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Dominique Serrani[a], Ilario Ferrocino[b], Cristiana Garofalo[a], Andrea Osimani[a], Maria Rita Corvaglia[b], Vesna Milanović[a], Lucia Aquilanti[a], Valeria Cardelli*[a], Andrea Salvucci[a], Stefania Cocco[a], Alves Rafael Rogerio Borguete[c], Giuseppe Corti[ad]

[a]Department of Agriculture, Food and Environmental Sciences – D3A; Polytechnic University of Marche, 60131 Ancona, Italy.

[b]Department of Agriculture, Forest and Food Sciences, University of Turin, 10095 Grugliasco, Italy.

[c]Department of Rural Engineering, Soil Science Division; Faculty of Agronomy and Forestry Engineering, University Eduardo Mondlane. Av. Julius Nyerere, No. 3435, P. Box 257, University Campus, Building #1, Maputo, Mozambique.

[d]CREA - Council for Agricultural Research and Analysis of the Agricultural Economy; Centre of Agricultural and Environmental Research, 50125 Firenze, Italy.

*Corresponding author: Department of Agriculture, Food and Environmental Sciences – D3A; Polytechnic University of Marche, 60131 Ancona, Italy. v.cardelli@univpm.it (V. Cardelli).

Abstract

This study provides a metataxonomic analysis of the fungal communities in soils under slash-and-burn agroforestry system and offers new insights into the relationships between fungal populations and soil physicochemical features such as pH, the particle size distribution, easily oxidizable organic carbon, total nitrogen, available phosphorus, and the mineralogical composition. Soils from three locations in central Mozambique—Vanduzi, Sussundenga, and Macate—that are subjected to slash and burn were considered to assess the effects of the forest fallow length (temporal variation) and of the land use (charcoal kiln, crop field, and forest; meaning horizontal variation) on the fungal community. The fungi of the genetic horizons (vertical variation) were also considered. Most of the detected fungi were decomposers, antagonists of plant pathogens, and plant-growth promoters; they were differently distributed in relation to the soil's physicochemical properties and the soil use. The variations in the fungi distribution among the locations and between the horizons were considerable, while there were few variations between the different land-use types. The limited differences between land uses indicate the inability of a forest fallow period shorter than 50 years to improve soil fertility and induce changes in the fungal community. The pedological approach used to identify and sample soil horizons allowed us to clearly distinguish the fungal community of the A horizons, those richest in organics and nutrients, and that of the Bo horizons, which have poor fertility.

Keywords: soil genetic horizons; Illumina sequencing; land-use change; soil fungi; 26S rRNA gene sequencing

1. Introduction

Slash and burn is a rotational agroforestry system that is widespread in the tropical and subtropical regions of the world (Mertz et al., 2009), where poorly fertile soils such as Oxisols occur (Soil Survey Staff, 2015). In rural areas, farmers use the slash-and-burn approach to a segment of forest to convert it into a cultivated field; to do so, they distribute several charcoal kilns per hectare where stems and branches are used to produce charcoal for the family. The burning activity and the charcoal production produce ashes as a byproduct; these are roughly distributed across the field. Such distribution has the effect of temporarily increasing soil fertility and boosting microbial activity (Gay-des-Combes et al., 2017). After two to four years of cultivation, when crop production is insufficient to maintain family supplies, the field is abandoned and natural reforestation is allowed to occur for decades until the land is cultivated again. Due to the absence of chemical fertilization (Rafael et al., 2018), the forest fallow period is considered essential to restoring a certain level of soil fertility (Gonçalves Lintemani et al., 2019) through soil organic matter (SOM) accumulation and mineralization (Andriamananjara et al., 2020; Silva-Forsberg and Fearnside, 1997). For centuries, the duration of the forest fallow was approximately 50–100 years or more, but the population growth and socio-economic changes that occurred in the second half of the 20th century shortened this period by a significant amount (Chowdhury et al., 2020; Nath et al., 2016), also reducing the ecosystem services provided by forests (Wood et al., 2016). Indeed, studies have established that gradual soil degradation (Gay-des-Combes et al., 2017; Thomaz et al., 2013; Zwartendijk et al., 2020) and the loss of flora, fauna, and microbial diversity (Aguilar-Fernández et al., 2009; Randriamalala et al., 2019) are triggered by the intense deforestation caused by the intensification of the slash-and-burn practice (Curtis et al., 2018).

After the effects of a slash-and-burn system on the soil bacterial community in Mozambique were studied (Serrani et al., 2023), it was considered useful to assess the fungal community's diversity in the same context. In fact, as argued by Arévalo-Gardini et al. (2020), due to the influence of microbial

activity on ecosystems' stability and fertility, variations in the fungal community may constitute a valid indicator of changes in soil health caused by land management. Fungi are significantly affected by physiographic conditions, environmental contexts related to climate and land management, and soil properties such as the SOM content and fertility level (Shah et al., 2016; Spurgeon et al., 2013; Oehl et al., 2017). Important soil fungi, such as saprotrophic varieties, are fundamentally important decomposers of lignocellulosic remnants (Clocchiatti et al., 2020, van der Wal et al., 2013), while entomopathogenic fungi are endophytes that can enhance plant defenses against harmful insects (Deaver et al., 2019; Vega, 2018). Many studies describe the diversity in the soil fungal population, but few consider fungi in soils submitted to slash and burn. To the best of our knowledge, only Aguilar-Fernández et al. (2009), Adeniyi (2010), Sharmah et al. (2014), and Barraclough and Olsson (2018) have studied fungi variations in soils subjected to slash and burn; these studies have mainly focused on the arbuscular mycorrhizal fungi (AMF) community, a group of fungi that have obligate symbiotic relationships with many plants and which play a specific role in nutrient uptake (e.g., Deveautour et al., 2018; Yang et al., 2011; Saliou Sarr et al., 2019; Rożek et al., 2020). Improving our knowledge of soil fungal diversity would allow us to understand the complexity of specific ecosystems and their responses to slash-and-burn practice.

