusion of Nitrospirae in the Bo horizons fitted with their preference to colonize soil compartments with neutral pH and scarce N.

4.5 Conclusions

Oxisols submitted to slash and burn differed in terms of spatial and vertical changes for their bacterial diversity. Interestingly, our study suggested that bacteria were affected by soil physicochemical properties reliant on both soil genesis and human activities. Actinobacteria, Nitrospirae, WS3, Chloroflexi, Verrucomicrobia, Planctomycetes, and Firmicutes varied among locations in conjunction with different pHs and nutrients availability, while Cyanobacteria abundance seemed to depend on quartz content. Also land use determined a strong selection of microbiota in particular under charcoal kilns, where soil physicochemical properties are changed by temperature and addition of charcoal and ash. Gemmatimonadetes, OD1, Armatimonadetes, Firmicutes, and Planctomycetes were also affected by the presence of the charcoal kiln while, Tenericutes and Chlamydiae proliferated, respectively, in soils under forest for the high organic matter content and moisture and in the soil under crop field at Macate because of mulching practices. Except for Tenericutes, no other significative differences in terms of taxa abundances and physicochemical properties were encountered between forests and crop fields, despite the forest fallow might let suppose a considerable soil fertility restoration – with consequent microbiota change – over time. Remarkable results were found along the soil profiles, confirming the importance of genetic horizons in determining microbiota composition. Actinobacteria, Planctomycetes, Verrucomicrobia, Bacteroidetes, Gemmatimonadetes, TM7, and WS3 were abundant in the A horizons, suggesting a predilection for eutrophic conditions, while AD3, GAL 15, Thermi, WPS-2, Proteobacteria, and Nitrospirae abounded in oligotrophic Bo horizons. Such results allowed us to recognize two main group of bacteria, the bacteria strongly affected by spatial, temporal, and vertical variations, so they showed significative differences and the group of bacteria homogeneously distributed in soil despite variations.

Our findings contribute to improve the knowledge on spatial, temporal, and vertical soil bacteria diversity, and its dependence from physicochemical properties in Oxisols. More studies are needed to better understand the relationships between microbiota and soil properties.

Chapter 5.

Fungal metataxonomic diversity under different land use

5.1 Introduction

After the study about the effect of slash and burn system on soil bacterial community in Mozambique, it appears useful to assess the fungal community diversity in the same situation. In fact, as claimed by (Arévalo-Gardini et al., 2020), due to the influence of microbial activity on ecosystem stability and fertility, variations in fungal community may represent a valid indicator of soil health changes caused by land management.

It is well-known that eumycetes are greatly related to physiographic conditions, environmental setting due to climate and land management, soil properties such as SOM content and fertility level (Oehl et al., 2017; Shah et al., 2016; Spurgeon et al., 2013; Yuste et al., 2011). Important soil eumycetes are the saprotrophic fungi, which are fundamental decomposers of ligno-cellulosic remnants (Clocchiatti et al., 2020; van der Wal et al., 2013), while the entomopathogenic fungi are endophytes that can enhance plant defence against harmful insects (Deaver et al., 2019; Vega, 2018). Many studies have dealt with soil eumycetes diversity, but a very few have studied eumycetes in soils submitted to slash and burn. As far as we know, only Aguilar-Fernández et al. (2009), Adeniyi (2010), Sharmah and Jha (2014), and Barraclough and Olsson (2018) studied mycobiota variations in slash and burn submitted soils, mainly focusing arbuscular mycorrhizal fungi (AMF) community, a group of obligate symbiotic fungi with many plants that exerts a specific role in nutrient uptake (Deveautour et al., 2019; Gai et al., 2009; Hansen et al., 2019; Hart et al., 2005; Rożek et al., 2020; Sarr et al., 2019; Yang et al., 2011). In particular, Barraclough and Olsson (2018) studying dry tropical forests of Madagascar, reported that slash and burn practices decrease AMF abundance. However, a better knowledge of the soil fungal diversity can contribute to understand the complexity of the ecosystems and their response to slash and burn practice.

The aim of this work was therefore to evaluate fungal diversity by a metataxonomic approach in soils of three locations in central Mozambique subjected to slash and burn considering the effect of *i*) the different duration of the forest fallow period (temporal variation); *ii*) the three land uses forming the slush and burn system: charcoal kiln, crop field, and forest (horizontal variation); and *iii*) the development of genetic soil horizons (vertical variation). Using the experimental design and the sampling sites reported for the bacteria community, the investigation on the temporal, horizontal, and vertical variations of the soil fungal populations was linked to the main soil physicochemical properties.

5.2 Materials and methods

Details on the study areas, slash and burn system, mineralogical and physicochemical methods and results can be found in paragraphs 4.2.1 and 4.2.2. Here it suffices to remember that within the Manica province, central Mozambique, three locations were selected: Vanduzi, Sussundenga, and Macate (Fig. 2.1). The different duration of the forest fallow period (temporal variation) formed the following chronosequence i) at Vanduzi the forest was ≈25-years old, the crop field was 1-year old, and the charcoal kiln was 4-years old; ii) at Sussundenga the forest was ≈35-years old, the crop field 2-years old, and the charcoal kiln 1-year old; iii) at Macate the forest was ≈50-years old, the crop field 16-years old, and the charcoal kiln 16-years old (Table S4.1). In each location, we took into consideration soils under charcoal kiln, crop field, and forest (horizontal variation) and, for each soil, we collected both A and Bo horizons (vertical variation).

5.2.1 Microbial DNA extraction and sequencing

Total microbial DNA was extracted from 100 mg of each soil sample using the E.Z.N.A. ® Soil DNA Kit (Omega Bio-Tek, Inc., Georgia, USA), following the manufacturer's instruction. DNA-based analysis was preferred to mRNA analysis because in complex matrices like soil, RNA can be rapidly degraded by RNAases, with a consequent less reliability of the soil microbial composition (Nannipieri et al., 2020). The extracted DNA was quantified using a Qubit dsDNA assay kit (Life Technologies, Milan, Italy) and standardized to 5 ng/µL. Then, 2.5 µL were used as a template to amplify the D1 domain of the 26S rDNA gene by using the primers and protocol described by Mota-Gutierrez et al. (2019); a negative control was included in the PCR reactions by replacing the DNA solution with water. The PCR amplicons were purified and sequenced according to the Illumina metagenomic pipeline instructions. The sequencing was performed with a MiSeq Illumina instrument (Illumina) with V3 chemistry and generated 250 bp paired-end reads according to the manufacturer's instructions. To prevent preferential sequencing of the smaller amplicons, the amplicons were cleaned using the Agencourt AMPure kit (Beckman coulter, Brea, USA) according to the manufacturer's instructions. Then, DNA concentrations of the amplicons were determined using the Quant-iT PicoGreen dsDNA kit (Invitrogen Life Technology) following the manufacturer's instructions. To ensure the absence of primer dimers and to assay the purity, the quality of generated amplicon libraries was evaluated by a Bioanalyzer 2100 (Agilent, Palo Alto, CA, USA) using the High Sensitivity DNA Kit (Agilent). Following the quantitation, cleaned amplicons were mixed and combined in equimolar ratios. Pair-end sequencing (2X250 bp) using the Illumina MiSeq system (Illumina, San Diego, USA) were carried out following the manufacturer's instructions.

5.2.2 Bioinformatic analysis

After sequencing, reads were analyzed by using the Quantitative Insights into Microbial Ecology QIIME2 (Bolyen et al., 2019). Primers and adapters were trimmed by Cutadapter and then quality filtered using the DADA2 algorithm (Callahan et al. 2016), removing low-quality bases and chimeric sequences by using the DADA2 denoise-paired plug in of QIIME2. Amplicon Sequence Variants (ASVs) generated by DADA2 were used for taxonomic assignment using the qiime feature-classifier plugin against the manually build database for the mycobiota Mota-Gutierrez et al. (2019). Fungal taxonomy assignment was double checked on BLAST suite tools. QIIME2 diversity script was used to perform alpha diversity analysis. The data generated by sequencing were deposited in the NCBI Sequence Read Archive (SRA) and are available under the Bioprojects Accession Number PRJNA631872.

5.2.3 Statistical analysis

The data obtained by the soil physicochemical analyses were the same used for the Chapter 4 and can be found in Tables S4.2 and S4.3 of Supplementary materials. ASVs table was used to build a principal-component analysis (PCA) as a function of the sampling time by using the *made4* package of R. Concerning fungal metataxonomic analysis, not-normally distributed variables were presented as median (range interquartile). Variables were compared by Mann-Withney U test or Kruskal-Wallis test, as appropriate. Mycobiota α-diversity were assessed by Chao1 index and by Shannon diversity index, calculated using the diversity function of QIIME2. ASVs table was then imported in R to build the heatmap by the function made4 and to perform the permutational multivariate analysis of variance (ANOSIM) by the "vegan" package in R environment. Spearman correlation analysis between physicochemical determinations and mycobiota was performed through the psyc package and plotted by using the function *corrplot* of R. The *P* values were adjusted for multiple testing using the Benjamini-Hochberg procedure, which assesses the false discovery rate (FDR).

5.3 Results and discussion

5.3.1 Soil general features

All the soils under study belonged to the order of Oxisols (Soil Survey Staff, 2014), and were made by an 18 to 40 cm thick A horizon (ochric) and a thick Bo horizon (Table S4.1). Generally, all the soil horizons showed a coarse texture (mainly loamy sand and sandy loam) and a good degree of aggregation mostly made of sub-angular and angular blocks that, associated with the absence of redoximorphic feature, indicated a good drainage and the consequent low water-holding capacity of these soils (e.g., Agrawal 1991; Suzuki et al. 2007).

5.3.2 Mycobiota diversity

In all the samples analysed, a total of 37 ASVs were detected, and these grouped into two main clusters: *i*) cluster 1 includes most of the samples coming from Macate and Vanduzi soils and from the A horizons; *ii*) cluster 2 includes most of the samples comprising the Sussundenga soil and the Bo horizons. Cluster 1 mainly contained fungi of the genera *Sarcinomyces*, *Catenulifera*, *Chaetomium*, *Zygoascus*, *Fusarium*, *Trichoderma*, and *Chaetomiaceae*, while cluster 2 consisted of fungi belonging to the genera *Aureobasidium, Cladosporium, Malassezia, Pichia, Aspergillus, Saccharomyces*, and *Acremonium* (Fig. 5.1). Toju et al., (2016), analysing the fungi network in cool-temperate forest, found that *Malassezia* and *Cladosporium* had a strong preference for the B horizons, as in our case. Analysing the alpha diversity values as a function of the locations, we observed that the index indicated the highest Shannon, Chao1, and number of ASV in the Macate soils (FDR < 0.05, data not shown). Alpha diversity as a function of the land use did not show significant differences, while the comparison between the horizons highlighted a major level of complexity in the A than in the Bo horizons (FDR < 0.05, data not shown). Alpha diversity referred to horizon comparison confirmed the fungi tendency to decrease in number and species with the increase of depth (Jumpponen et al., 2010; Warcup, 1951). Furthermore, some studies have demonstrated that an increase of nitrogen results in an increased fungal richness and diversity (Mueller et al., 2014; Weber et al., 2013), thus explaining the highest indexes in the Macate soils and in the A horizons, which were characterized by higher N contents.

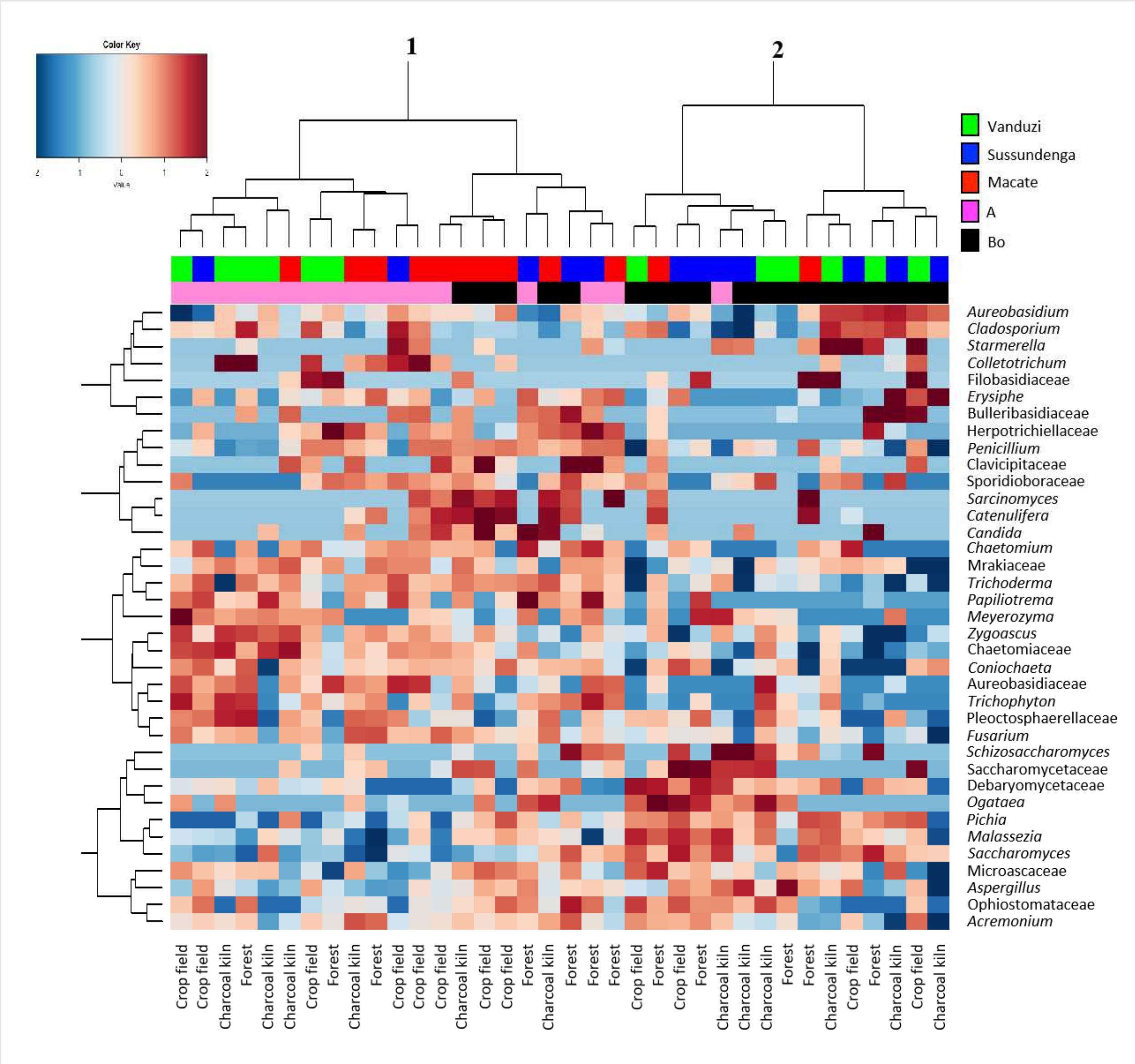

Fig. 5.1. Average-linkage clustering of soil samples based on ASVs relative abundance at the highest taxonomical rank, for A and Bo horizons, different land use, and locations. Manica province, central Mozambique. The colour scale represents the ASVs abundance denoted as Z-score, with brown indicating high abundance and blue indicating low abundance.

5.3.3 Different forest fallow period effect (temporal variation)

While pH values and available P were the greatest in the soils of Vanduzi, EOOC and total N showed the highest contents in those of Macate (Table 4.1). Particle-size distribution was always dominated by sand, which was higher in the soils of Vanduzi and Sussundenga than in those of Macate. The main mineralogical composition underlined the large dominance of quartz in all the soils (Table 4.1).

By comparing the three locations, differences in ASVs distribution were observed. The principal component analysis (PCA) based on the relative abundance of the main ASVs showed a partial sharing of the mycobiota as function of the locations in Vanduzi and Sussundenga; however, it was possible to ascertain a certain degree of separation in Macate (Fig. S5.1, P < 0.01). Looking at the relative frequency across locations, Vanduzi soils showed the highest frequency of *Cladosporium* (Fig. S5.2, FDR < 0.05), while Macate soils were characterized by the highest frequency of *Catenulifera*, *Fusarium*, *Penicillium*, *Sarcinomyces*, *Trichoderma*, and *Zygoascus*. The results of fungi diversity among locations were schematically synthesized in Fig. 5.2.

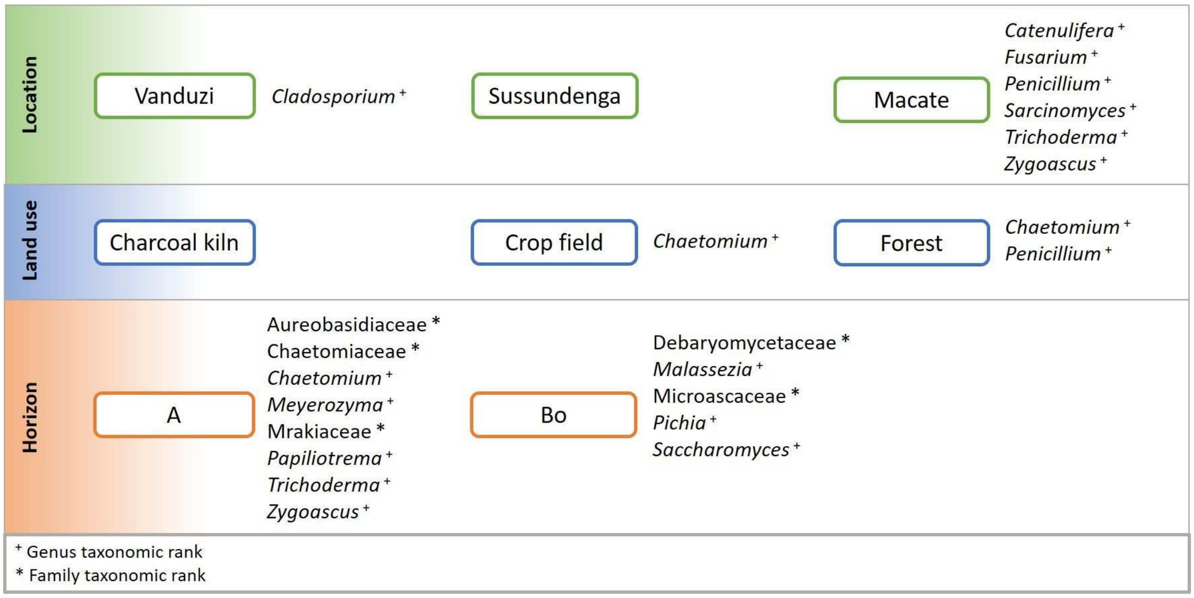

Fig. 5.2 Graph showing the statistically most abundant ASVs in soils at the highest taxonomical rank according to location, land use, and horizon. Manica province, central Mozambique. Abundances significantly differ at FDR ≤ 0.05.