The aim of this work was therefore to use a metataxonomic approach to evaluate the fungal diversity in the soils of three locations in central Mozambique that are subject to slash and burn, considering the effect of *i*) the three locations as representing different durations of the forest fallow period (temporal variation); *ii*) the land uses forming the slash-and-burn system: charcoal kiln, crop field, and forest (horizontal variation); and *iii*) the development of genetic soil horizons (vertical variation). In so doing, we hypothesized that the soil fungal community can differentiate horizontally and/or vertically, according to land management and soil changes.

2. Materials and methods

2.1. Locations and morphological description of the studied areas

Three locations from the Manica province, central Mozambique, were selected: Vanduzi, Sussundenga, and Macate (see Fig. S1 of Supplementary Materials in Serrani et al., 2023). The selected locations all fall into the Agro-Ecological Zone R4, which includes areas between 200 and 1000 m above sea level (Maria and Yost, 2006), with the mean annual rainfall ranging from 1000 to 1200 mm and the mean annual air temperature around 21°C (Climate Data, 2019). The geology of the zone is dominated by the Mesoproterozoic Southern Irumide Belt (950-1060 Ma), a litho-tectonic unit made up of metamorphic rocks (Chaúque et al., 2019). The predominant soil type belongs to the order of *Oxisols*, which is characterized by primary low fertility and strong erosion due to the topography of the terrain (Maria and Yost, 2006). Furthermore, the soils were recognized as having an aridic moisture regime and a thermic temperature regime (Soil Survey Staff, 2014). Such pedoclimatic conditions have led to the formation of typical tropical woodland (open forest), which is common in the studied locations, comprising savannas and shrublands made up of sparse trees of the leguminous trees *Brachystegia spiciformis* Benth., *Brachystegia tamarindoides* Benth., and *Julbernardia globiflora* (Benth.) with a more or less thick grass understorey of *Themeda triandra* Forssk., *Panicum maximum* Jacq., *Hyparrhenia filipendula* (Hochst.) Stapf, and *Andropogon gayanus* Kunth, referred to as *miombo* (Sitoe, 2004).

The three locations were chosen as the slash-and-burn system has been and is still being practised there, but with forest fallow periods of different durations (temporal variation), so as to form the following chronosequence: *i*) in Vanduzi, the forest was ≈25 years old, the crop field was 1 year old, and the charcoal kiln was 4 years old; *ii*) in Sussundenga, the forest was ≈35 years old, the crop field was 2 years old, and the charcoal kiln was 1 year old; *iii*) in Macate, the forest was ≈50 years old, the crop field was 16 years old, and the charcoal kiln was 16 years old (see Table S1 of Supplementary Materials in Serrani et al., 2023). In each location, we took into consideration the soils under the

charcoal kiln, the crop field, and forest (horizontal variation), and soil samples from each pedogenic horizon were collected (vertical variation).

Further details on the study areas, slash-and-burn systems, and study sites are reported in Serrani et al. (2023).

2.2. Sampling campaigns and soil characteristics

After a brief geomorphological and soil survey was conducted in March 2017, the sampling sites were selected in a relatively flat area (plateau) with a gentle slope (2–4%), featuring mostly Oxisols (Soil Survey Staff, 2014) developed from similar metamorphic parent rocks (Chaúque et al., 2019; Wijnhoud, 1997) (see Table S1 of Supplementary Materials in Serrani et al., 2023). To account for the eventual differences in terms of the fungal community across the agricultural seasons, the first sampling campaign was run in March 2017 (autumn) and the second one in November 2017 (spring). For each sampling campaign, soil profiles were opened in a representative area after the preliminary manual opening of mini-pits and auger holes. In the charcoal kilns and agricultural fields, the soil profiles were opened in approximately the middle of their extension, while those in the *miombo* were opened at ≈1 m from the trunk of one of the biggest *Brachystegia spiciformis* trees. Once excavated, each profile was described according to Schoeneberger et al. (2012) and sampled according to genetic horizons. In all sites, the studied soils were constituted by a brownish A horizon (umbric) and a reddish Bo (oxic) horizon with a coarse texture, a good degree of aggregation, and the absence of the redoximorphic feature, indicating good drainage and, consequently, a low water-holding capacity (e.g., Agrawal 1991; Suzuki et al., 2007) (see Table S1 of Supplementary Materials in Serrani et al., 2023). About 4 kg of samples were collected from each horizon and stored inside a portable fridge during the field operations. Once in the laboratory, the samples were air-dried and then sieved at 2 mm to remove the skeletal particles and coarse vegetal residues.

To summarize, for each location (Vanduzi, Sussundenga, and Macate), 12 soil samples were collected (3 land uses x 2 horizons x 2 replicates) from each campaign, for a total of 36 samples.

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149 *2.3. Soil analyses and microbial DNA extraction and sequencing*

150 The physicochemical and mineralogical analyses run on the soil samples are reported in Table

151 1, which synthesizes information that is fully explained in Serrani et al. (2023).