Cladosporium is a genus that includes 993 heterogeneous and ubiquitous members of hyphomycetes well-known as common endophytes, and in our case was found with the highest frequency in the soils of Vanduzi. Several bioactive molecules that are active against bacteria and fungi have been isolated from endophytic *Cladosporium* species, thus indicating the main role of this fungal group in producing antimicrobial compounds involved against plant pathogens (Yehia et al., 2020). Also because of the generally higher content of N, the high prevalence of *Cladosporium* its often associated with intensive cultivation systems and it is reported to be an important taxon of the phyllosphere population (Abdelfattah et al., 2016). *Cladosporium* is also involved in plant phosphorus absorption (Shi et al., 2020), and the highest frequency of this fungi in the Vanduzi soils was probably associated with the highest amount of available phosphorus of these soils, despite no significant correlation to soil physiochemical properties was found (Fig. 5.3).

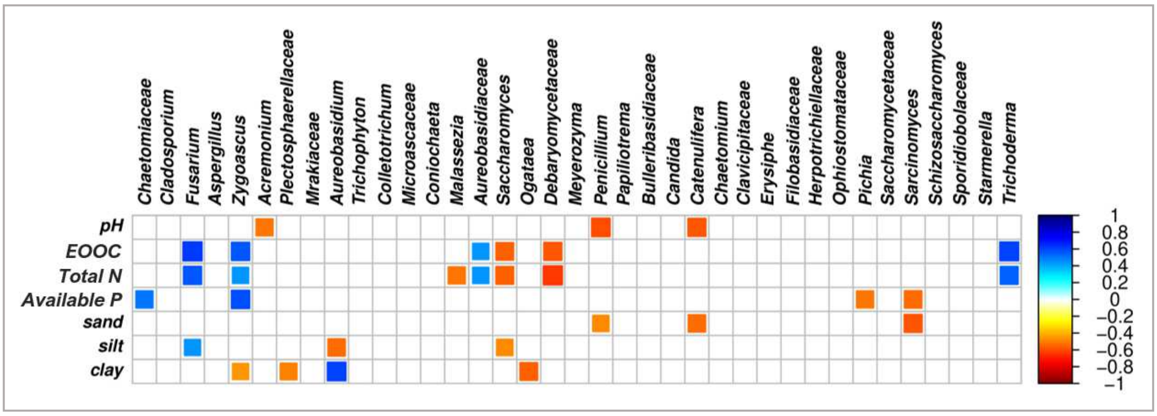

Fig. 5.3 Correlation between fungi and physiochemical soil properties in the A and Bo horizons of the soils under charcoal kiln, crop field, and forest at Vanduzi, Sussundenga, and Macate. Manica province, central Mozambique.

The genus *Catenulifera* includes anamorphs of four species of *Hyphodiscus*, a genus of discomycetes that was found associated with decaying wood and the fruit bodies of other fungi (Bogale et al., 2010; Hosoya, 2002). As far as we know, no information exists about the interaction between *Catenulifera* requirements and soil properties but, looking at the correlation plot (Fig. 5.3), *Catenulifera* was negatively related to pH and sand, which assumed the lowest values in the Macate soils. This let us to hypothesise that *Catenulifera* abounded in the Macate soils because they prefer acidophilic soil environments where organics and N abound.

The genus *Fusarium* includes over 1000 species and, among these, many are known as soilborne phytopathogenic and mycotoxigenic filamentous fungi able to infect crops (A. H. Ge et al., 2021; C. Ge et al., 2021; Goncharov et al., 2020), but also to act as saprotrophic fungi and /or colonizers of the rhizosphere in response to plant exudates (Goncharov et al., 2020). Further, many *Fusarium* species belong to the ecological group of fast-growing colonizers that, with their metabolism, enhance the N content of the soil litter (Goncharov et al., 2020). This reports agreed with our findings since *Fusarium* was positively correlated with total N and EOOC (Fig. 5.3), which abounded in the Macate soils where these fungi prospered. This abundance was probably favoured by the accumulation of decaying organic materials due to mulching in the crop field and to the presence of relatively well-developed and poorly disturbed litter in the forest.

Penicillium is a common soil fungal genus that includes beneficial microrganisms with a role in the plant-growth due to their ability to solubilize phosphate and Zn, and to produce useful secondary metabolites, extracellular enzymes, siderophores, and plant-growth regulators (Altaf, 2018; Das et al., 2021; (Efthymiou et al., 2018b, 2018a). *Penicillium* is also known for growing in extreme environments, including very acidic soils (Diao et al., 2019; Houbraken et al., 2020; Yadav et al., 2018). These properties of *Penicillium* well explained our results since the genus ASVs showed an inverse relation with pH (Fig. 5.3), which appeared the lowest in the Macate soils.

The free-living yeast-like fungi *Sarcinomyces* are known to be endophytic fungi playing important roles in enhancing plant growth and promoting resistance to abiotic and biotic stresses such as drought, salinity, and pathogens, because of their close interaction with plants. Because of this, the highest frequency of *Sarcinomyces* in the soils of Macate was ascribed to the relatively high presence of decaying organic material due to mulching and forest development, as also reported by Li et al. (2018). The fact that *Sarcinomyces* frequency was inversely related to available P and sand (Fig. 5.3) was probably due to their role of endophytic plant growth promoters, which implies the presence of mycelium in the abundant dead roots (Table S4.1).

Species of the genus *Trichoderma* are common soilborne fungi known as plant growth promoters and biocontrol agents able to increase plant resistance to phytopathogens and abiotic stresses through the production of the indole acetic acid (IAA) and volatile organic compounds (VOCs) (Das et al., 2021; Ji et al., 2020; Oskiera et al., 2017; F. Zhang et al., 2020). *Trichoderma* can also improve availability of N and P by increasing the activity of urease, phosphatase, catalase, and cellulolase (Ji et al., 2020;

Makhuvele et al., 2017). This evidence well agreed with the positive correlation of these fungi with EOOC and the total N (Fig. 5.3), which abounded in the soils of Macate.

Members of genera *Zigoascus* have been reported to have a role as biofertilizer since they are able to solubilize soil phosphates (Das et al., 2021). The highest abundance of *Zigoascus* in the Macate soils and their positive correlation with EOOC, total N, and available P (Fig. 5.3) let us to hypothesise that they prefer soil niches enriched in organics.

5.3.4 Land use effect (horizontal variation)

The highest pH values were detected in the charcoal kiln soils of Vanduzi and Sussundenga, while the available P, although in small amounts, was the highest in the charcoal kiln and forest soils (Table 4.2). Sand was always the most represented separate, followed by clay and silt, and quartz was the most abundant mineral, followed by clay minerals and plagioclases (Table 4.2).

The principal component analysis (PCA) showed a partial sharing of the mycobiota as function of the land use, for crop field and forest (Fig. S5.3, $P < 0.01$). Comparing different land uses, only two out of 37 fungi expressed different ASV distributions, *Chaetomium* and *Penicillium*, and their frequency was higher in the crop field and forest soils than in the charcoal kilns soils (Fig. S5.4, FDR < 0.05). This fungi distribution was synthetized in Fig. 5.2. *Chaetomium* genus belong to the family *Chaetomiaceae,* known to be producers of antimicrobial metabolites against plant pathogens pests, including fungi and insects (Chovanova and Zamocky, 2016; Mohammed *et al.*, 2019). The *Chaetomiaceae* family is also linked to the degradation of complex soil organic matter (Paula et al., 2020), and in particular the genus *Chaetomium* abounds in soils rich of cellulosic biomass due to their cellulose degrading capabilities. These characteristics well explained their highest frequency in crop field and forest soils, where they have been favoured by the presence of crop residues and litter accumulation (Ahmed et al., 2016; Soytong et al., 2001). The highest *Penicillium* distribution in the soils under crop fields and forests was ascribed to their adaptability to low pHs, which characterised these soils, as previously reported in the paragraph 3.3 and suggested by corrplot (Fig. 5.3).

Papiliotrema was the only taxon that resulted to be associated with the charcoal kiln soils of Macate (Fig. S5.5, FDR < 0.05). Few data are available for *Papiliotrema* yeast genus, formerly *Cryptococcus*. Member of this genus were found as predominant in rice storage granaries (Shi et al., 2021), while in soil *Papiliotrema laurentii* was observed to develop a synergic interaction with AMF to improve plant uptake of N and P (del V. Leguina et al., 2019) and the solubilization of scarcely soluble forms of phosphate (apatites) and zinc (ZnO and $ZnCO_3$) (Kumla et al., 2020). The presence of *Papiliotrema* in the charcoal kiln soils of Macate was tentatively attributed to the possible presence of phosphatic minerals that could have generated by repeated by combustion on the same area; the higher P availability in this soil could be taken as a support of this hypothesis.

5.3.5 Horizon effect (vertical variation)

The highest values of pH, EOOC, total N, and available P were detected in the A horizons, while, as expected for Oxisols, the Bo horizons contained more clay than the A horizons (Table 4.3). Mineralogy assemblage was similar in all cases, with quartz always more abundant in the A than in the Bo horizons, and the reverse occurring to clay minerals.

As reported in paragraph 5.3.2, fungi tend to create distinguished networks along the soil profile and, indeed, a clear separation of mycobiota between A and Bo horizons was observed by PCA (Fig. S5.6, $P < 0.01$). As synthesized in Fig. 5.2. ASVs mainly associated with A horizons were Aureobasidiaceae, Chaetomiaceae, *Chaetomium, Meyerozima*, Mrakiaceae, *Papiliotrema, Trichoderma* and *Zygoascus* (Fig. S5.7, FDR < 0.05), while the Bo horizons displayed the highest association with Debaryomycetaceae, *Malassezia*, Microascaceae, *Pichia* and *Saccharomyces* (Fig. S5.7, FDR < 0.05).

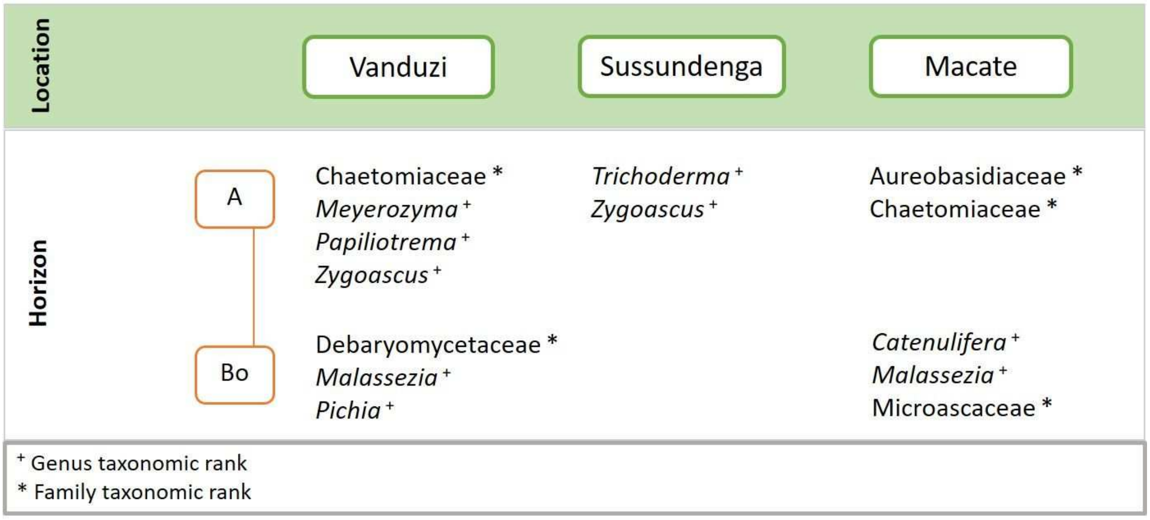

Fig. 5.4 Graph showing the statistically most abundant ASVs in soils at the highest phylum rank between horizons within locations. Manica province, central Mozambique. Abundances significantly differ at FDR ≤ 0.05.

For the A horizons, members of Aureobasidiaceae, Chaetomiaceae and *Chaetomium* are endophytic fungi particularly abundant in leaves and stems (Habtewold et al., 2020; Khan et al., 2016), whereas *Meyerozyma*, *Thricoderma* and *Zygoascus* were found in soil with the role of phosphate-solubilization (Gizaw et al., 2017; Kim et al., 2016; Nakayan et al., 2013; Saravanakumar et al., 2013). These reports rather agreed with our corrplot, which underlined several positive relations: *i*) Aureobasidiaceae and *Trichoderma* with EOOC and total N, *ii*) Chaetomiaceae with available P, and *iii*) *Zygoascus* with EOOC, total N and available P (Fig. 5.3). The Mrakiaceae family includes the *Makria* genus that, according to K. H. Zhang et al. (2020), contains species able to survive at low temperature because of the production of enzymes like lipases, amylases, proteases, pectinases, cellulases, chitinases, and ligninolytic. and the ability to use nitrate and nitrite. The findings of Mrakiaceae in the A horizon of our soils indicated that not all the members of this family are adapted to cold environments, and their ability to produce a large spectrum of degradative enzymes could explain their presence in the A horizon where organic matter abounded. Therefore, the whole group of fungi prospering in the A horizons were favoured by the abundance of organic matter and nutrients.

For the Bo horizons, the associated fungi showed inverse relations for Debaryomycetaceae and *Saccharomyces* with EOOC and total N, *Malassezia* with total N, and *Pichia* with available P; Microascaceae did not show any correlation with the analytical parameters. Although not sufficient information is available for Debaromycetaceae that fact that they abounded in the Bo horizons indicated that these fungi prefer oligotrophic environments scarce in organics. For *Saccharomyces,* the wild species are commonly associated with tree substrates such as bark, soil, leaves, exudates, and litter (Alsammar and Delneri, 2020), but they are also known to be zinc and phosphate solubilizers, N and S oxidizers, phytohormones producers, inhibitors of plant pathogens, and siderophore producers in both the bulk soil and the rhizosphere (Das et al., 2021). Because of this, the presence of *Saccharomyces* in the Bo horizons can be justified by the conspicuous amount of roots in the Bo horizons of several soil (the charcoal kilns of Sussundenga and Macate, and the forests of Vanduzi and Macate). *Malassezia* fungi can colonize a wide range of extreme habitats, from polar regions to deep-sea (Amend, 2014), but (Toju et al., 2016) found *Malassezia* especially diffused in the Bo horizons as in our case. The inverse relation with total N and the abundance in the Bo horizons indicated that these fungi prefer scarcely fertile soil environments. To some fungi belonging to *Pichia* genus were assigned the ability to produce siderophores and, similarly to *Saccharomyces*, to solubilize zinc and phosphates (Kumla et al., 2020; Nakayan et al., 2009), so explaining the inverse relation with available P. Microascaceae was not correlated with the analytical parameters, but its abundancy in Bo horizons may be explained by large amount of roots in the Bo horizons of several soils (Sandoval-Denis et al., 2016). Therefore, the whole group of fungi harbouring the Bo horizons were probably favoured by the oligotrophic environment they represented and, possibly, by the presence of large amount of roots.

For the vertical variation among land uses, no significant differences were observed, while several differences were observed between mycobiota and soil horizons within each location (Fig. 5.4). At Vanduzi, Chaetomiaceae, *Meyerozima, Papiliotrema* and *Zygoascus* were the most abundant in A horizons, while Debaryomycetaceae*,* *Malassezia* and *Pichia* in Bo horizons (Fig. S5.8, FDR < 0.05). At Sussundenga only *Trichoderma* and *Zygoascus* proliferated in A horizons (Fig. S5.9, FDR < 0.05), while at Macate, Aureobasidiaceae and Chaetomiaceae were the most frequent in A horizons, in contrast with *Catenulifera, Malassezia*, and Microascaceae, predominant in Bo horizons (Fig. S5.10, FDR < 0.05).

5.3.6 Mycobiota correlated to physicochemical soil properties

In addition to the above-mentioned correlations, the Fig. 5.3 revealed other relations between soil properties and fungi of the studied soils. In detail, inverse relations were underlined for *Acremonium* and pH, and for Plectosphaerellaceae and *Ogataea* with clay content (FDR < 0.05), whereas *Aureobasidium* showed a negative relation with silt but a positive relation with clay content (FDR < 0.05).

Members of the genus *Acremonium* includes plant pathogens, wood saprotrophs and mycoparasitic species (Nguyen et al., 2016). An interesting study found *Acremonium* more abundant in fertilizer treatments with a relatively acidic pH (4.6 and 4.8), and have been found to be more abundant in N and P fertilized soils with a relatively acidic pH (4.6 and 4.8) than in others with higher pH (Zhou et al., 2016), in accordance with the result enhanced by our corrplot (Fig. 5.3).

The Plectosphaerellaceae family comprises numerous plant pathogenic genera and soil-born species, detected in many substrates, which include sandy soils and loamy soil (Giraldo and Crous, 2019). The genus *Ogataea* is characterized by thermotolerant, nitrate-assimilating methylotrophic yeasts (Limtong et al., 2008; Suh and Zhou, 2010). Considering these findings, the negative correlation between Plectosphaerellaceae and *Ogataea* with clay may suggest the tendency of these fungi to colonize soils with a coarser texture.

Aureobasidium is a genus of hyphomycetes fungi that inhabit various extreme environments (Bozoudi and Tsaltas, 2018; Zalar et al., 2008), including stones and rocks in moderate or humid climate

(Sterflinger, 2010). In our soils, their distribution suggested they prefer soils with fine texture, able to retain more humidity.

5.4 Conclusions

This study provides the first metagenomic analysis of the soil-associated fungi in soils submitted to slash and burn and offer new insights into the relation of fungal populations and the soil physicochemical properties. Results highlighted the differentiation of fungi in two main groups: those affected by temporal, spatial, and vertical variations and those that has a homogeneous distribution in all the investigated soils. Within the diverse abundances, the main differences were found among locations and between horizons. In the first case, the fungi distribution was ascribed to the soil management and to genetic soil properties rather than the different length of the forest fallow period. This was corroborated also by the scarce difference detected among land uses and the homogeneity of fungi community in soils under crop field and forest. Different was the situation along the soil profile, where the changes in physicochemical properties determined a clear fungi clustering.

This work has clarified that soils submitted to slash and burn may display a certain fungal variability that only partially depends on the agroforestry system, and that forest fallow is ineffective to produce substantial changes in the fungal community. After these observations, the application of agronomic and forestry practices able to preserve soil fertility may play a crucial role for the soil ecosystem restoration and for the sustainability of slash and burn. Further studies are needed to further disclose the role of fungi in soil, but it appears that fungal diversity soils submitted to slash and burn mostly depends on soil genesis and management, rather than to the length of the forest fallow period.

Chapter 5.

Concluding Remarks

Oxisols submitted to slash and burn differed for morphological, physicochemical, and biological properties among locations (temporal variation), among land use (horizontal variation), and between horizons (vertical variation). The biotic properties detected in the three locations did not show a directly proportional trend with the forest fallow length; in particular, the location with the longest fallow period (Macate) did not show better soil characteristics compared to the other locations. Furthermore, no significant difference appeared between crop field and forest within each location, remarking the strong effect of intrinsic soil properties despite different land uses.

Bacteria and fungi are affected by soil physicochemical properties reliant on both soil genesis and human activities. Two main groups of microrganisms have been recognized: a group of bacteria and fungi strongly affected by spatial, temporal, and vertical variations, and a group of microbes homogeneously distributed in soils despite variations.

Principal variations on bacteria and fungi community are underlined among locations, influenced by agronomical practices actuated in the crop field and the forest management, and between horizons. Significant differences are detected in soils under the charcoal kiln, while slight differences are found between crop field and forest soils. This may suggest the inability of a shorter than 50 years forest fallow period to induce changes in microbial community.

Results of analyses obtained for the soil genetic horizons of the different land uses have revealed *i*) the strong influence exercised by parent material in determining soil properties; *ii*) the strong soils depletion, due to the combination of biotic and abiotic factors; *iii*) the homogeneity of soil ecosystem under crop fields and forests; *iv*) the irrelevance of less than 50 years of forest fallow period to produce differences in soil fertility; *v*) the positive effect of the mulching in accumulating organic matter and limiting soil depletion. In this context, the slash and burn agro-forest system can be still considered as essential for rural populations, but it results unsustainable for the soil fertility, and it is therefore advisable to adopt agronomical practices (e.g. crop selection, agronomic techniques, and application of fertilizers) aimed at providing nutrients to improve the soil fertility, to guarantee sufficient production for family sustenance and protection of soil and soil functions.

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Publications

List of on working papers:

- "What future for the soils submitted to slash and burn?" based on Chapter 3; almost ready to be submitted to *Science of the Total Environment.*
- "Soil bacteria communities under slash and burn in Mozambique as revealed by metataxonomic approach" based on Chapter 4; under review to *Pedosphere* after major revision.
- "Soil fungi communities under slash and burn in Mozambique – A metataxonomic approach" based on Chapter 5; ready to be submitted to *Pedosphere*.

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Appendix

Chapter 3.

Appendix 3.1 Mean values of soluble anions for the A and Bo horizons of the soils under crop field and forest in the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique. Numbers in parentheses are the standard deviations (n=2). For each column within land use and location, mean values with different letters significantly differ for $P < 0.05$.

	Horizons	Bicarbonate		Chloride		Sulphate		Nitrate		Phosphate		Fluoride		Nitrite		Bromide		Acetate		Oxalate		Formate	
		$\mu eq\ kg^{-1}$																					
		Vanduzi																					
Crop field	Ap	751(391)		433(46)		106(64)		282(372)		60(67)		12(7)		2(3)		<LOD		<LOD		<LOD		<LOD	
	Bo1	424(316)	aA	377(52)	aA	120(77)	aA	67(94)	abA	13(14)	aA	7(1)	aA	4(6)	aA	<LOD	aA	3(5)	aA	11(15)	aA	<LOD	-
	Bo2	428(167)		413(81)		128(108)		59(65)		3(0)		6(1)		4(5)		<LOD		1(1)		<LOD		<LOD	
Forest	A	880(579)		330(10)		99(3)		1(1)		68(77)		6(2)		<LOD		<LOD		<LOD		2(2)		<LOD	
	Bo1	366(285)	**a**A	253(132)	**ab**B	46(3)	**a**A	3(5)	**b**B	12(17)	**a**A	9(1)	**a**A	2(3)	**a**A	<LOD	**a**A	<LOD	**a**A	13(7)	**a**A	<LOD	-
	Bo2	334(137)		372(35)		125(66)		11(16)		7(10)		10(6)		6(8)		<LOD		<LOD		<LOD		<LOD	
		Sussundenga																					
Crop field	Ap	768(380)		1030(983)		265(198)		107(61)		35(49)		4(3)		2(2)		<LOD		122(173)		6(8)		<LOD	
	Bo1	222(314)	aA	217(45)	aA	70(22)	aA	38(42)	bA	7(10)	aA	2(1)	bA	1(1)	aA	<LOD	aA	343(485)	aA	1(1)	aA	<LOD	-
	Bo2	465(475)		775(754)		198(162)		27(11)		<LOD		1(1)		<LOD		<LOD		21(29)		5(7)		<LOD	
Forest	A	830(479)		282(126)		62(30)		35(8)		37(52)		3(1)		2(2)		<LOD		1(0)		5(2)		<LOD	
	Bo1	618(545)	**a**A	227(55)	**b**A	43(42)	**a**A	21(10)	**ab**A	14(19)	**a**A	4(4)	**b**A	5(3)	**a**A	<LOD	**a**A	29(41)	**a**A	8(12)	**a**A	<LOD	-
	Bo2	146(206)		253(34)		47(37)		28(2)		4(6)		3(1)		6(9)		<LOD		491(694)		57(77)		<LOD	
		Macate																					
Crop field	Ap	353(499)		476(296)		148(93)		609(249)		2(3)		11(7)		<LOD		1(1)		314(443)		3(4)		<LOD	
	Bo1	314(388)	aA	408(85)	aA	144(37)	aA	252(204)	aA	<LOD	aA	7(1)	aA	2(0)	aA	<LOD	aA	3(4)	aA	<LOD	aA	<LOD	-
	Bo2	317(364)		315(42)		105(21)		164(36)		<LOD		6(2)		<LOD		<LOD		10(14)		<LOD		<LOD	
Forest	A	420(65)		444(21)		196(141)		1861(2435)		1(1)		10(4)		3(4)		<LOD		23(32)		<LOD		<LOD	
	Bo1	434(17)	**a**A	352(26)	**a**A	92(69)	**a**A	222(206)	**a**A	<LOD	**a**A	13(2)	**a**A	1(1)	**a**A	<LOD	**a**A	5(7)	**a**A	12(16)	**a**A	<LOD	-
	Bo2	85(82)		403(8)		56(31)		329(136)		<LOD		5(0)		3(2)		<LOD		<LOD		<LOD		<LOD	

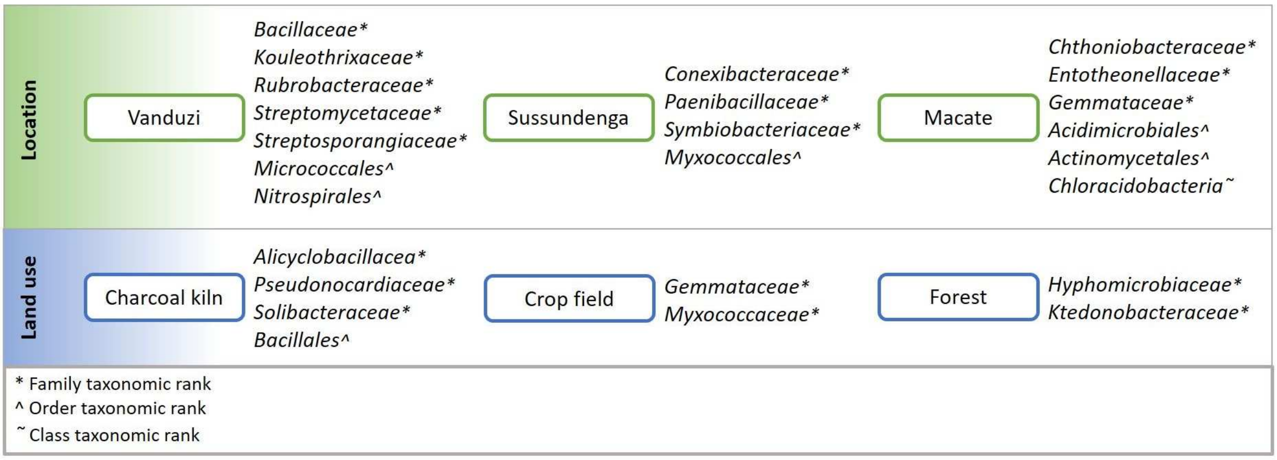
LOD = limit of detection.
Lowercase normal letters = comparison between crop field soils of the three locations.
Lowercase bold letters = comparison between forest soils of the three locations.
Capital letters = comparison between forest and crop field soils within each location

Appendix 3.2 Mean values of soluble cations for the A and Bo horizons of the soils under crop field and forest in the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique. Numbers in parentheses are the standard deviations (n=2). For each column within land use and location, mean values with different letters significantly differ for $P < 0.05$.

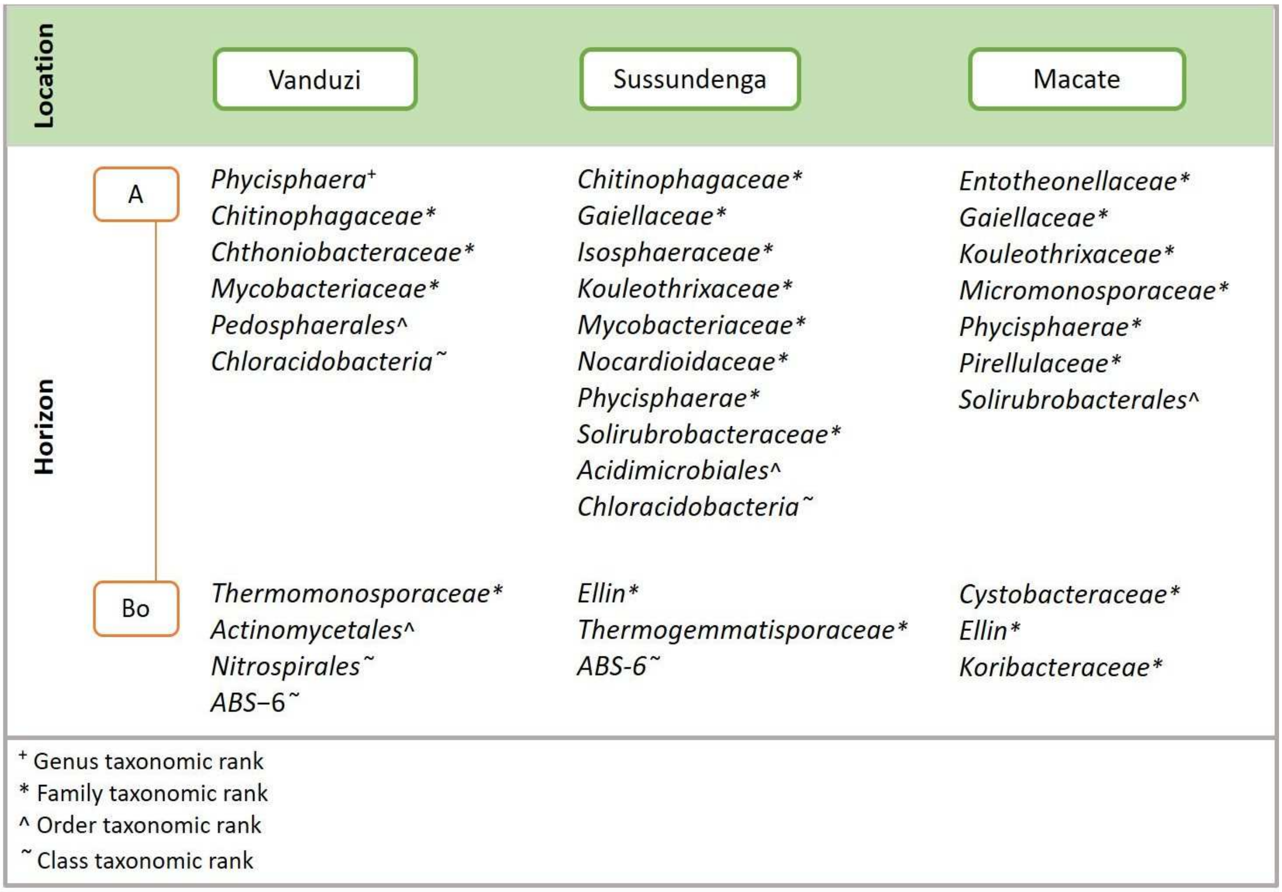
	Horizons	Calcium		Magnesium		Potassium		Sodium		Ammonium		Lithium	
		μeq kg^{-1}											
Vanduzi													
Crop field	Ap	521(85)		150(63)		680(17)		285(62)		9(13)		<LOD	
	Bo1	249(4)	aA	71(33)	aA	373(354)	aA	298(155)	aA	35(49)	bA	<LOD	-
	Bo2	245(21)		65(6)		355(384)		357(206)		18(25)		<LOD	
Forest	A	726(352)		160(102)		403(102)		194(60)		12(3)		<LOD	
	Bo1	359(188)	**a**A	62(8)	**a**A	219(37)	**a**A	217(54)	**a**A	6(8)	**b**A	<LOD	**-**
	Bo2	240(16)		65(12)		300(119)		270(84)		38(54)		<LOD	
Sussundenga													
Crop field	Ap	418(12)		114(25)		390(110)		1328(1665)		88(33)		<LOD	
	Bo1	476(88)	aA	81(69)	aA	632(728)	aA	271(200)	aA	360(488)	aA	<LOD	-
	Bo2	290(139)		91(17)		123(72)		926(1159)		63(53)		<LOD	
Forest	A	456(80)		118(26)		303(77)		175(25)		206(223)		<LOD	
	Bo1	397(253)	**a**A	120(88)	**a**A	145(106)	**a**A	142(6)	**a**A	166(154)	**a**A	<LOD	**-**
	Bo2	679(463)		115(110)		731(962)		394(395)		408(465)		<LOD	
Macate													
Crop field	Ap	589(231)		201(83)		626(342)		252(35)		247(139)		<LOD	
	Bo1	300(70)	aA	72(15)	aA	280(73)	aA	255(80)	aA	221(31)	aA	<LOD	-
	Bo2	283(110)		72(27)		185(49)		220(70)		158(97)		<LOD	
Forest	A	732(696)		595(721)		1097(966)		263(12)		272(121)		<LOD	
	Bo1	291(47)	**a**A	71(1)	**a**A	401(322)	**a**A	199(16)	**a**A	170(98)	**a**A	<LOD	**-**
	Bo2	294(138)		45(11)		208(91)		203(42)		132(187)		<LOD	

Lowercase normal letters = comparison between crop field soils of the three locations.
Lowercase bold letters = comparison between forest soils of the three locations.
Capital letters = comparison between forest and crop field soils within each location

Chapter 4.



Appendix 4.1 Graph showing the statistically most abundant OTUs at the lowest taxonomical rank in soils according to location and land use. Manica province, central Mozambique. Abundances significantly differ at FDR ≤ 0.05.



Appendix 4.2 Graph showing the statistically most abundant OTUs at the lowest taxonomical level in soils between horizons within locations. Manica province, central Mozambique. Abundances significantly differ at FDR ≤ 0.05.

Supplementary materials

Tables

Chapter 3.

Table S3.1 Results of Levene's test for equality of variances and Shapiro-Wilk test on residuals for normality, both at 5% significance level, for mineralogy in the soils of the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique, for the two sampling campaigns.

	Schedasticity	Normality	p-value
Vanduzi			
Crop field	0.94*	0.00*	0.88[3]
Forest	0.99*	0.00*	0.73[3]
Sussundenga			
Crop field	0.94*	0.00*	0.58[3]
Forest	0.98*	0.00*	0.10[3]
Macate			
Crop field	0.93*	0.00*	0.20[3]
Forest	0.97*	0.00*	0.78[3]

Sampling campaigns = First (March), Second (November).

* BoxCox transformation before statistic test.

[1] One Welch ($P < 0.05$).

[2] Tukey test ($P < 0.05$).

[3] Kruskall-Wallis test ($P < 0.05$).

Table S3.2 Results of Levene's test for equality of variances and Shapiro-Wilk test on residuals for normality, both at 5% significance level, for the physicochemical properties of the soils from the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique, for the two sampling campaigns.

	Schedasticity	Normality	p-value
Vanduzi			
Crop field	0.96*	0.02*	0.77[1]
Forest	0.68*	0.06*	0.97[2]
Sussundenga			
Crop field	0.77*	0.01*	0.88[1]
Forest	0.77*	0.02*	0.59[1]
Macate			
Crop field	0.37*	0.01*	0.77[1]
Forest	0.50*	0.00*	0.71[1]

Sampling campaigns = First (March), Second (November).

* BoxCox transformation before statistic test.

[1] Kruskall-Wallis test ($P < 0.05$).

[2] One-way ANOVA test ($P < 0.05$).

Table S3.3 Results of Levene's test for equality of variances and Shapiro-Wilk test on residuals for normality, both at 5% significance level, for aluminum and iron in the soils of the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique, for the two sampling campaigns.

	Schedasticity	Normality	p-value
Vanduzi			
Crop field	0.00	0.61	0.05[1]
Forest	0.15*	0.01*	0.16[2]
Sussundenga			
Crop field	0.58	0.06	0.11[2]
Forest	0.07*	0.00*	0.38[3]
Macate			
Crop field	0.15*	0.04*	0.43[3]
Forest	0.50*	0.00*	0.26[3]

Sampling campaigns = First (March), Second (November).

* BoxCox transformation before statistic test.

[1] One Welch ($P < 0.05$).

[2] Tukey test ($P < 0.05$).

[3] Kruskall-Wallis test ($P < 0.05$).

Table S3.4 Results of Levene's test for equality of variances and Shapiro-Wilk test on residuals for normality, both at 5% significance level, for anions and cations in the soils between the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique, for the two sampling campaigns.

	Schedasticity	Normality	p-value
Vanduzi			
Crop field	0.22*	0.00*	0.55[1]
Forest	0.15*	0.00*	0.70[1]
Sussundenga			
Crop field	0.32*	0.00*	0.11[1]
Forest	0.34*	0.00*	0.09[1]
Macate			
Crop field	0.97*	0.00*	0.64[1]
Forest	0.21*	0.00*	0.37[1]

Sampling campaigns = First (March), Second (November)

* BoxCox transformation before statistic test.

[1] Kruskall-Wallis test ($P < 0.05$).

Table S3.5 Results of Levene's test for equality of variances and Shapiro-Wilk test on residuals for normality, both at 5% significance level, for minerals in the soils from the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique.

	Quartz		Plagioclases		Orthoclase		Micas		2:1 clay minerals		Kaolinite	
	Sche	Nor	Sche	Nor	Sche	Nor	Sche	Nor	Sched	Norm	Sched	Nor
Crop field†	0.03[1]	0.50[1]	0.01[1]	0.09[1]	-	-	0.00[1]	0.00[1]	0.05[1]	0.01[1]	0.00	0.12
Forest†	0.03[2]	0.56[2]	0.25[3]	0.07[3]	-	-	0.00[1]	0.00[1]	0.00[1]	0.02[1]	0.22[1]	0.02[1]
Vanduzi‡	0.14[3]	0.19[3]	0.35[3]	0.13[3]	-	-	-	-	0.16[3]	0.10[3]	0.64[3]	0.14[3]
Sussundenga	0.15[3]	0.08[3]	0.00[2]	0.15[2]	-	-	-	-	0.41[1]	0.00[1]	0.44[1]	0.00[1]
Macate‡	0.03[2]	0.26[2]	0.05[3]	0.11[3]	-	-	-	-	0.13[1]	0.02[1]	0.63[3]	0.44[3]

† Statistical analysis among soils from different locations.