Table 1. Methods adopted to assess physicochemical properties of each soil sample collected according to locations, land uses, and horizons within Manica province, central Mozambique.

Property	Procedure	Bibliography
pH in water	Potentiometric method, using a combined glass-calomel electrode immersed into the suspension (1:2.5 solid:liquid ratio).	Thomas, 1996
Particle-size distribution	After dissolution of organic cements by Na-hypochlorite (NaOCL)solution at 6% of active chlorine adjusted to pH 9 with HCL, sand (2-0.05 mm) was recovered by wet sieving, while silt (0.05-0.002 mm) was separated from clay (< 0.002 mm) by sedimentation maintaining the columns at 19-20°C.	Lavkulich and Wiens, 1970
Easily oxidizable organic carbon (EOOC)	Walkley-Black method by K-dichromate digestion without application of heating.	Nelson and Sommers, 1996
Total nitrogen (N)	Semi-micro Kjeldahl method.	Bremmer, 1996
Potentially plant-available phosphorous (P)	Olsen method.	Olsen et al., 1954
Mineralogical assemblage	Assessed by X-ray diffractometry on manually compressed powdered samples by using a Philips PW 1830 diffractometer (Fe-filtered Co Kα1 radiation, 35 kV and 25 mA). Minerals were identified on the basis of their characteristic peaks, and 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.	Brindley and Brown, 1980; Dixon and Schulze, 2002

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153 Total microbial DNA was extracted from 250 mg of each soil sample using the E.Z.N.A. ® Soil DNA

154 Kit (Omega Bio-Tek, Inc., Georgia, USA), following the manufacturer's instructions. The extracted

155 DNA was quantified using a Qubit dsDNA assay kit (Life Technologies, Milan, Italy) and

156 standardized to 5 ng μL^{-1}. Then, 2.5 µL were used as a template to amplify the D1 domain of the 26S

157 rDNA gene by using the primers and the protocol described by Mota-Gutierrez et al. (2019); a

158 negative control was included in the PCR reactions by replacing the DNA solution with water. The

159 26S gene region provides a higher alpha diversity index and greater fungal rRNA taxonomic depth

160 and robustness results compared with ITS2 (Mota-Gutierrez et al., 2019). The PCR amplicons were

purified, tagged, and sequenced according to the Illumina metagenomic pipeline instructions. The sequencing was performed using a MiSeq Illumina instrument (Illumina, San Diego, USA) with V3 chemistry and generated 2x250 bp paired-end reads, according to the manufacturer's instructions.

2.4. Bioinformatic analysis

After sequencing, reads were analyzed using the Quantitative Insights into Microbial Ecology QIIME2 (Bolyen et al., 2019). Primers and adapters were trimmed using Cutadapter and then filtered for quality using the DADA2 algorithm (Callahan et al., 2016), removing low-quality bases and chimeric sequences with the DADA2 denoise-paired plug-in of QIIME2. A total of 3.820.038 clean reads were used for downstream analysis (99% of the sample coverage). Amplicon Sequence Variants (ASVs) generated by DADA2 were used for a taxonomic assignment using the QIIME feature-classifier plug-in against the SILVA-implemented database for fungi (Mota-Gutierrez et al., 2019). Briefly, the database was obtained using the large subunit rRNA gene sequences from the Silva database and from NCBI. The fungi taxonomic assignment was double-checked using BLAST suite tools. The 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: biosample accession numbers from SAMN14895437 to SAMN14895491 and from SAMN14895517 to SAMN14895548.

2.5. Statistical treatment of the data

Statistical analyses of the soil's physicochemical properties are reported in Serrani et al. (2023) and briefly reported below. Physicochemical soil data were statistically treated using the R program (vv 1.3.1093) workspace. ANOVA was used to test the similarity of the two sampling campaigns for physicochemical soil properties [pH, particle size distribution, easily oxidizable organic carbon (EOOC), total N, and available P] (see Table S2 of Supplementary Materials in Serrani et al., 2023; $P > 0.05$). Once it was confirmed that the samples collected in the two sampling campaigns were

187 replicates, ANOVA was run to test significative differences for sampling locations, land uses, and
188 horizons (see Table S3 of Supplementary Materials in Serrani et al., 2023; $P > 0.05$). The contrasted
189 results of the whole profiles were obtained from the weighted mean of each outcome for the thickness
190 of the A and Bo horizons of each soil sample. To apply the parametric test, we verified the normal
191 distribution of the data using the Shapiro–Wilk statistical test (stats R package) and the equal
192 variances using Levene's test (car R package), both at a 5% of significance level. When the data were
193 non-normally distributed, each numerical variable was transformed using the Box–Cox procedure
194 (Meloun et al., 2005). When the normality assumption was validated, a post hoc Tukey's Honest
195 Significant Difference (HSD) test with $P \leq 0.05$ was used to compare the means; in contrast, the
196 Kruskal–Wallis non-parametric test was used to assess the significance of the differences. In the case
197 of heteroscedasticity, the Welch one-way ANOVA test was used ($P \leq 0.05$), while, in case of
198 heteroscedasticity and non-normality, the Friedman test (rstatix package) combined with Kendall's
199 W were used to measure the Friedman test effect size and pairwise Wilcoxon signed-rank tests.
200 Fungal α-diversity was assessed using the Chao1 index and the Shannon diversity index, calculated
201 using the diversity function of QIIME2 on an ASV table rarefied at the lowest feature count/sample.
202 A Bray–Curtis distance matrix was generated by QIIME2 and used to build the principal coordinate
203 analysis (PCoA) and to perform PERMANOVA as a function of location, land use, or horizon.
204 Variables that were not normally distributed were presented as the median (interquartile range).
205 Variables were compared using the Mann–Whitney U test or the Kruskal–Wallis test, as appropriate.
206 An ASVs table was then imported in R to build the heatmap using the *made4* function. Spearman
207 correlation analysis between physicochemical properties and fungi was performed with
208 the *psych* package and *corrplot*() from corrplot R package. The *P* values were adjusted for multiple
209 testing using the Benjamini–Hochberg procedure, which assesses the false discovery rate (FDR).
210 The arithmetic means and relative standard deviations for physicochemical properties (see Tables S4,
211 S5, and S6 of the Supplementary Materials in Serrani et al., 2023) and ASVs were calculated for the