‡ Statistical analysis between soils under crop field and forest within the same location.

Sched = Schedasticity; Norm = Normality.

[1] Kruskall-Wallis test ($P < 0.05$).

[2] Welch one-way ANOVA test ($P < 0.05$).

[3] One-way ANOVA test ($P < 0.05$).

Table S3.6 Results of Levene's test for equality of variances and Shapiro-Wilk test on residuals for normality, both at 5% significance level for physicochemical properties of the soils from the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique, for the two sampling campaigns.

	pH		Particle-size distribution						TOC		Humic C		Total N		Available P	
			Sand		Silt		Clay									
	Sched	Norm	Sched	Norm	Sched	Norm	Sched	Norm	Sched	Norm	Sched	Norm	Sched	Norm	Sched	Norm
Crop field†	0.35[1]	0.39[1]	0.00[2]	0.84[2]	0.01[3]	0.01[3]	0.03[2]	0.31[2]	0.40[1]	0.52[1]	0.36[1]	0.11[1]	0.44[1]	0.18[1]	0.52[1*]	0.89[1*]
Forest†	0.47[1]	0.95[1]	0.61[1]	0.10[1]	0.14[1*]	0.21[1*]	0.68[1]	0.09[1]	0.08[1]	0.39[1]	0.24[1]	0.89[1]	0.07[1]	0.29[1]	0.04[2]	0.09[2]
Vanduzi‡	0.72[1]	0.20[1]	0.03[2]	0.26[2]	0.09[1]	0.86[1]	0.06[1]	0.30[1]	0.48[1]	0.08[1]	0.34[1]	0.07[1]	0.76[1]	0.06[1]	0.54[1]	0.09[1]
Sussundenga‡	0.20[1]	0.46[1]	0.96[3]	0.02[3]	0.29[1]	0.67[1]	0.99[3]	0.02[3]	0.98[1]	0.05[1]	0.94[1]	0.07[1]	0.32[1]	0.09[1]	0.09[1]	0.51[1]
Macate‡	0.86[1]	0.88[1]	0.40[1]	0.17[1]	0.79[1]	0.99[1]	0.75[1]	0.10[1]	0.20[1]	0.25[1]	0.54[1]	0.90[1]	0.51[1]	0.80[1]	0.06[1]	0.39[1]

† Statistical analysis among soils from different locations.

‡ Statistical analysis between soils under crop field and forest within each location.

Sched = Schedasticity; Norm = Normality.

[*] BoxCox transformation before statistic test.

[1] One-way ANOVA test ($P < 0.05$).

[2] Welch one-way ANOVA test ($P < 0.05$).

[3] Kruskall-Wallis test ($P < 0.05$).

Table S3.7 Results of Levene's test for equality of variances and Shapiro-Wilk test on residuals for normality, both at 5% significance level, for the aluminum and iron in the soils from the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique.

	Aluminium		Iron	
	Schedasticity	Normality	Schedasticity	Normality
Crop field†	0.00[1]	0.24[1]	0.00[1]	0.50[1]
Forest†	0.18[2]	0.00[2]	0.19[2]	0.00[2]
Vanduzi‡	0.02[1]	0.53[1]	0.02[1]	0.40[1]
Sussundenga‡	0.04[1]	0.79[1]	0.05[1]	0.68[1]
Macate‡	0.75[3]	0.22[3]	0.92[3]	0.69[3]

† Statistical analysis among soils from different locations.

‡ Statistical analysis between soils under crop field and forest within the same location.

[1] Welch one-way ANOVA test ($P < 0.05$).

[2] Kruskall-Wallis test ($P < 0.05$).

[3] Tukey test ($P < 0.05$).

Table S3.8 Results of Levene's test for equality of variances and Shapiro-Wilk test on residuals for normality, both at 5% significance level for the water-extractable anions in the soils from the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique.

	Bicarbonate		Chloride		Sulphate		Nitrate		Phosphate		Fluoride		Bromide		Nitrite		Acetate		Oxalate	
	Sche	Nor	Sche	Nor	Sche	Nor	Sche	Nor	Sche	Nor	Sche	Nor	Sche	Nor	Sche	Nor	Sche	Nor	Sche	Nor
Crop field†	0.63[1]	0.43[1]	0.05[1]	0.41[1]	0.29[1]	0.15[1]	0.12[1]	0.86[1]	0.28[1]	0.26[1]	0.81[2]	0.00[2]	0.26[2]	0.00[2]	0.00[3]	0.20[3]	0.18[2]	0.00[2]	0.65[2]	0.00[2]
Forest†	0.33[1]	0.19[1]	0.80[1]	0.40[1]	0.20[1]	0.39[1]	0.24[2]	0.00[2]	0.21[1]	0.24[1]	0.09[1]	0.51[1]	0.30[2]	0.00[2]	0.78[2]	0.01[2]	0.36[2]	0.00[2]	0.41[2]	0.00[2]
Vanduzi‡	0.69[1]	0.07[1]	0.93[1]	0.13[1]	0.11[1]	0.21[1]	0.97[2]	0.00[2]	0.21[1]	0.06[1]	0.74[1]	0.95[1]	0.34[2]	0.00[2]	0.75[2]	0.01[2]	0.25[2]	0.00[2]	0.77[2]	0.00[2]
Sussundenga‡*	0.68[1]	0.32[1]	0.14[1]	0.05[1]	0.14[1]	0.19[1]	0.06[1]	0.56[1]	0.58[1]	0.57[1]	0.85[1]	0.07[1]	0.19[2]	0.00[2]	0.14[1]	0.11[1]	0.93[2]	0.00[2]	0.32[2]	0.00[2]
Macate‡	0.04[3]	0.15[3]	0.22[1]	0.06[1]	0.43[1]	0.07[1]	0.59[1]	0.99[1]	0.56[2]	0.00[2]	0.31[1]	0.29[1]	0.25[2]	0.00[2]	0.22[1]	0.32[1]	0.35[2]	0.00[2]	0.43[2]	0.00[2]

† Statistical analysis among soils from different locations.

‡ Statistical analysis between soils under crop field and forest within the same location.

Sched = Schedasticity; Norm = Normality.

* BoxCox transformation before statistic test.

1 One-way ANOVA test ($P < 0.05$).

2 Kruskall-Wallis test ($P < 0.05$).

3 Welch one-way ANOVA test ($P < 0.05$).

Table S3.9 Results of Levene's test for equality of variances and Shapiro-Wilk test on residuals for normality, both at 5% significance level, for water-extractable cations in the soils from the three locations of Vanduzi, Sussundenga, and Macate Districts, Manica province, central Mozambique.

	Calcium		Magnesium		Potassium		Sodium		Ammonium	
	Sche	Nor	Sche	Nor	Sche	Nor	Sche	Nor	Sche	Nor
Crop field†	0.73[1]	0.24[1]	0.92[1]*	0.99[1]*	0.81[1]	0.15[1]	0.08[2]	0.00[2]	0.06[1]*	0.22[1]*
Forest†	0.71[1]*	0.87[1]*	0.70[1]*	0.95[1]*	0.19[1]*	0.81[1]*	0.56[2]	0.00[2]	0.04[2]	0.01[2]
Vanduzi‡	0.28[1]	0.05[1]	0.61[1]*	0.82[1]*	0.35[1]	0.09[1]	0.11[1]	0.69[1]	0.70[2]	0.00[2]
Sussundenga‡	0.18[1]	0.13[1]	0.10[1]	0.75[1]	0.84[1]*	0.74[1]*	0.14[1]	0.05[1]	0.84[1]	0.87[1]
Macate‡	0.64[1]*	0.75[1]*	0.64[1]*	0.95[1]*	0.38[1]*	0.89[1]*	0.32[1]	0.82[1]	0.40[1]	0.99[1]

† Statistical analysis among soils from different locations.

‡ Statistical analysis between soils under crop field and forest within the same location.

Sched = Schedasticity; Norm = Normality.

* BoxCox transformation before statistic test.

[1] One-way ANOVA test ($P < 0.05$).

[2] Kruskall-Wallis test ($P < 0.05$).

Chapter 4.

Table S4.1. General features and morphology of the soils from three locations in Manica province, central Mozambique. For symbols see legend.

Average data for the period 1982-2012 – Mean annual precipitation: 1036 mm. Mean annual air temperature: 21.2°C; winter (J-J-A) mean air temperature: 16.9°C; spring (S-O-N) mean air temperature: 22.5°C; summer (D-J-F) mean air temperature: 24.1°C; autumn (M-A-M) mean air temperature: 22.5°C.

Horizon	Depth cm	Thickness cm	Boundary[a]	Color[b]	Texture[c]	Rock fragments %, by sight	Structure[d]	Consistence[e]	Roots[f]	Other observations[g]

VANDUZI (37S 19°04'002" S, 033°21'45" E WGS84). Altitude: 658 m; parent rock: granulite.
In the charcoal kiln area. Slope: 3%; Exposure: W. Management: 4 years old charcoal kiln. Vegetation – Bushes: *Vangueria infausta* Burch.; herbaceous: *Panicum maximum* Jacq.. Drainage class: well-drained.
Soil: *coarse-loamy, mixed, thermic, Typic Eutrotorrox* (Soil Survey Staff, 2014).

A	0-38	35-40	C, W	7.5YR 3/2	ls	0	0sg to 2,3f,m,co abk-sbk & pl	m(fr)	0	CH ≈30%, burned grass; popping and crunchy structure at places
Bo	38-121+	-	-	7.5YR 4/3	ls	0	2f,m abk-sbk	m(fr)	0	Popping and crunchy, FMN ≈5%, nuciform structure

Crop field. Slope: 3%; Exposure: N-NW. Management: 1 year old intercropping with different varieties of *Musa paradisiaca* L., *Moringa oleifera* Lam., *Sorghum vulgare* Pers.. Vegetation - herbaceous: *Panicum maximum* Jacq., *Euphorbia* spp., *Convolvulus arvensis* L.. Drainage class: well-drained.
Soil: *fine, mixed, thermic, Typic Eutrotorrox* (Soil Survey Staff, 2014).

A	0-40	36-43	C, W	7.5YR 3/4	ls	0	2f gr & 3f,m,co sbk	m(fr)	3vf, 2f, 1m	CH <1%; TU (termites)
Bo	40-100+	-	-	7.5YR 4/6	sc	0	3m,co sbk	m(fr)	2f, 1m,f	FMN ≈5%, TU (termites)

Forest. Slope: 3%; Exposure: NW. Management: 27 years old spontaneous forest with patches that have been burnt by low fire and occasionally pastured and used to obtain firewood, timber, and charcoal. Vegetation ("open miombo" forest with rests of previous cultivation) – Trees: *Brachystegia spiciformis* Benth., *Brachystegia tamarindoides* Benth., *Julbernardia globiflora* (Benth.) Troupin, *Mangifera indica* L; bushes: *Psidium guajava* L., *Lantana camara* L., *Vangueira infausta* Burch; herbaceous: *Themeda triandra* Forssk., *Panicum maximum* Jacq., *Hyparrhenia filipendula* (Hochst.) Stapf, *Andropogon gayanus* Kunth, *Dichrostachys cinerea* (L.) Wight & Arn., *Combretum* spp.. Drainage class: well-drained.
Soil: *coarse-loamy, mixed, thermic, Typic Eutrotorrox* (Soil Survey Staff, 2014).

A	0-34	30-35	C, W	7.5YR 2.5/3	s	0	3co pl & 2m,co abk	m(fr)	3vf, 2f	
Bo	34-100+	-	-	7.5YR 4/4	scl	0	2f,m abk	m(fr)	2vf, 2f, 3m,co	FMN ≈5%

SUSSUNDEGA (37S 19°18'45.328"S, 33°13'21.050"E WGS84). Altitude: 649 m; parent rock: granulite.
In the charcoal kiln area. Slope: 2-4%; Exposure: E. Management: 1 year old charcoal kiln. Vegetation - Trees: sparse plants of *Apocinaceae* spp.. Drainage class: well-drained.
Soil: *fine-loamy, mixed, thermic, Typic Eutrotorrox* (Soil Survey Staff, 2014).

A	0-33	32-35	C, W	5YR 2.5/2	ls	0	0sg & 2m,co sbk	m(fr)	0	Medium gravelly CH ≈40%, popping and crunchy structure at places, FMN <1%, dead roots
Bo	33-98+	-	-	5YR 5/6	scl	0	2f,m abk-sbk	m(fr)	2vf, 1f, 2m,co	Dead roots, fine gravelly FMN <1%

Crop field. Slope: 2 %; Exposure: NE; Management: 2 years old crop field (*Zea Mais* L.) Vegetation – Trees: sparse plants of *Apocinaceae* spp.; herbaceous: *Panicum miliaceum* L., *Panicum maximum* Jacq., *Mucuna pruriens* DC. Drainage class: well-drained.
Soil: *coarse-loamy, mixed, thermic, Typic Eutrotorrox* (Soil Survey Staff, 2014).

A	0-18	15-19	C, W	7.5YR 2.5/1	ls	0	1,2f,m,co sbk	m(fr)	2-3vf,f	CH 1-2%
Bo	18-93+	-	-	7.5YR 3/4	sl	0	1,2m,co sbk-abk	m(fr)	2vf, 2f,m	Rare CH, fine FMN 3-5%, leopard skin features 20%, popping

Forest. Slope: 3%; Exposure: NW. Management: 35 years old spontaneous forest with burnt patches, occasionally pastured and used to obtain firewood and timber. Vegetation: "open miombo" forest – Trees: *Brachystegia spiciformis* Benth., *Brachystegia tamarindoides* Benth., *Julbernardia globiflora* (Benth.) Troupin, *Burkea africana* Hook.; bushes: *Annona senegalensis* Pers., *Parinari curatellifolia* Planch. ex Benth.,

Brackenridgea zanguebarica Oliv.; herbaceous: *Cynodon* spp., *Themeda triandra* Forssk., *Panicum maximum* Jacq., *Hyparrhenia filipendula* (Hochst.) Stapf, *Trichilia capitata* Klotzsch., *Andropogon gayanus* Kunth. Drainage class: well-drained.
Soil: *coarse-loamy, mixed, thermic, Typic Eutrotorrox* (Soil Survey Staff, 2014).

A	0-34	31-36	C, W	7.5YR 3/2	ls	0	2co gr & 1,2f,m,co abk-sbk	m(fr)	3vf,f,m, co	FMN, TU (termites)
Bo	34-100+	-	-	7.5YR 5/3	ls	0	1,2f,m,co abk-sbk	m(fr)	2vf, 1f, 2m, 1co	Rare CH, friable FMN <1%, TU (termites)

MACATE (37S 19°41'405" S, 33°51'513" E WGS84). Altitude: 555 m; parent rock: granulitic gneiss.
In the charcoal kiln area. Slope: 3%; Exposure: W. Management: 16 years old charcoal kiln. Vegetation - herbaceous: absent. Drainage class: well-drained.
Soil: *coarse-loamy, mixed, thermic, Typic Eutrotorrox* (Soil Survey Staff, 2014).

A	0-22	18-23	C, W	5YR 2.5/1	sl	0	3f,m,co sbk	m(fr)-m(vfr)	2vf, 1f	CH 30%, QUA 30%, dead wood
Bo	29-96+	-	-	5YR 4/3	sl	0	1,2f,m,co abk-sbk	m(fr)	2vf, 1f, 2m,co	CH traces, fine gravelly QUA, soot traces

Crop field. Slope: 3%; Exposure: W. Management: 16 years old crop field in preparation (*Zea mays* L.) Vegetation - herbaceous: *Mucuna pruriens* DC. Drainage class: well-drained.
Soil: *fine-loamy, mixed, thermic, Typic Eutrotorrox* (Soil Survey Staff, 2014).

A	0-22	18-23	C, W	5YR 3/2	scl	0	3f,m,co vc sbk	m(fr)-m(fi)	0	CH <1%; Dead roots, QUA
Bo	22-96+	-	-	2.5YR 3/4	scl	0	2f,m sbk	m(fr)	0	Dead roots

Forest. Slope: 3%; Exposure: W. Management: 50 years old spontaneous forest with burnt patches, occasionally pastured and used to obtain firewood and timber and for hunting small animals. Vegetation: "open miombo" forest – Trees: *Brachystegia spiciformis* Benth., *Julbernardia globiflora* (Benth.) Troupin, *Albitia versicolor* Welw. Ex Oliv., *Brachystegia tamarindoides* Benth., *Acacia nilotica* (L.) Willd. ex Del., *Brachystegia microphylla* Harms; bushes: *Psidium guajava* L., *Zanthoxylum* sp., *Senna petersiana* (Bolle) Lock, *Lantana camara* L.; herbaceous: *Cassia* sp., *Themeda triandra* Forssk., *Panicum maximum* Jacq., *Hyparrhenia filipendula* (Hochst.) Stapf, *Andropogon gayanus* Kunth, *Maytenus senegalensis* Lam. (Exell). Drainage class: well-drained.
Soil: *fine-loamy, mixed, thermic, Typic Eutrotorrox* (Soil Survey Staff, 2014).

A	0-18	15-18	C, W	5YR 3/2	sl	4	3f,m,co sbk	m(fr)	2vf, 1f	Leaves and twigs with mycelia
Bo	18-91+	-	-	2.5YR 3/6	scl	1	2 to 3f,m sbk-abk	m(fr)-m(fi)	2vf, 1f, 2m,co	Biological activity, QUA, F3M ≈1%

[a] C=clear, D=diffuse; S=smooth, W=wavy

[b] moist and crushed, according to the Munsell Soil Color Charts.

[c] ls=loamy sand, sl=sandy loam, scl=sandy clay loam, sc=sandy clay, s=sand

[d] 0=structureless, 1=weak, 2=moderate, 3=strong; vf= very fine, f=fine, m=medium, c=coarse, vc=very coarse; sg= single grain, gr=granular, abk=angular blocky, sbk=sub-angular blocky, pl=platy.

[e] m(vfr)=very friable, moist; m(fr)=friable, moist; m(fi)=firm, moist.

[f] 0=absent, 1=very few, moderately few, 2=common, 3=many; vf=very fine, f=fine, m=medium, co=coarse.

[g] CH=charcoal fragments; QUA=quartz fragments; F3M=Masses of oxidized FeIII; FMN=iron-manganese nodules; TU=tubular pores.

Table S4.2. Results of the test for equality of variances and normality by Levene's test and by the Shapiro-Wilk statistical test on residuals, respectively, both at 5% significance level.

	Schedasticity	Normality	p-value
Sampling campaigns: first in March 2017, second in November 2017	0.36[*]	0.00[*]	0.95[**]

[*] BoxCox transformation before statistic test.

[**] Kruskall-Wallis test ($P < 0.05$).

Table S4.3. Results of the test for equality of variances and normality by Levene's test and by the Shapiro-Wilk statistical test on residuals, respectively, both at 5% significance level.

	pH		Particle-size distribution						EOOC*		Total N		Available P	
			Sand		Silt		Clay							
	Sched	Norm	Sched	Norm	Sched	Norm	Sched	Norm	Sched	Norm	Sched	Norm	Sched	Norm
Location	0.53[1*]	0.16[1*]	0.09[2*]	0.03[2*]	0.00[4]	0.00[4]	0.97[2*]	0.00[2*]	0.21[1]	0.82[1]	0.06[1]	0.84[1]	0.01[4]	0.02[4]
Land use														
Total	0.62[1]	0.93[1]	0.98[2*]	0.04[2*]	0.39[1*]	0.45[1*]	0.58[1*]	0.17[1*]	0.66[2*]	0.02[2*]	0.88[1*]	0.23[1*]	0.02[4]	0.02[4]
Vanduzi	0.85[1*]	0.09[1*]	0.05[1]	0.99[1]	0.90[1]	0.66[1]	0.14[1]	0.99[1]	0.24[1]	0.40[1]	0.46[1]	0.13[1]	0.79[1]	0.24[1]
Sussundeng	0.22[1]	0.79[1]	0.77[1]	0.71[1]	0.71[2*]	0.00[2*]	0.02[3]	0.49[3]	0.07[1]	0.23[1]	0.77[1]	0.25[1]	0.47[1]	0.05[1]
Macate	0.49[1]	0.99[1]	0.80[1*]	0.50[1*]	0.40[1]	0.52[1]	0.50[1]	0.15[1]	0.95[1]	0.42[1]	0.51[1]	0.88[1]	0.82[1]	0.06[1]
Horizons														
Total	0.61[1]	0.43[1]	0.09[1]	0.11[1]	0.72[1*]	0.35[1*]	0.84[1*]	0.16[1*]	0.35[1*]	0.09[1*]	0.26[1*]	0.09[1*]	0.87[1*]	0.70[1*]
Vanduzi	0.42[1]	0.45[1]	0.76[1*]	0.15[1*]	0.68[1]	0.44[1]	0.60[1]	0.07[1]	0.39[1*]	0.46[1*]	0.49[1]	0.99[1]	0.60[1]	0.69[1]
Sussundeng	0.42[1]	0.27[1]	0.24[1]	0.09[1]	0.39[1]	0.93[1]	0.35[2*]	0.02[2*]	0.57[1]	0.26[1]	0.22[1]	0.75[1]	0.67[1*]	0.23[1*]
Macate	0.64[1]	0.37[1]	0.63[1]	0.39[1]	0.01[3]	0.94[3]	0.17[1]	0.40[1]	0.81[1]	0.67[1]	0.53[1]	0.69[1]	0.15[1]	0.86[1]
Charcoal	0.73[1]	0.18[1]	0.34[1]	0.36[1]	0.35[1*]	0.13[1*]	0.05[1]	0.60[1]	0.54[1*]	0.13[1*]	0.51[1*]	0.25[1*]	0.27[1]	0.40[1]
Crop field	0.63[1]	0.56[1]	0.90[1]	0.11[1]	0.75[1]	0.09[1]	0.58[1]	0.33[1]	0.48[1]	0.31[1]	0.29[1]	0.73[1]	0.58[1*]	0.79[1*]
Forest	0.63[1]	0.27[1]	0.88[1*]	0.07[1*]	0.69[1*]	0.74[1*]	0.71[1]	0.29[1]	0.27[1]	0.10[1]	0.62[1*]	0.16[1*]	0.34[1]	0.46[1]

*EOOC = easily oxidizable organic carbon.

Location = Vanduzi, Sussundenga, and Macate; Land use = Charcoal kiln, crop field, and forest; Horizons = A and Bo.

Sched = Schedasticity; Norm = Normality.

[1] One-way ANOVA test ($P < 0.05$).

[2] Kruskall-Wallis test ($P < 0.05$).

[3] Welch one-way ANOVA test ($P < 0.05$).

[4] Friedman test ($P < 0.05$).

[*] BoxCox transformation before statistic test.

Figures

Chapter 3.

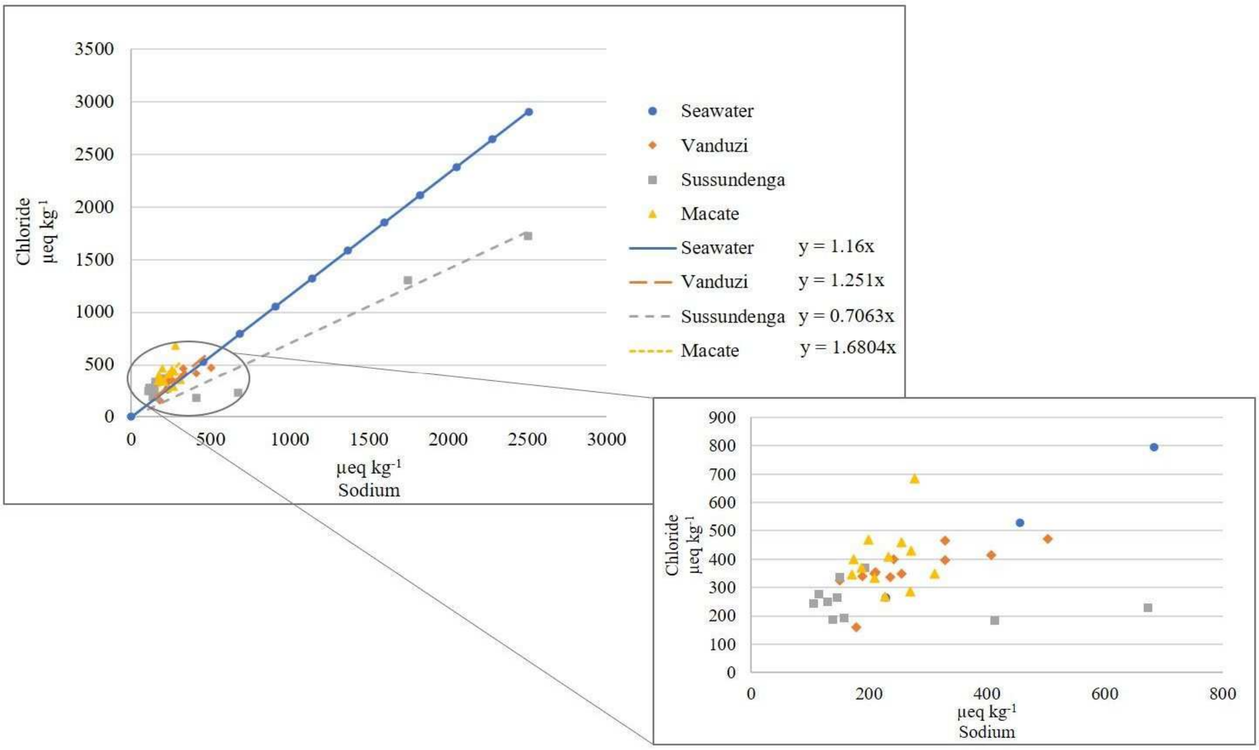


Fig. S3.1 Relationship between chloride and sodium in seawater (blue line) and in the soils under crop field and forest at Vanduzi (orange colour), Sussundenga (grey colour), and Macate (yellow colour). Manica province, central Mozambique.

Chapter 4.

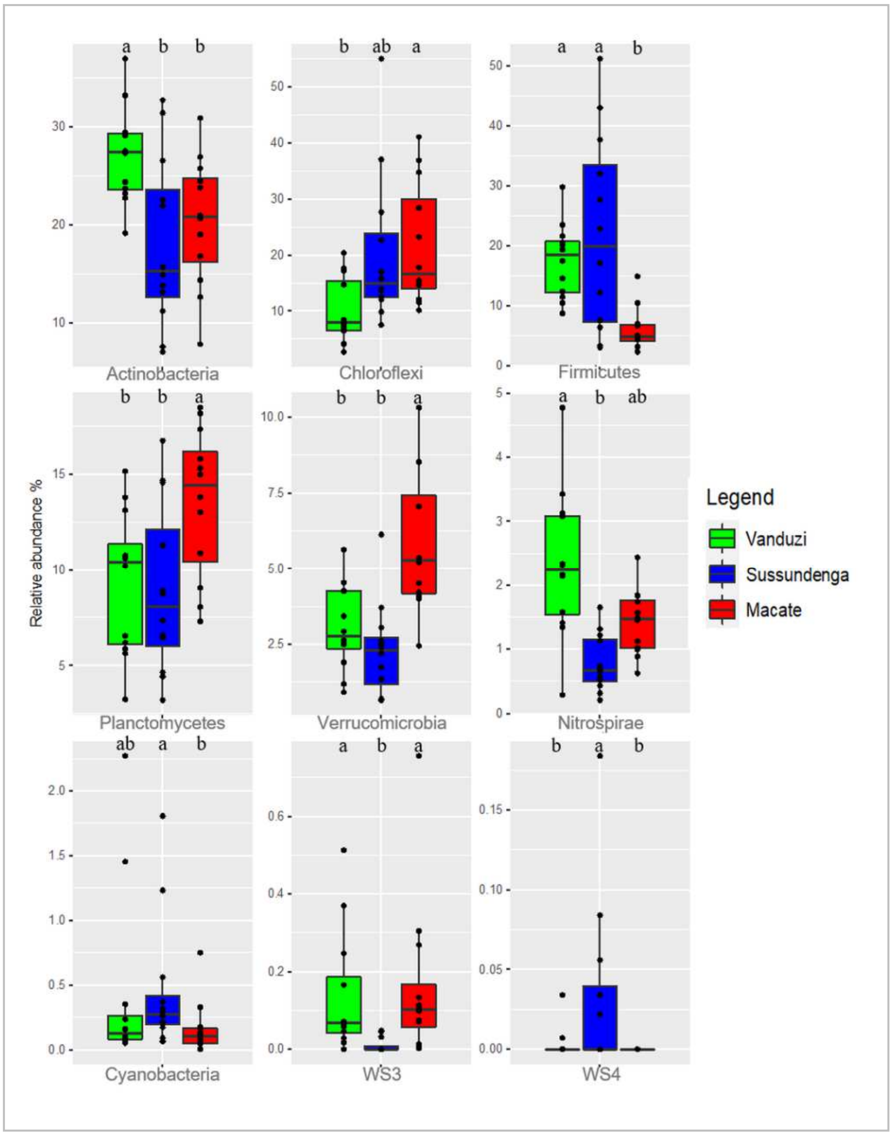


Fig. S4.1 Boxplots showing the relative abundance of the OTUs differential abundance of soils from Vanduzi, Sussundenga, and Macate. Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

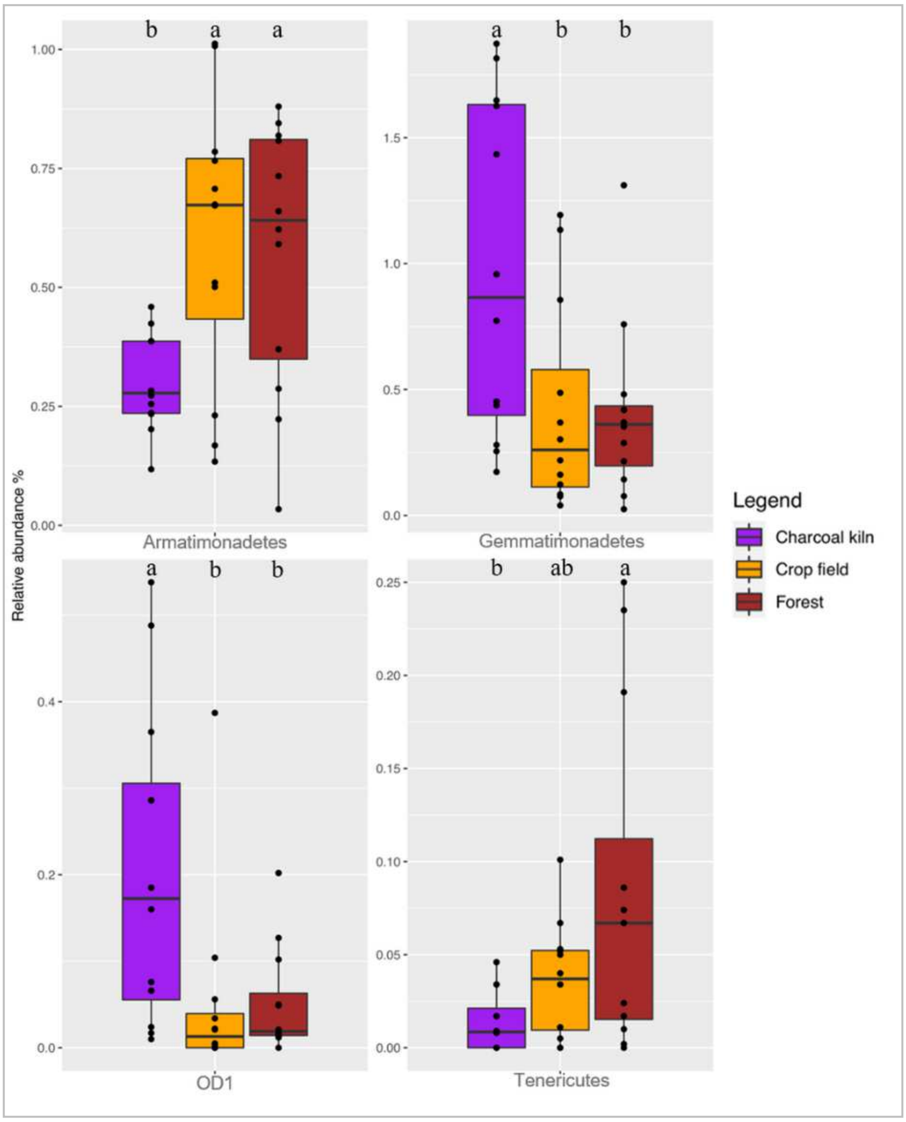


Fig. S4.2 Boxplots showing the relative abundance of the of soils for different land uses: Charcoal kiln, Crop field and Forest. Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

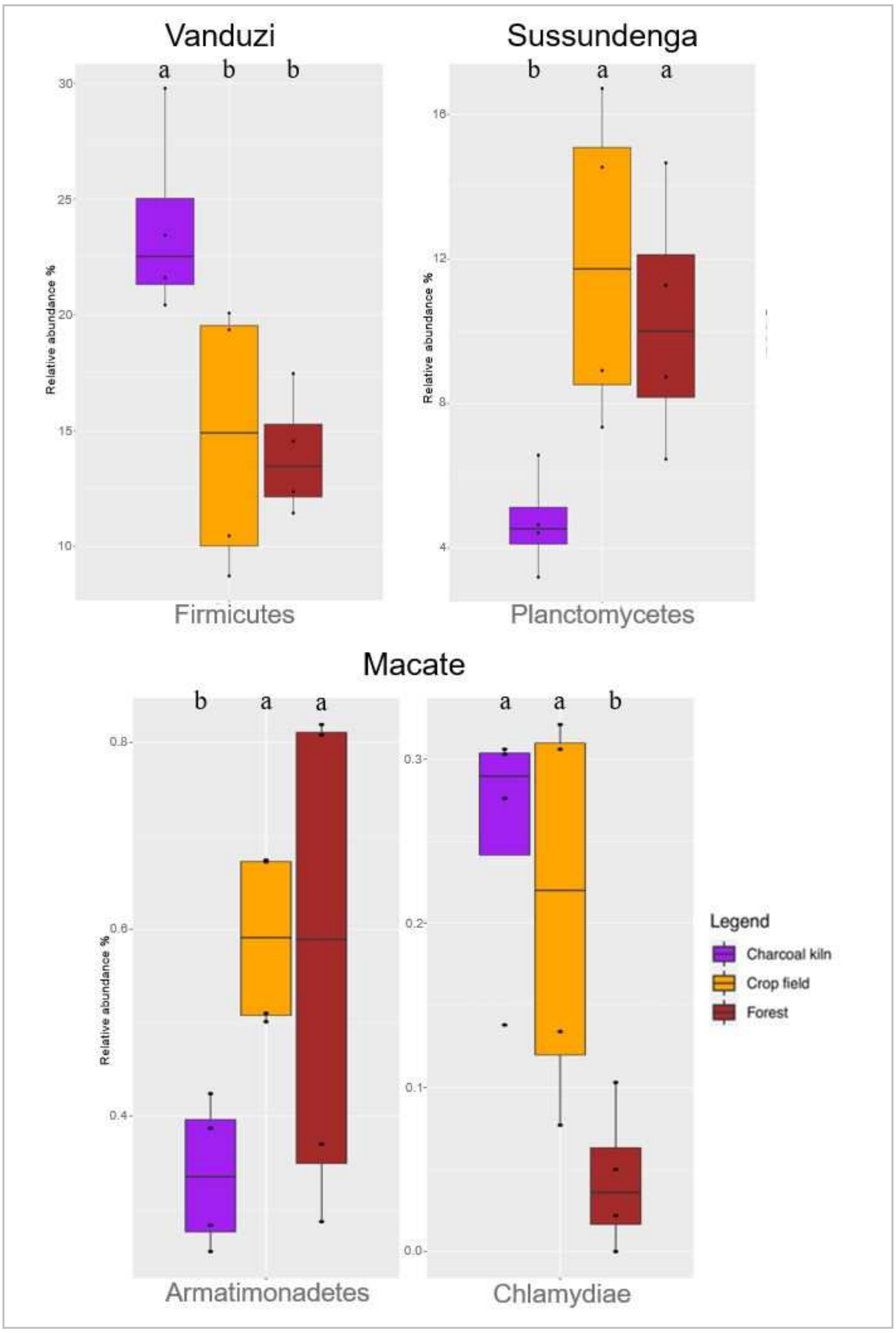


Fig. S4.3 Boxplots showing the OTUs differential abundance of soils for different land uses: Charcoal kiln, Crop field, and Forest. Vanduzi, Sussundenga and Macate, Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