212 sampling locations (n=12), total land use (n=12), land use of each area (n=4), total horizons (n=18),
213 and the horizon of each site (n=6).
214
215 **3. Results and discussion**
216 *3.1. Fungal diversity*
217 Differences in fungal composition as a function of location, land use, and horizons were
218 examined at the highest taxonomic resolution reached, namely, at the genus or family level (Fig. 1).
219 ASVs were detected in the dataset and grouped into two main clusters: *i*) Cluster 1 was characterized
220 by the highest frequency of *Sarcinomyces*, *Catenulifera*, *Chaetomium*, *Zygoascus*, *Fusarium*,
221 *Trichoderma*, and *Chaetomiaceae* and included most of the samples from the Macate and Vanduzi
222 soils and the A horizons; *ii*) Cluster 2 exhibited the highest frequency of *Aureobasidium*,
223 *Cladosporium*, *Malassezia*, *Pichia*, *Aspergillus*, *Saccharomyces*, and *Acremonium* and included most
224 of the samples from the Sussundenga soils and the Bo horizons. Toju et al. (2016) analyzed the fungal
225 network in a cool–temperate forest in Hokkaido (Japan) and found that, as in our case, *Malassezia*
226 and *Cladosporium* had a strong preference for the B horizons. Elsewhere, Chen et al. (2019) found
227 an abundance of saprotroph fungi in organic soil and an abundance of symbiont fungi in the mineral
228 topsoil under a subtropical forest.
229 Analysing the alpha diversity values as a function of the locations, we observed the highest levels of
230 richness (the Shannon and Chao1 indices) and ASVs in the Macate soils (FDR<0.05, data not shown).
231 Alpha diversity as a function of land use did not show significant differences, while the comparison
232 between horizons highlighted greater complexity in the A horizon than in the Bo horizon (FDR<0.05,
233 data not shown). The alpha diversity comparison referring to horizons showed the fungi to decrease
234 in both number and species from the A to the Bo horizons, that is, with increasing depth; this finding
235 was also reported by Warcup (1951) and Jumpponen et al. (2010). Some studies have reported that
236 soils with high fungal richness and diversity showed a relatively large content of N (Mueller et al.,

2014; Weber et al., 2013), and this could explain why the highest Shannon and Chao1 indexes were found in the Macate soils and in the A horizons, where relatively high total N content occurred (see Tables S4 and S6 of the Supplementary Materials in Serrani et al., 2023). Since the physicochemical changes occurring along the soil profile induce the development of spatial niches that are able to accommodate different fungal communities (Chen et al., 2019), we assume this happened in our soils where, from the A to the Bo horizons, nutrients decreased and roots increased (see Tables S1 and S6 of the Supplementary Materials in Serrani et al., 2023).

3.2. Effect of location (temporal variation) on fungal diversity

PCoA based on the Bray–Curtis distance matrix showed a partial overlapping of fungi for the Vanduzi and Sussundenga soils, which were separated from the Macate soils (Fig. S1 of Supplementary Materials, $P<0.001$). Considering the relative frequency across locations, Vanduzi soils showed the highest frequency of *Cladosporium* (Fig. 2, FDR<0.05), while Macate soils were characterized by the highest frequencies of *Catenulifera*, *Fusarium*, *Penicillium*, *Sarcinomyces*, *Trichoderma*, and *Zygoascus* (Fig. 2, FDR<0.05).

Cladosporium is a genus that includes 993 heterogeneous and ubiquitous kinds of hyphomycetes that are well-known as common endophytes (Bensch et al., 2012). Several bioactive molecules that are active against bacteria and fungi have been isolated from endophytic *Cladosporium* species, thus indicating the main role of this group of fungi in producing antimicrobial compounds that are involved in the control of plant pathogens (Yehia et al., 2020). Additionally, because of the generally higher N content, the highest prevalence of *Cladosporium* is often associated with intensive cultivation systems, but it has been also reported to be an important taxon of the phyllosphere microbial community (Abdelfattah et al., 2016). *Cladosporium* is also involved in plant P absorption (Shi et al., 2020), and the highest frequency of these fungi were likely present in the Vanduzi soils due to the highest content levels of available P in these soils (see Table S4 of Supplementary Materials in Serrani

et al., 2023), despite no significant correlation to the soil's physicochemical properties being found (Fig. 3).

The genus *Catenulifera* includes anamorph species of *Hyphodiscus*, a genus of discomycetes that has been found to be associated with decaying wood and the fruit bodies of other fungi (Bogale et al., 2010; Hosoya et al., 2002). As far as we know, no information exists about the interaction between *Catenulifera* requirements and soil properties; however, based on the correlation plot (Fig. 3), *Catenulifera* appears to be negatively related to pH and sand, which displayed the lowest values in the Macate soils. This led us to hypothesize that *Catenulifera* were abundant in Macate because they prefer soil environments with acidophilic reactions and relatively high contents of silt and clay; however, the Macate soils also showed the highest levels of organics and N content (see Table S4 of Supplementary Materials in Serrani et al., 2023), even though no significant correlation between *Catenulifera* and these parameters was found (Fig. 3).

Fusarium is a genus of saprotrophic fungi and/or fast-growing colonizers of the rhizosphere in response to plant exudates (Goncharov et al., 2020), and its proliferation through the formation of both macroconidia and ascospores may be favored by soil moisture conditions (Lemmens et al., 2004). In our soils, the positive correlation of *Fusarium* with total N and EOOC (Fig. 3), which abounded in the Macate soils, was ascribed to the accumulation of decaying organic matter provided by the mulching in the crop field and by the presence of relatively well-developed and poorly disturbed litter in the forest, with both mulching and dense forest being able to maintain a certain level of soil moisture.

Penicillium is a common soil fungi genus that includes plant-beneficial microorganisms (Altaf et al., 2018; Das et al., 2021, Efthymiou et al., 2018a,b); it is also known for growing in extreme environments, including highly acidic soils (Diao et al., 2019; Yadav et al., 2019; Warcup, 1951). These properties of *Penicillium* effectively explain our results, since the ASVs of this genus showed an inverse relation with pH (Fig. 3), which was the lowest in the Macate soils.

As *Sarcinomyces* endophytic fungi, their highest frequency in the soils of Macate was ascribed to the relatively pronounced presence of decaying organic matter due to mulching (in the crop field) and forest development, as also reported by Li et al. (2018). Moreover, the correlation plot showed that the frequency of *Sarcinomyces* was inversely correlated to available P and sand (Fig. 3). Given that there are no specific indications for *Sarcinomyces*, since endophytic fungi are often isolated from sandy soils as they produce growth-promoting metabolites that help the host plants to survive under soil stress conditions, the observed inverse correlation was ascribed to these fungi's general resistance to drought and salinity (e.g., Hamayun et al., 2010; Khan et al., 2012, 2016).

Species belonging to the genus *Trichoderma* are considered plant-growth promoters, biocontrol agents (Ji et al., 2020; Oskiera et al., 2017; Zhang et al., 2020a), and improvers of N and P availability as they increase the activity of urease, phosphatase, catalase, and cellulase (Ji et al., 2020; Makhuvele et al., 2017). This evidence is aligned with the positive correlation of these fungi with EOOC and total N (Fig. 3), which were abundant in the soils of Macate.

Members of the genus *Zygoascus* have been reported to play a role as biofertilizers since they can solubilize soil phosphates (Das et al., 2021). The highest abundance of *Zygoascus* in the Macate soils and their positive correlation with EOOC, total N, and available P (Fig. 3) allowed us to hypothesize that they have a preference for soil niches enriched with organic matter.

To summarize, the partial overlapping of fungi in the Vanduzi and Sussundenga soils suggested the irrelevance of the different durations of the forest fallow period for these two locations: 25 and 35 years, respectively. In the Macate soils, the different fungal compositions and the highest ASV abundance were probably favored by the higher levels of nutrients, which are due to the pedogenic conditions and soil management (mulching in the crop field, few disturbances in the forest), rather than the different forest fallow period. Considering the fungi's ecosystem/ecological functions (Table 2), the most abundant fungi in the Macate soils played important roles, acting as decomposers, antagonists of plant pathogens, and plant-growth promoters.

Table 2. The most abundant fungi (ASVs) and their ecosystem/ecological functions in soils according to locations, land uses, and horizons within Manica province, central Mozambique. Abundances significantly differ at FDR ≤ 0.05.