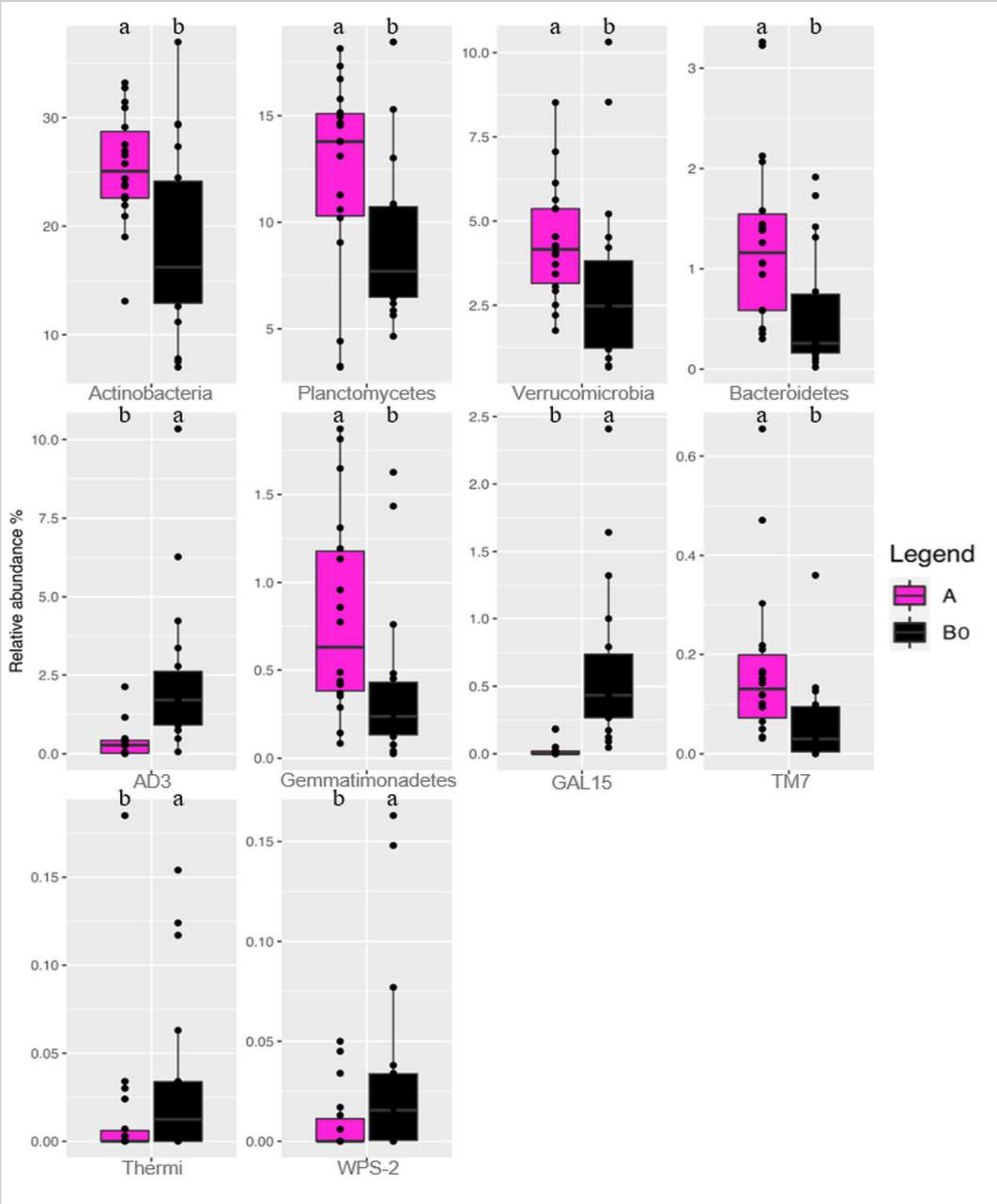


Fig. S4.4. Boxplots showing the OTUs differentially abundant of A and Bo horizons. Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

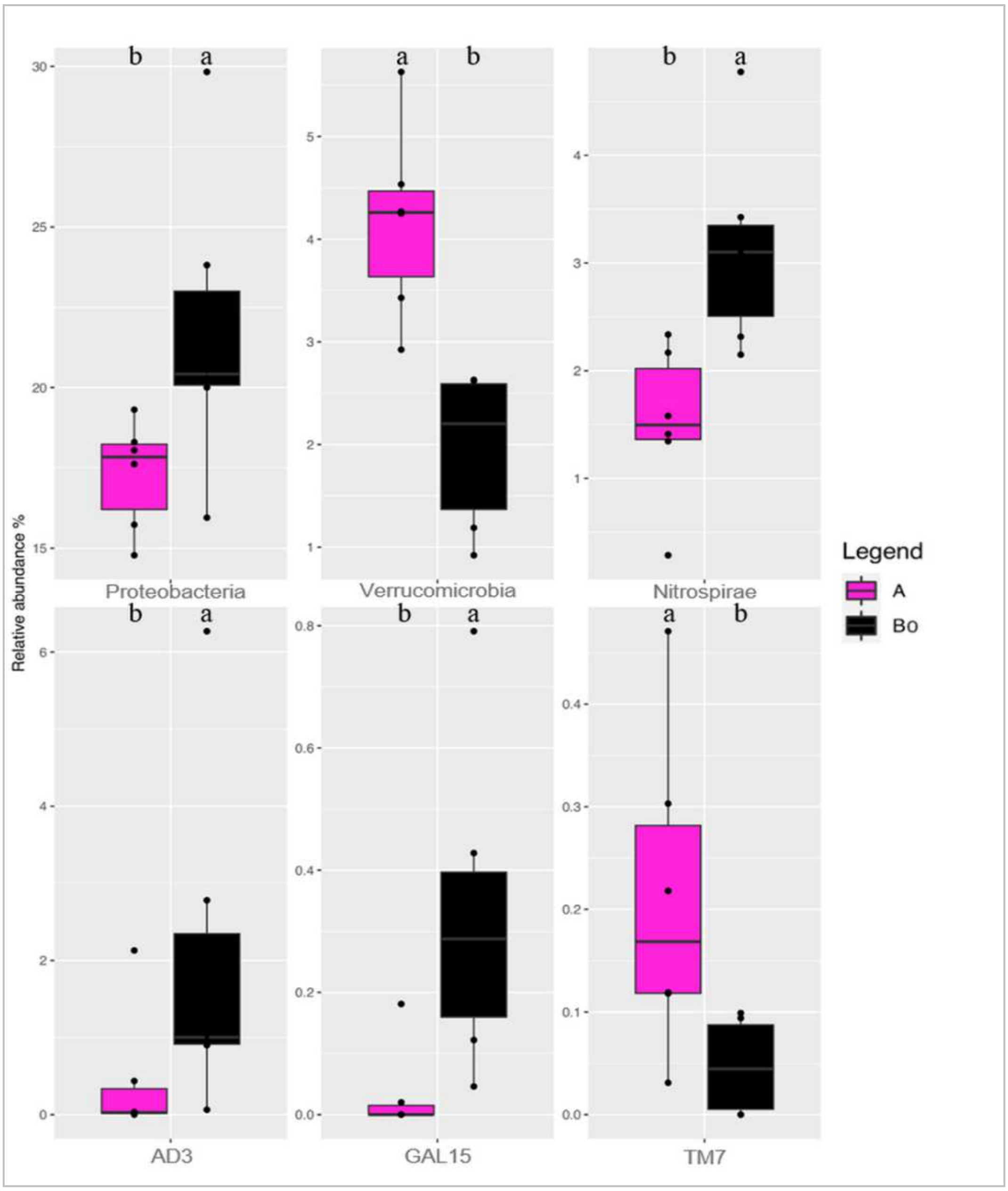


Fig. S4.5 Boxplots showing the OTUs differentially abundant of A and Bo horizons. Vanduzi, Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

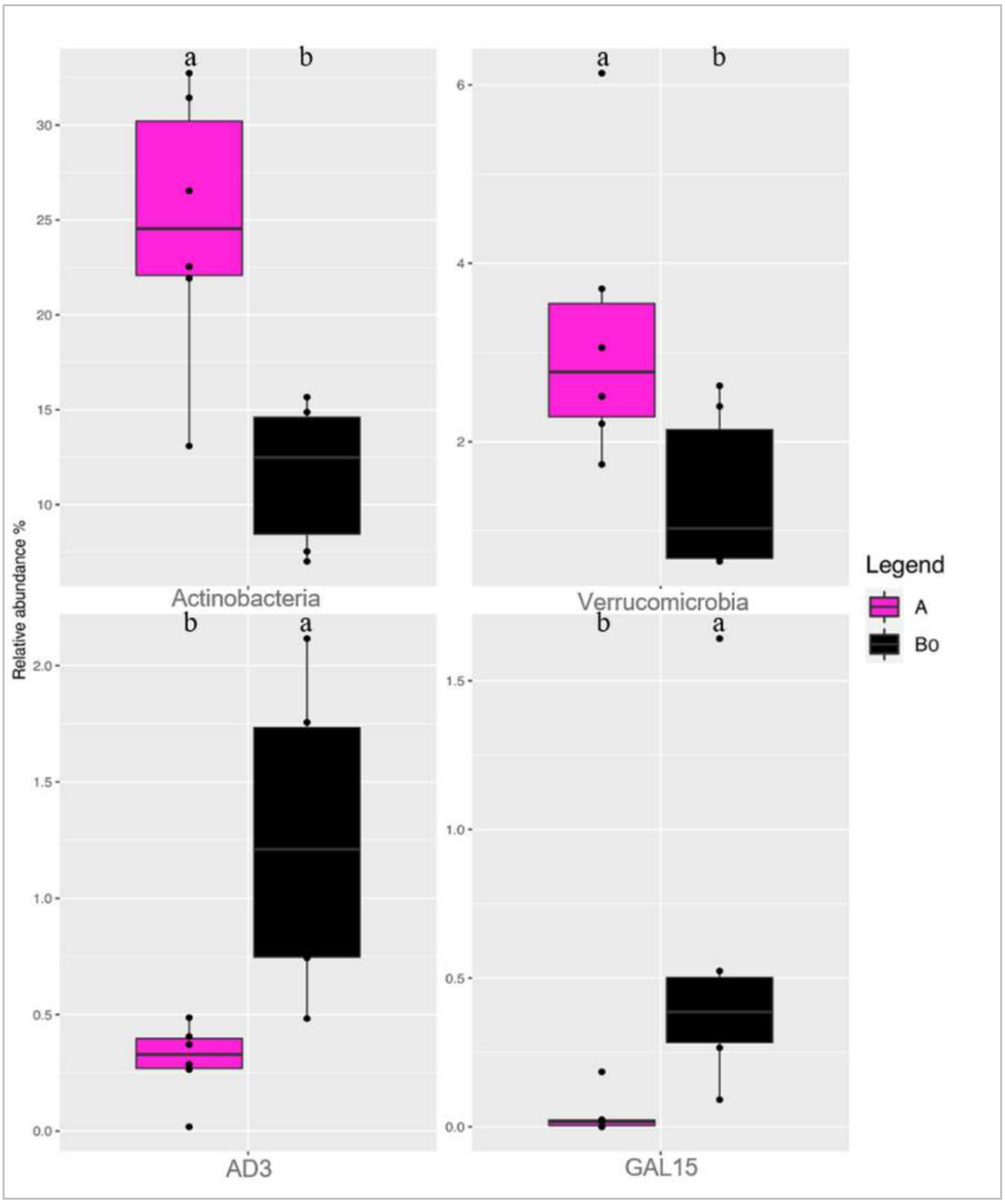


Fig. S4.6 Boxplots showing the OTUs differentially abundant of A and Bo horizons. Sussundenga, Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

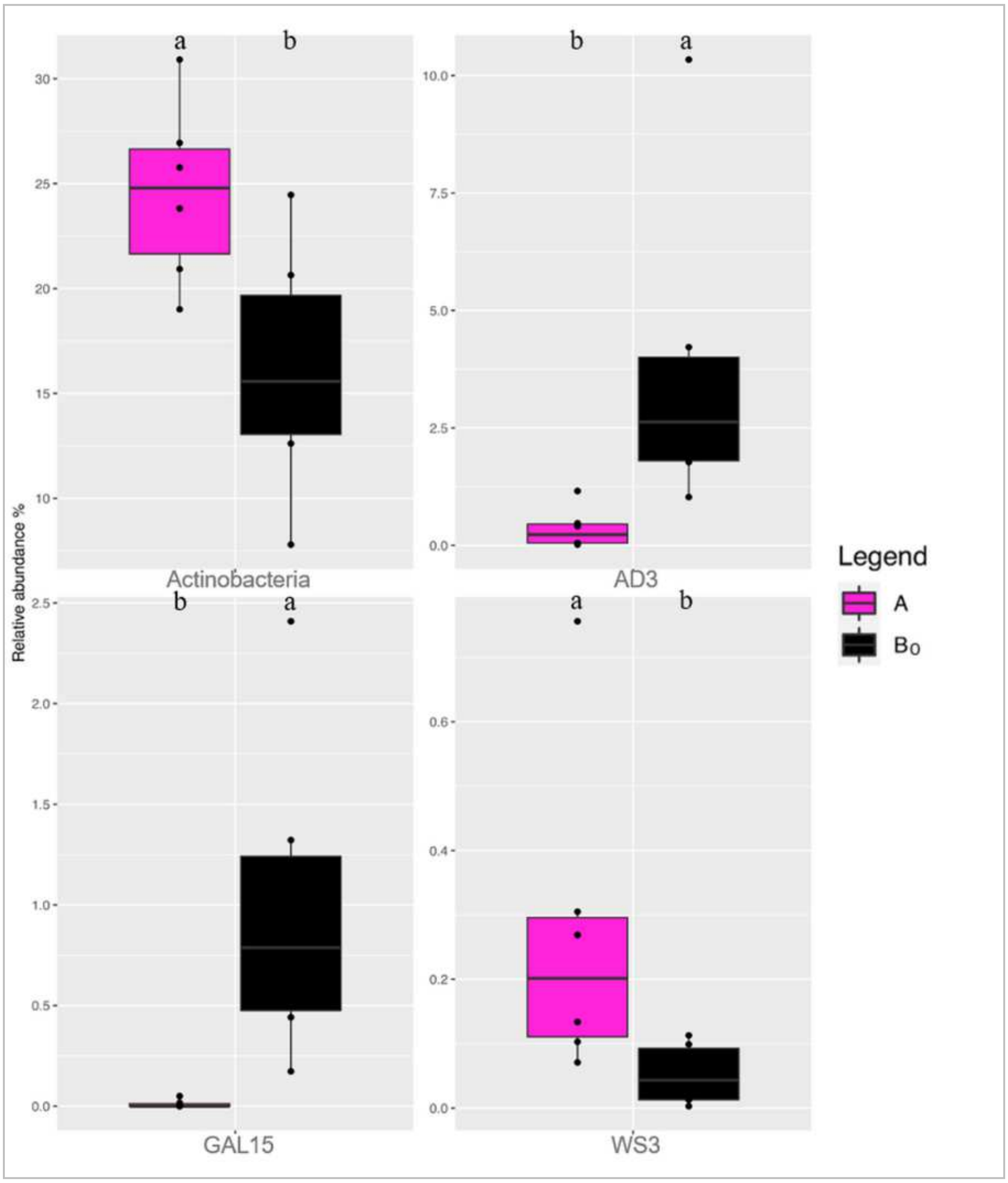


Fig. S4.7 Boxplots showing the OTUs differentially abundant of A and Bo horizons. Macate, Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

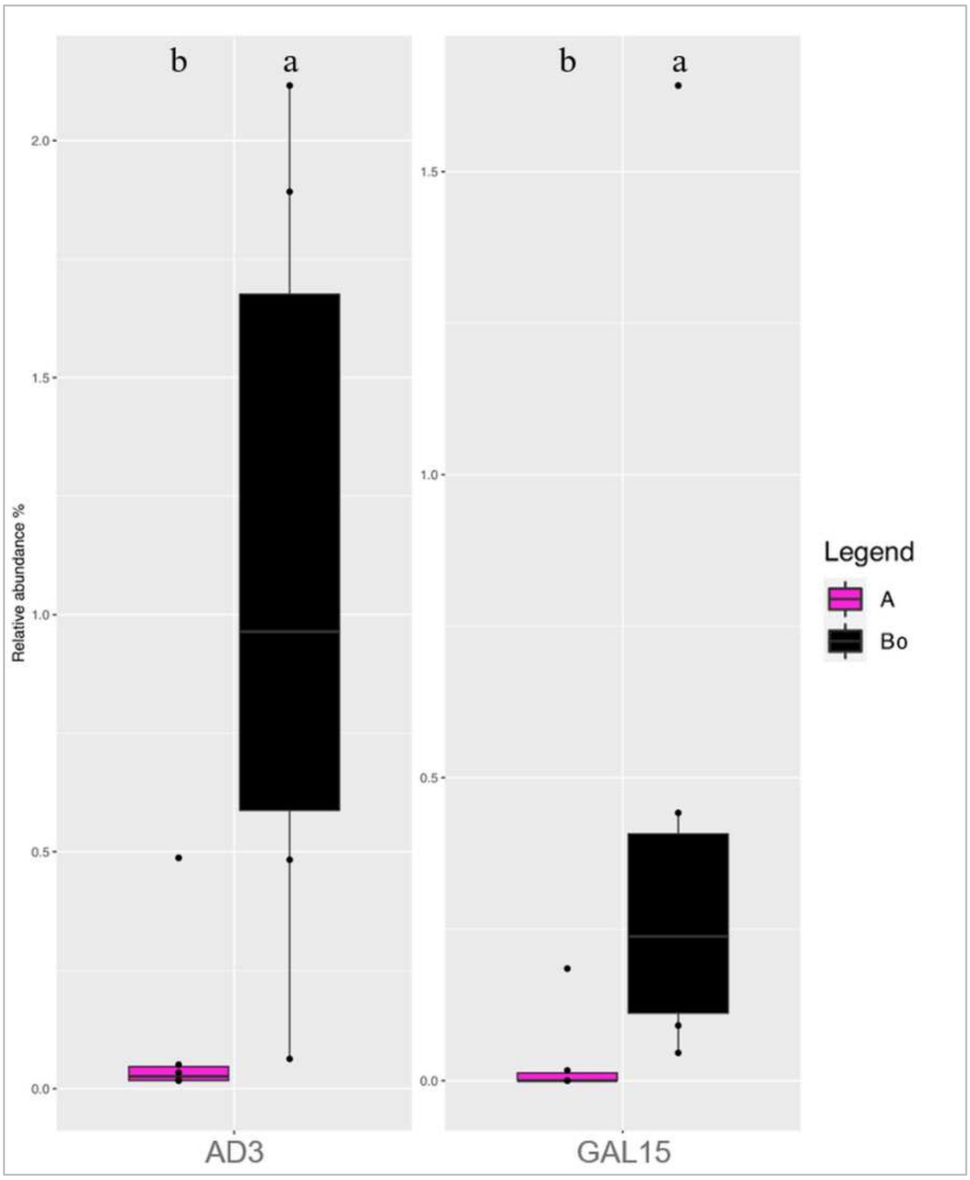


Fig. S4.8 Boxplots showing the OTUs differentially abundant of A and Bo horizons under charcoal kilns. Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