	Clade	Family/Genus	Ecosystem/ecological functions	Bibliography
Location				
Vanduzi	Ascomycota	*Cladosporium*	Antagonistics of plant pathogens; litter and wood saprotrophs; foliar endophytes	Frac et al., 2018; Yehia et al., 2020
Macate	Ascomycota	*Catenulifera*	Decomposers and fungi pathogens; wood saprotrophs	Bogale et al., 2010; Frac et al., 2018; Hosoya et al., 2002
		Fusarium	Soil-borne root pathogenic fungi; litter saprotrophs; foliar endophytes	Frac et al., 2018; Ge et al., 2021a,b; Goncharov et al., 2020
		Penicillium	Increase in fertilized soils; antagonistics of plant pathogens; plant-growth promoters; litter saprotrophs; foliar endophytes	Altaf, 2018; Das et al., 2021; Efthymiou et al., 2018a,b; Frac et al., 2018
		Sarcinomyces	Ectomycorrhizal mutualists; adapted to high temperatures and low water activity; litter saprotrophs; foliar endophytes	Li et al., 2018; Sterflinger, 1998; Volkmann et al., 2003
		Trichoderma	Increase in fertilized soils; antagonistics of plant pathogens; improvers of the plant health and root growth; litter saprotrophs; foliar endophytes	e.g. Frac et al., 2018; Oskiera et al., 2017; Vinale et al., 2008
	Saccharomyceta	*Zygoascus*	Biofertilizers	Das et al., 2021; Frac et al., 2018
Land use				
Crop field	Sordariales	*Chaetomium*	On cellulose-rich soil materials or on dung; adapted to arid climate; litter saprotrophs; foliar endophytes	Ahmed et al., 2016; Frac et al., 2018
Forest	Sordariales	*Chaetomium*	On cellulose-rich soil materials or on dung; adapted to arid climate; litter saprotrophs; foliar endophytes	Ahmed et al., 2016; Frac et al., 2018
	Ascomycota	*Penicillium*	Increase in fertilized soils; antagonistics of plant pathogens; plant-growth promoters; litter saprotrophs; foliar endophytes	Altaf, 2018; Das et al., 2021; Efthymiou et al., 2018a,b; Frac et al., 2018
Horizon				
A	Dothideomycetes	Aureobasidiaceae	Fungal endophytes. Dominant in forest soil; decomposers in agricultural soils; increase after nitrogen fertilization	Frac et al., 2018; Khan et al., 2016
	Sordariales	Chaetomiaceae	Antagonistics of plant pathogens; degraders of complex SOM	Chovanova and Zamocky, 2016; Frac et al., 2018; Mohammed et al., 2019
		Chaetomium	On cellulose-rich soil materials or on dung; adapted to arid climate; litter saprotrophs; foliar endophytes	Ahmed et al., 2016; Frac et al., 2018
	Saccharomyceta	*Meyerozyma*	Involved in the solubilization of phosphates and xylose fermentation; antagonistics of plant pathogens; epiphytes; foliar endophytes	Arumugam et al., 2020; Frac et al., 2018; Kim et al., 2016; Nakayan et al., 2013; Procópio and Barreto, 2021
	Tremellomycetes	Mrakiaceae	Adapted to low temperatures; nitrate and nitrite utilizers; dominant in forest soil; saprotrophic and parasitic fungi	Frac et al., 2018; Sannino et al., 2020; Zhang et al., 2020b
		Papiliotrema	Contains species able to interact with AMF† to improve plant N and P uptake; litter saprotrophs; mycoparasites; fungal decomposers	Frac et al., 2018; Leguina et al., 2019

		Trichoderma	Increase in fertilized soils; antagonistics of plant pathogens; improvers of the plant health and root growth; litter saprotrophs; foliar endophytes	e.g. Frac et al., 2018; Oskiera et al., 2017; Vinale et al., 2008
	Saccharomyceta	*Zygoascus*	Biofertilizers	Das et al., 2021; Frac et al., 2018
Bo	Saccharomyceta	Debaryomycetaceae	Involved in xylose fermentation; able to produce bioethanol	Arumugam et al., 2020; Hui et al., 2014
	Basidiomycota	*Malassezia*	Able to colonize a wide range of habitats, including oligotrophic soils; soil saprotrophs; root-associated fungi	Amend, 2014; Frac et al., 2018; Toju et al., 2016
	Sordariomycetes	Microascaceae	Saprobic and plant pathogens; decomposers in agricultural soils; increase after nitrogen fertilization	Frac et al., 2018; Sandoval-Denis et al., 2016
	Saccharomyceta	*Pichia*	Phosphate- and zinc-solubilizers; thermotolerant yeasts; involved in xylose fermentation; able to produce bioethanol; antagonistics of plant pathogens	Frac et al., 2018; Chamnipa et al., 2018; Kumla et al., 2020; Pongcharoen et al., 2018; Procópio and Barreto, 2021
		Saccharomyces	Phosphate- and zinc-solubilizers; thermotolerant yeasts; involved in glucose fermentation; able to produce bioethanol	Frac et al., 2018; Kumla et al., 2020; Pongcharoen et al., 2018;

†AMF = Arbuscular micorrhizal fungi

3.3. Effect of land-use (horizontal variation) on fungal diversity

The PCoA showed a partial overlapping of fungi as function of land use (Fig. S2, $P<0.001$). Comparing the different land uses, only 2 out of 37 fungi showed different ASV distributions, *Chaetomium* and *Penicillium*, which showed the highest frequencies in both crop fields and forest soils (Fig. 4, FDR < 0.05). Since the samples were small, the frequency of *Penicillium* for crop field soils was slightly higher than that of the charcoal kiln soils, but this was not statistically different. The *Chaetomium* genus belongs to the *Chaetomiaceae* family and is known to be a producer of antimicrobial metabolites against plant pathogens, including fungi and insects (Chovanova and Zamocky, 2016; Mohammed et al., 2019). The *Chaetomiaceae* family is also linked to the degradation of complex SOM (Paula et al., 2020); in particular, the genus *Chaetomium* abounds in soils rich in cellulosic biomass because of the cellulose-degrading capabilities of this genus's members (Ahmed et al., 2016). These characteristics effectively explain why the highest frequency of *Chaetomium* was found in crop fields and forest soils, where they are likely favored 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 forests (and crop fields) can be ascribed to their adaptability

328 to the low pH values that characterized these soils, as previously reported and as suggested by the
329 correlation analysis (Fig. 3).
330 *Papiliotrema* was the only taxon associated with the charcoal kiln soils of Macate (Fig. S3 of
331 Supplementary Materials, FDR<0.05). Few data are available for *Papiliotrema*, formerly
332 *Cryptococcus*. Members of this genus were found to be predominant in rice-storage granaries (Shi et
333 al., 2021) while, in soil, *Papiliotrema laurentii* was observed to develop a synergic interaction with
334 AMF to improve plants' uptake of N and P (Leguina et al., 2019) and the solubilization of scarcely
335 soluble forms of phosphate (apatites) and zinc (ZnO and $ZnCO_3$) (Kumla et al., 2020). The presence
336 of *Papiliotrema* in the charcoal kiln soils of Macate can be attributed to the possible presence of
337 phosphatic minerals, which could have been generated by repeated combustions in the same area; the
338 higher availability of P in this soil supports this hypothesis.
339 However, the low number of variations in the fungal composition between charcoal kilns, crop fields,
340 and forests indicate that the different land uses had little influence.
341
342 *3.4. Effect of the horizon (vertical variation) on fungal diversity*
343 As reported above, fungi tend to create distinct networks throughout the soil; indeed, a certain
344 degree of separation of fungi between the A and Bo horizons was highlighted by the PcoA (Fig. S4,
345 $P<0.001$). The ASVs that were mainly associated with the A horizons were *Aureobasidiaceae*,
346 *Chaetomiaceae*, *Chaetomium*, *Meyerozima*, *Mrakiaceae*, *Papiliotrema*, *Trichoderma*, and *Zygoascus*
347 (Fig. 5, FDR<0.05), while the Bo horizons displayed the strongest association with
348 *Debaryomycetaceae*, *Malassezia*, *Microascaceae*, *Pichia*, and *Saccharomyces* (Fig. 5, FDR<0.05).
349 For the A horizons, members of *Aureobasidiaceae*, *Chaetomiaceae*, and *Chaetomium* are endophytic
350 fungi that are particularly abundant in leaves and stems (Habtewold et al., 2020, Khan et al., 2016),
351 whereas *Meyerozyma*, *Trichoderma*, and *Zygoascus* were found to play a role in the soil in the
352 solubilization of phosphates (Gizaw et al., 2017; Kim et al., 2016; Saravanakumar et al., 2013). These
353 reports agree somewhat with the correlations we found, which highlighted the following positive

354 relations: *i*) *Aureobasidiaceae* and *Trichoderma* with EOOC and total N, *ii*) *Chaetomiaceae* with
355 available P, and *iii*) *Zygoascus* with EOOC, total N, and available P (Fig. 3). The fungi belonging to
356 the *Mrakiaceae* family are known to be able to adapt their physiology to low temperatures (Sannino
357 et al., 2020) because of their ability to use nitrates and nitrites and to produce enzymes such as lipases,
358 amylases, proteases, pectinases, cellulases, and chitinases, and ligninolytic enzymes (Zhang et al.,
359 2020b). The presence of *Mrakiaceae* in the A horizons of all the soils indicated that not all of the
360 members of this family are adapted to cold environments and that their ability to produce a broad
361 spectrum of degradative enzymes enables these fungi to perform well where organic matter abounds.
362 Therefore, it appeared that the group of fungi associated with the A horizons was favored by the
363 abundance of organic matter and nutrients and, from an ecosystem/ecological point of view (Table
364 2), that they play the roles of decomposers, antagonists of plant pathogens, and plant-growth
365 promoters.
366 For the Bo horizons, the associated fungi showed inverse relations for *Debaryomycetaceae* and
367 *Saccharomyces* with EOOC and total N, *Malassezia* with total N, and *Pichia* with available P.
368 Although little information is available for *Debaryomycetaceae*, this family of yeasts is involved in
369 the xylose fermentation of biomass with the potential to produce bioethanol (Hui et al., 2014;
370 Arumugam et al., 2020). They probably abound in the Bo horizons due to their large number of roots,
371 which constitute a lignocellulosic substrate from which xylose can be freed during root decay (e.g.,
372 Cheshire et al., 1990; Machinet et al., 2009) and which excrete exudates containing xylose (e.g.,
373 Graystone and Campbell, 1996). For *Saccharomyces,* the wild species are commonly associated with
374 tree substrates (bark, leaves, exudates, and litter) and soil (Alsammar and Delneri, 2020), but they are
375 also known as *i*) siderophore producers in both bulk and rhizosphere soils, and *ii*) being responsible
376 for various processes that are beneficial to plants (Das et al., 2021). Because of this, the presence of
377 *Saccharomyces* in the Bo horizons was ascribed to the conspicuous quantity of roots in the sub-
378 surface horizons of several soils (those under the charcoal kilns of Sussundenga and Macate and the
379 forests of Vanduzi and Macate). *Malassezia* can colonize a wide range of extreme habitats (Amend,

2014), but Toju et al. (2016) found that *Malassezia* diffused in soil, especially in the Bo horizons, as in our case. The inverse relationship with total N and the abundance in the Bo horizons indicate that these fungi prefer soil environments with low fertility. Some fungi belonging to the *Pichia* genus are known to be able to produce siderophores and, similarly to *Saccharomyces*, to solubilize zinc and phosphates (Kumla et al., 2020; Nakayan et al., 2009), thus explaining the inverse relation with available P. In addition, the *Pichia* genus was recognized for its ability to ferment xylose and produce bioethanol (Arumugam et al., 2020, Chamnipa et al., 2018; Pongcharoen et al., 2018), as was the case for *Debaryomycetaceae*; because of this, their larger concentrations in the Bo horizons were explained by the notable presence of roots. *Microascaceae* is a scarcely known fungi taxon that includes saprobes and plant pathogens (Sandoval-Denis et al., 2016) and degraders of labile organics (Lueders et al., 2006; Zhang et al., 2018). This taxon showed no correlation with the analytical parameters, but its abundance in the Bo horizons was explained by the large number of roots generally present in these horizons, which provided suitable organic materials during root decay. Therefore, the group of fungi harboring the Bo horizons is probably favored by the presence of many roots and the oligotrophic conditions; it also appeared to be involved in xylose fermentation (Table 2).