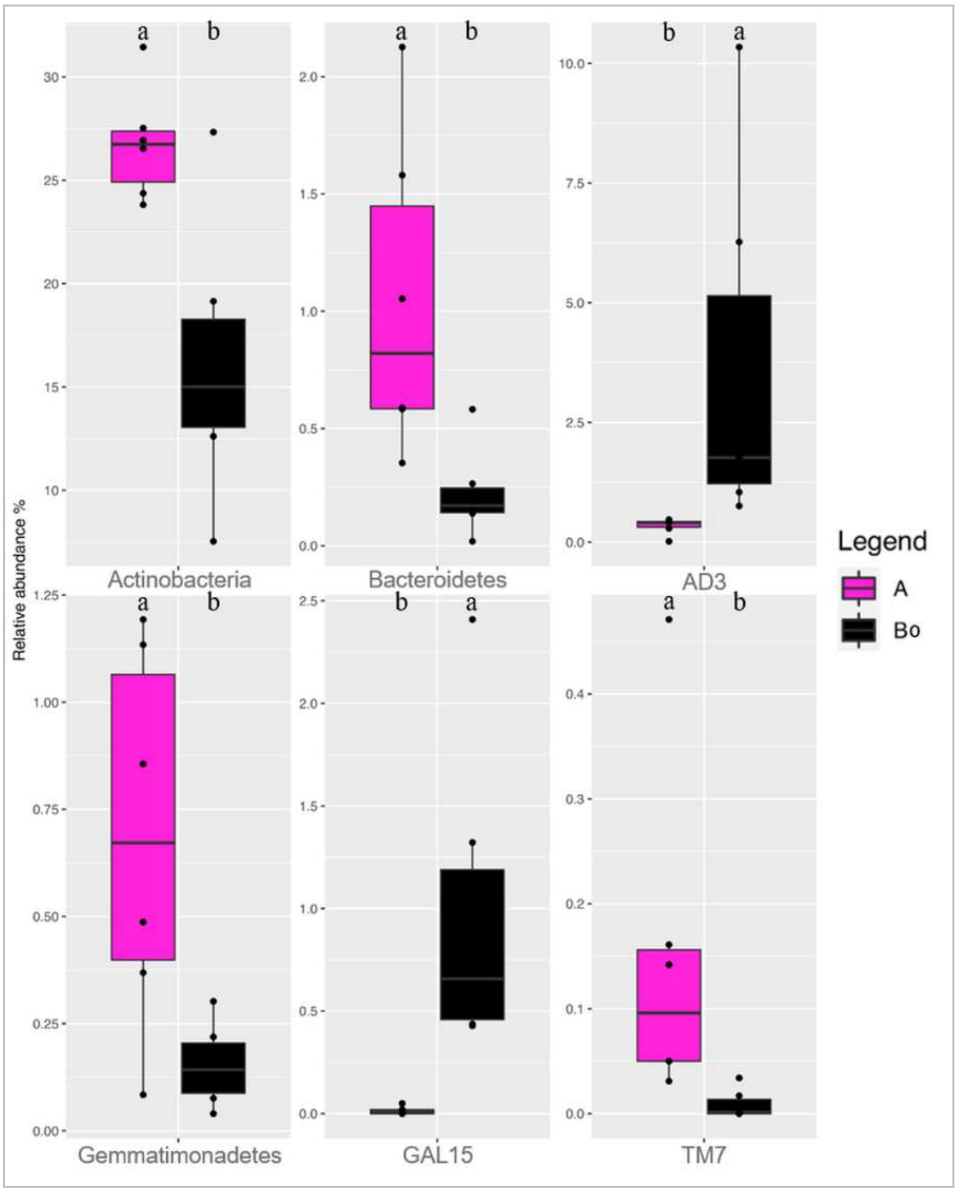


Fig. S4.9 Boxplots showing the OTUs differentially abundant of A and Bo horizons under crop fields. Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

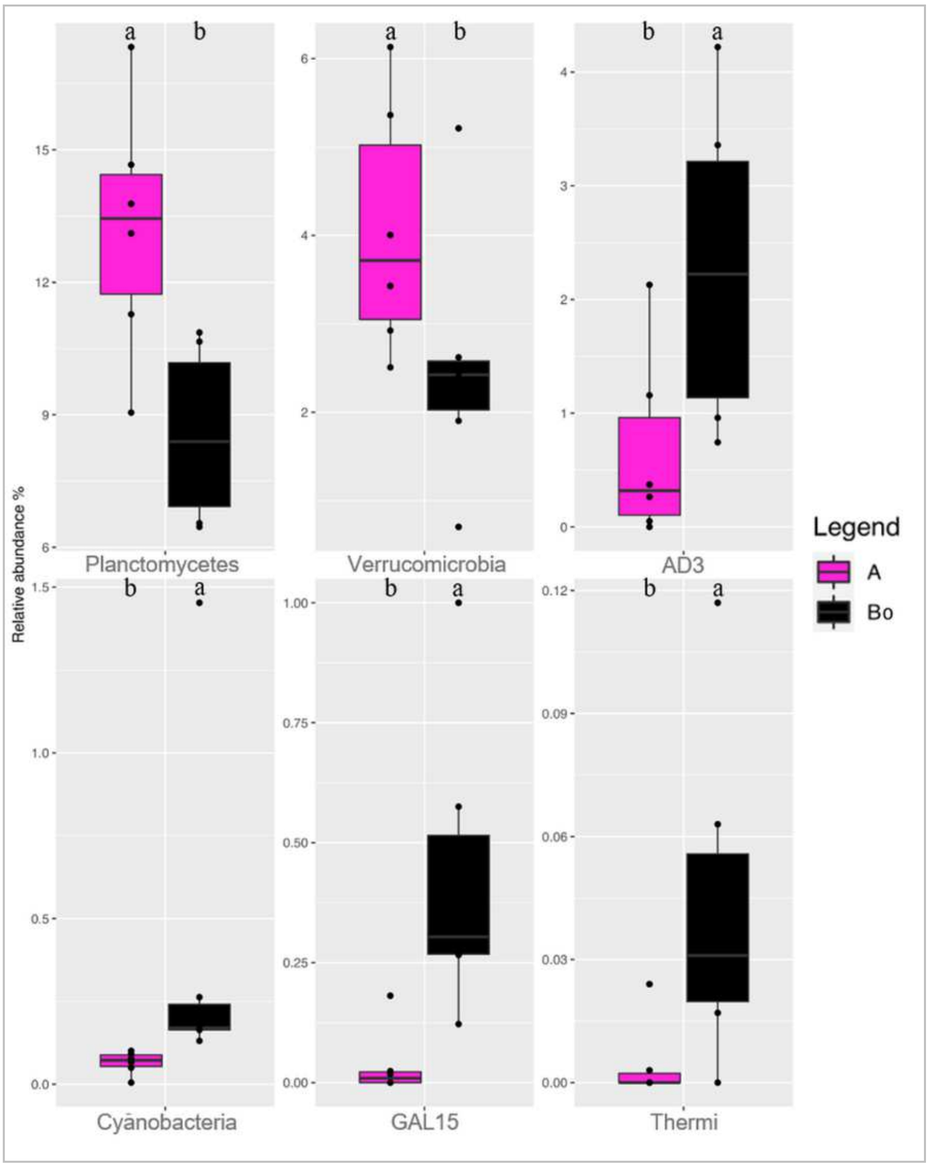


Fig. S4.10 Boxplots showing the OTUs differentially abundant of A and Bo horizons under forests. Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

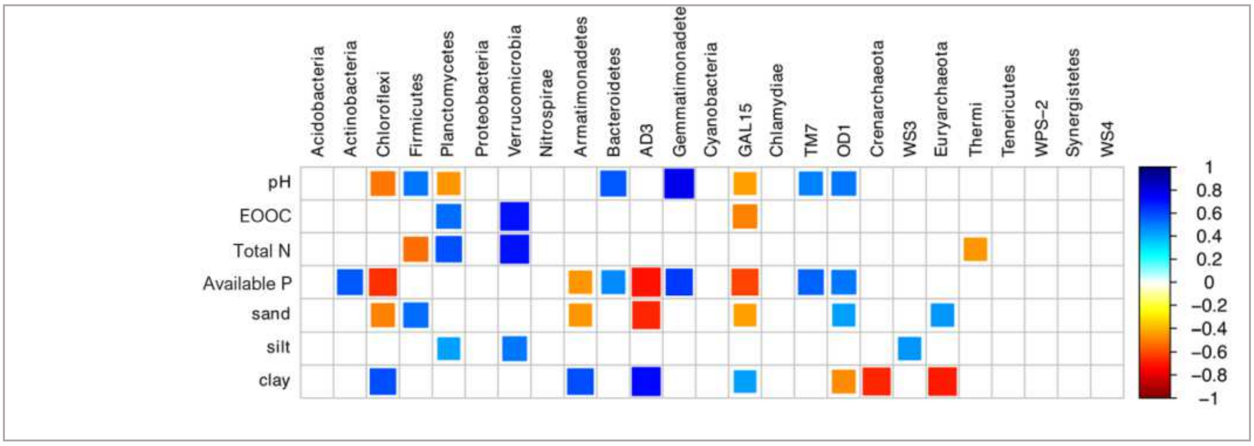


Fig. S4.11 Correlation between phyla and physiochemical soil properties in the A and Bo horizons of soils under charcoal kiln, crop field, and forest at Vanduzi, Sussundenga, and Macate. Manica province, Central Mozambique.

Chapter 5.

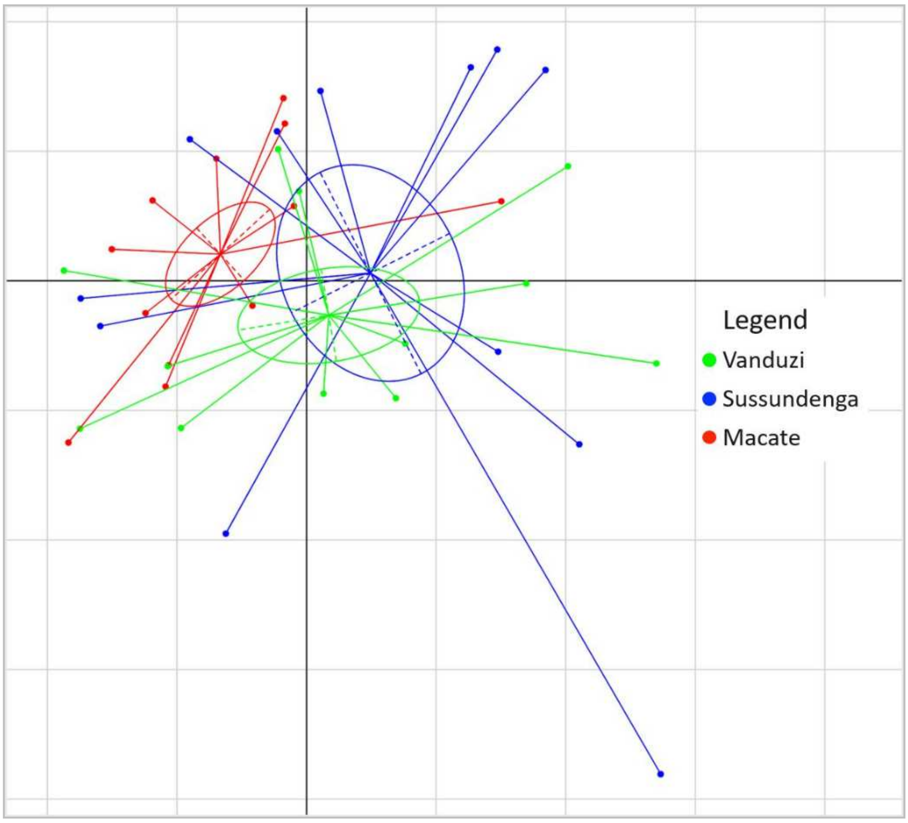


Fig. S5.1 PCA showing the relative ASV fungi distribution in the soils from Vanduzi, Sussundenga, and Macate. Manica province, Central Mozambique.

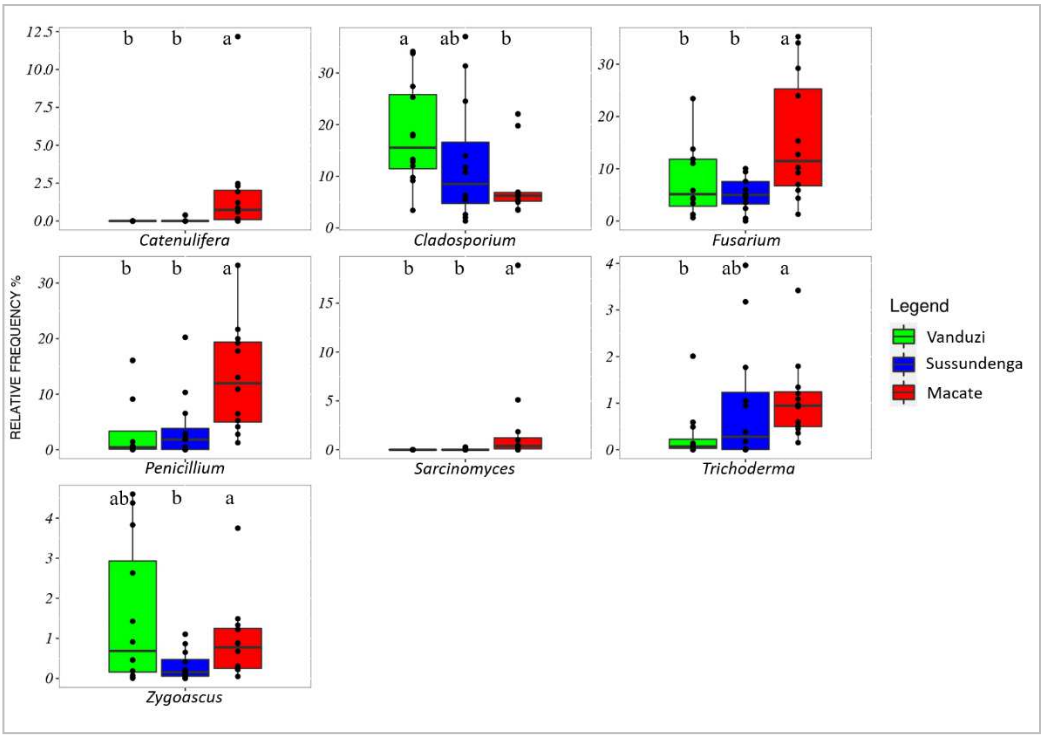


Fig. S5.2 Boxplots showing the relative abundance of the differentially abundant fungal ASVs of the soils from Vanduzi, Sussundenga, and Macate. Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

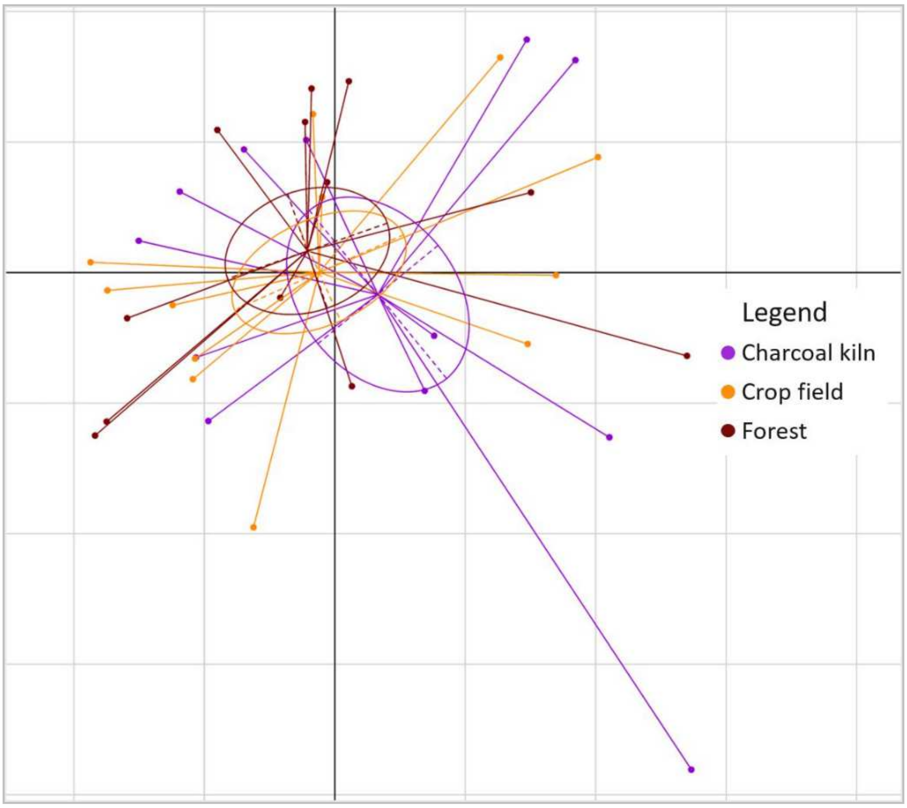


Fig. S5.3 PCA showing the relative ASV fungi distribution in the soils from different land uses: Charcoal kiln, Crop field and Forest. Manica province, Central Mozambique.

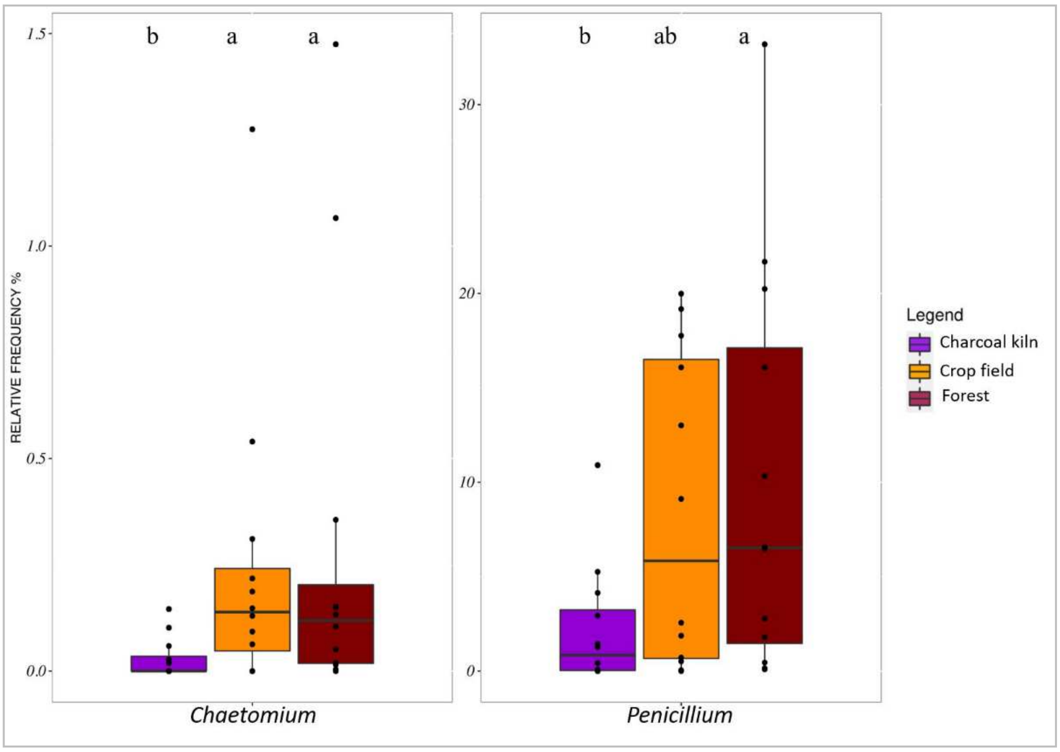


Fig. S5.4 Boxplots showing the differentially abundant soil fungal ASVs for different land uses: Charcoal kiln, Crop field, and Forest. Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

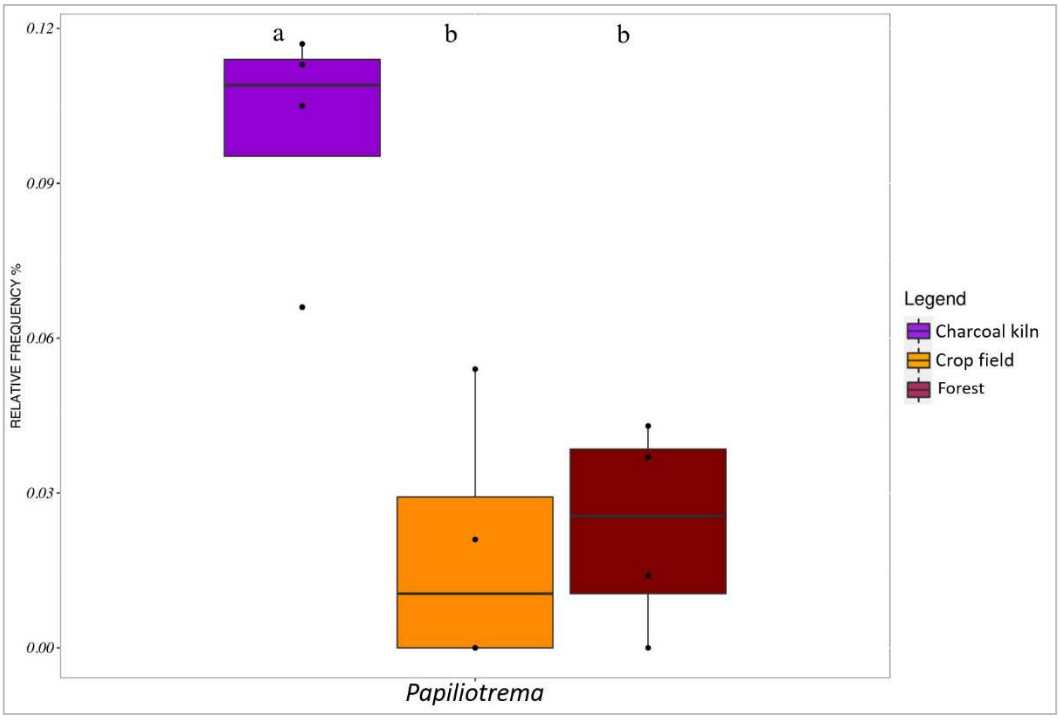


Fig. S5.5 Boxplots showing the differentially abundant soil fungal ASVs for different land uses: Charcoal kiln, Crop field, and Forest. Macate, Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

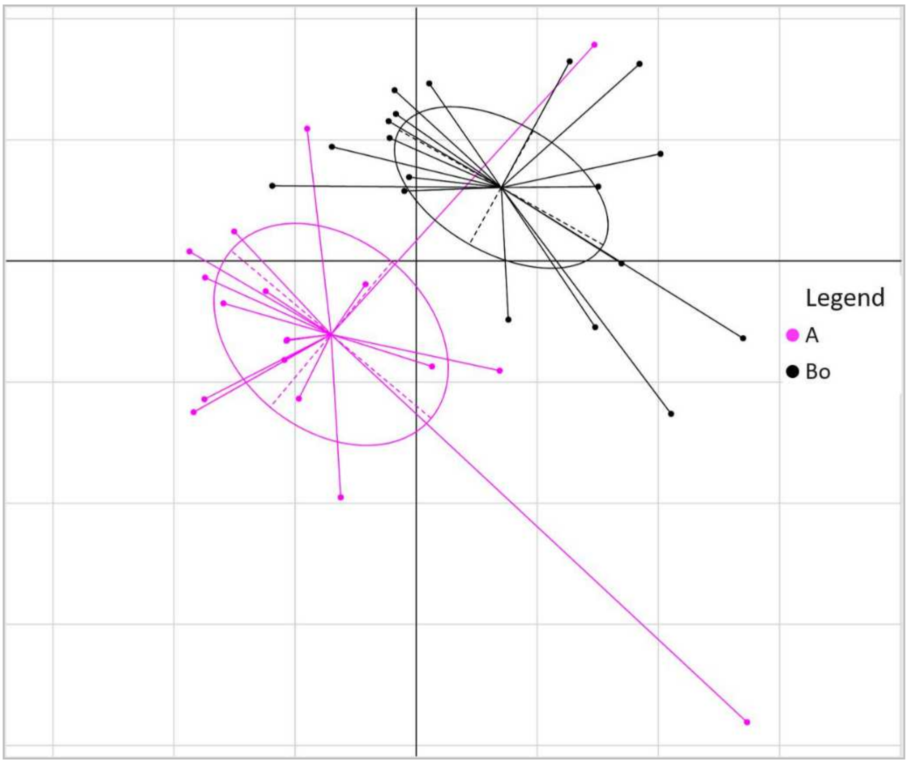


Fig. S5.6 PCA showing the relative soil fungal ASV distribution between A and Bo horizons. Manica province, Central Mozambique.

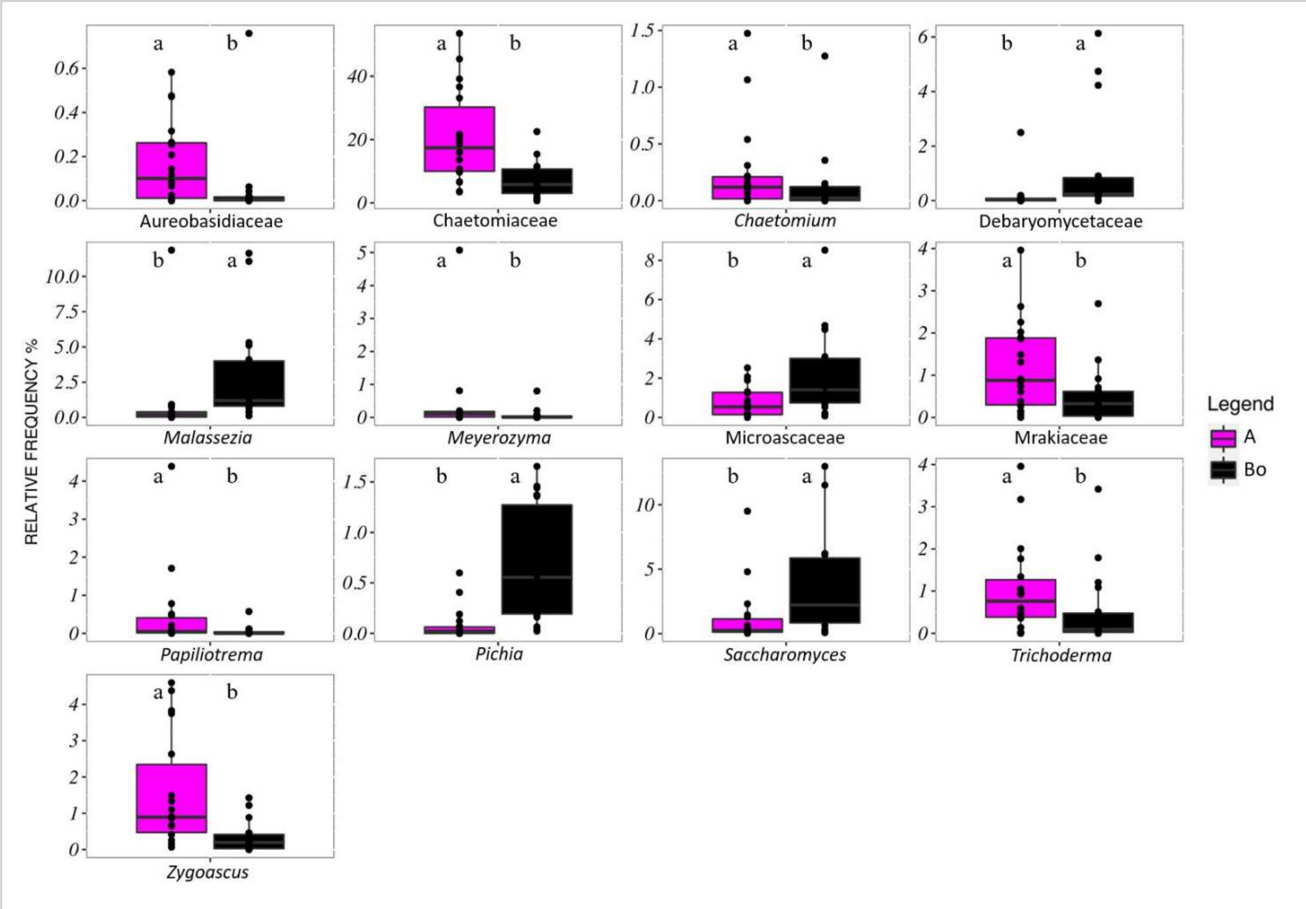


Fig. S5.7 Boxplots showing the differentially abundant soil fungal ASVs between A and Bo horizons. Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

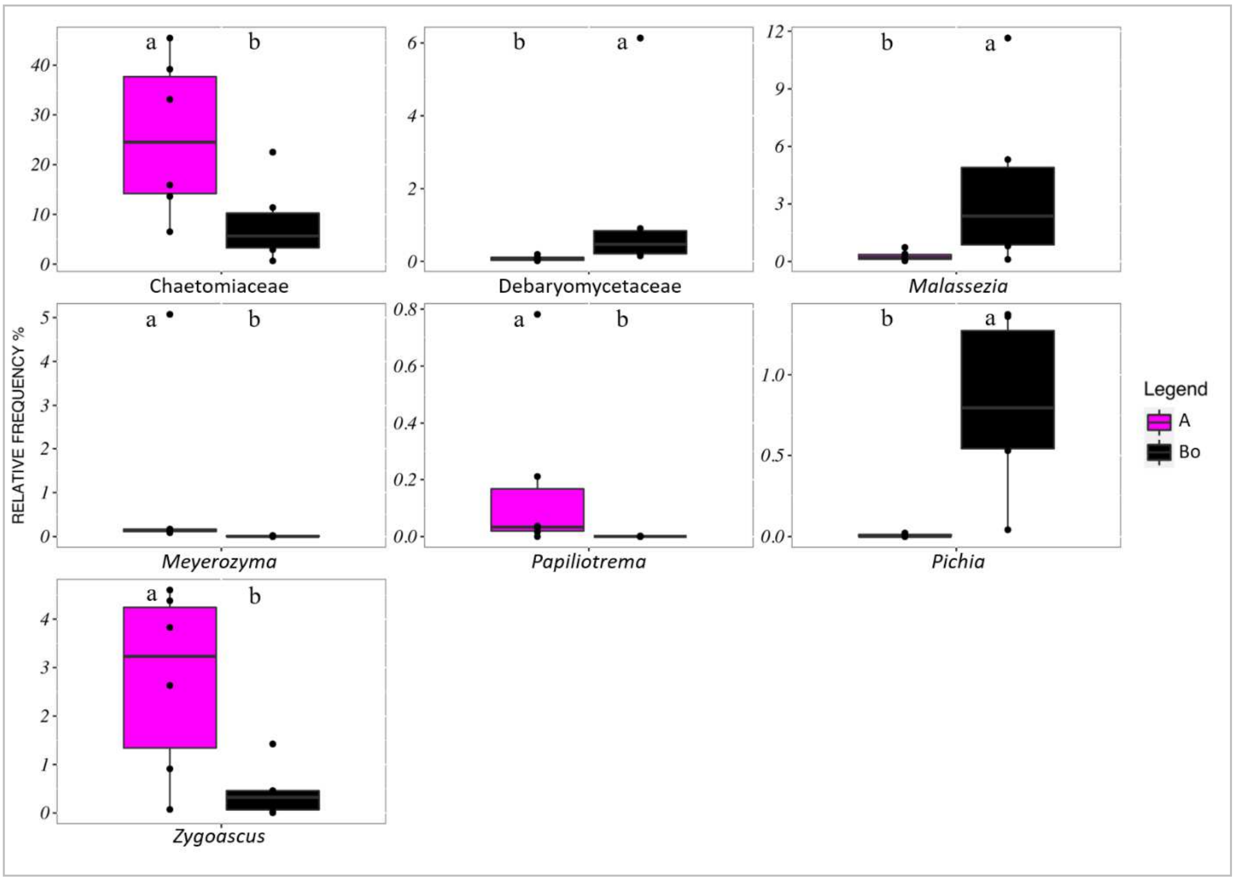


Fig. S5.8 Boxplots showing the differentially abundant fungal ASVs between A and Bo horizons in the soils of Vanduzi, Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

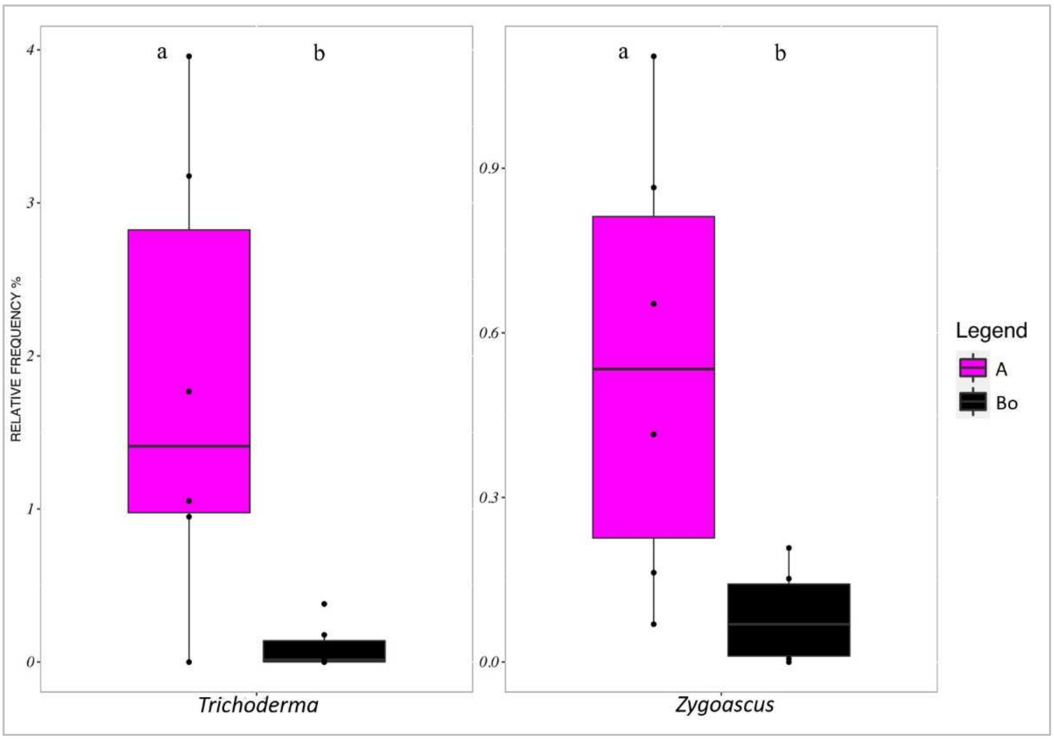


Fig. S5.9 Boxplots showing the differentially abundant fungal ASVs between A and Bo horizons in the soils of Sussundenga, Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.

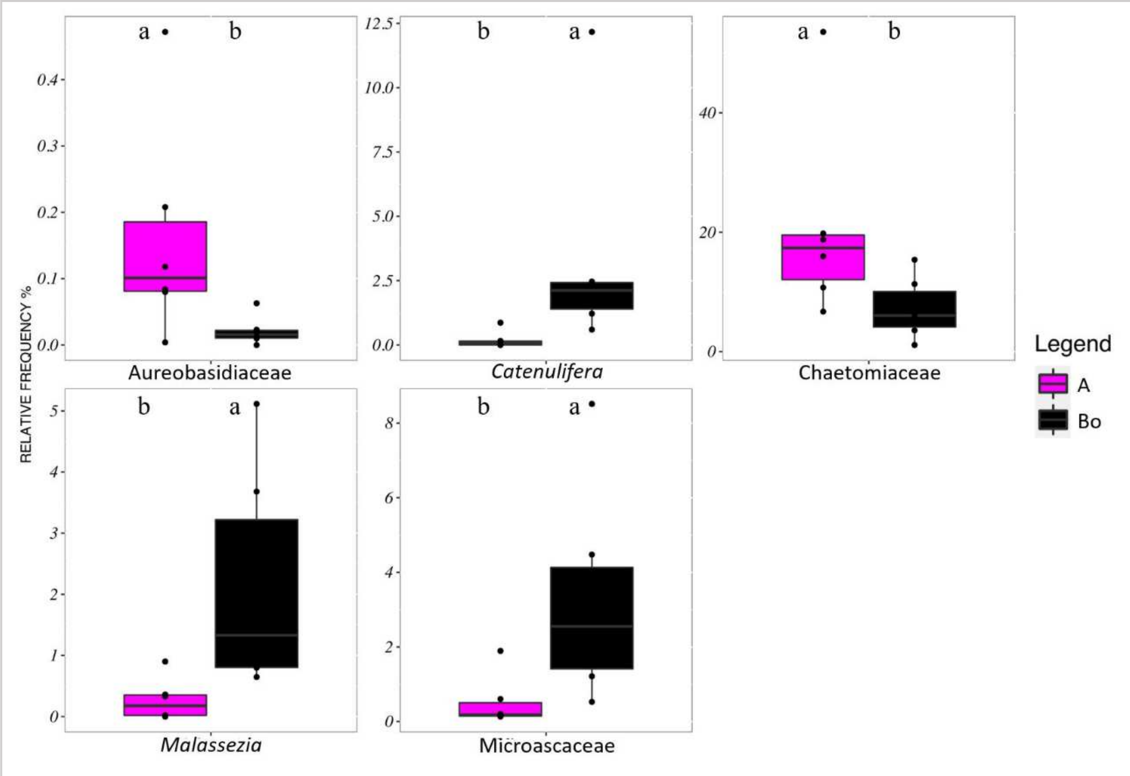


Fig. S5.10 Boxplots showing the differentially abundant fungal ASVs between A and Bo horizons in the soils of Macate, Manica province, Central Mozambique. Boxplots with different letters significantly differ at FDR ≤ 0.05.