No significant difference was observed for the vertical variation among land uses, while several differences were observed between the fungi and soil horizons within each location. In Vanduzi, *Chaetomiaceae*, *Meyerozima*, *Papiliotrema*, and *Zygoascus* were associated with the A horizons, while *Debaryomycetaceae*, *Malassezia*, and *Pichia* were associated with the Bo horizons (Fig. S5 of Supplementary Materials, FDR<0.05). At Sussundenga, *Trichoderma* and *Zygoascus* prospered in the A horizons (Fig. S6 of Supplementary Materials, FDR<0.05); meanwhile, in Macate, *Aureobasidiaceae* and *Chaetomiaceae* were the most abundant in the A horizons, with *Catenulifera,* *Malassezia*, and *Microascaceae* predominating in the Bo horizons (Fig. S7 of Supplementary Materials, FDR<0.05). As mentioned before, *Chaetomiaceae*, *Aureobasidiaceae*, *Meyerozyma*, *Trichoderma*, and *Zygoascus* were related to the presence of SOM and available nutrients, and their abundance in the A horizons is explained by their relatively high contents of EOOC, total N, and

406 available P. On the contrary, *Debaryomycetaceae, Malassezia*, and *Pichia* seemed to prefer
407 oligotrophic environments, which, in these soils, are represented by the Bo horizons. The tendency
408 of *Microascaceae* to proliferate in presence of roots may be explained by the significant amount of
409 living and dead roots observed in the Bo horizons in Macate (see Table S1 of the Supplementary
410 Materials in Serrani et al., 2023). In summary, the fungal community exhibited significant vertical
411 variations with a clear separation between the A and Bo horizons, which was mostly driven by the
412 distribution of nutrients and roots.
413
414 *3.5. Correlation between fungi and the soil's physicochemical properties*
415 In addition to the above-mentioned correlations, Fig. 3 shows the other relationships between fungi
416 and soil properties in the studied soils. Specifically, inverse relations were observed for *Acremonium*
417 and pH, and for *Plectosphaerellaceae* and *Ogataea* with clay content (FDR<0.05), whereas
418 *Aureobasidium* showed a negative relation with silt and a positive relation with clay content
419 (FDR<0.05).
420 Members of the genus *Acremonium* include plant pathogens, wood saprotrophs, and mycoparasitic
421 species (Nguyen et al., 2016), and they were found to be more abundant in N- and P-fertilized soils
422 with an acidic pH (4.6 and 4.8) than in soils with a higher pH (Zhou et al., 2016). These findings
423 agree with the results of our corrplot (Fig. 3).
424 The *Plectosphaerellaceae* family comprises numerous plant pathogen genera and soil-borne species
425 that have been detected in sandy and loamy soils (Giraldo and Crous, 2019), thus explaining the
426 inverse correlation between *Plectosphaerellaceae* and clay. The genus *Ogataea* is characterized by
427 thermotolerant and nitrate-assimilating methylotrophic yeasts (Limtong et al., 2008; Suh and Zhou,
428 2010) that are probably more suited to coarse-textured soils where nitrate availability is higher than
429 in clay-rich soils.
430 *Aureobasidium* is a genus of hyphomycetes fungi that inhabit various extreme environments (Bozoudi
431 et al., 2018; Zalar et al., 2008), including the stones and rocks of moderate or humid climates

(Sterflinger, 2010). This suggests that their distribution in our soils was enabled by the fine separates, possibly because of their ability to retain humidity.

4. Conclusions

This study provides one of the first metataxonomic analyses of soil-associated fungi in soils undergoing slash-and-burn practices and offers new insights into the relationship between fungal populations and soil physicochemical properties. The results highlighted the separation of fungi into two main groups: those affected by temporal, spatial, and vertical soil variations and those that are homogeneously distributed in all the investigated soils. Within these diverse abundances, the main differences were found among locations and between horizons. In the first case, the fungal distribution was ascribed to genetic soil properties and soil management rather than to the different lengths of the forest fallow period; in the second case, the ecological pressures responsible for fungal differentiation were recognized in the different dotation of SOM, nutrients, and living and decaying roots between the A and Bo horizons. In contrast, land use exerted negligible influence in determining differences in the fungal community, especially for the soils under crop fields and forests. Our findings indicate that temporal, horizontal, and vertical fungal distributions mainly depend on soil genesis and management, and that forest fallow is ineffective in producing substantial changes in the fungal community and, consequently, recovering soil biological fertility. Because of this, the fungi harbored in different soil environments have the potential to be considered ecosystem/ecological indicators of soil conditions and health. However, even though our approach is a commonly used method for characterizing fungi, we are aware of the limitations of our study. For example, the extraction method is not equally efficient for the different forms of fungi (simple cell, hyphae, or spore) and significant variation exists between methods. Thus, the metataxonomic technique may lead to possible biases due to amplification and may produce over- or underestimations of ASVs. In addition, sexual or asexual forms can produce different classifications in taxonomy. Because of this,

457 we believe that additional studies are needed to further disclose the role of fungi in various soil
458 horizons and the role of well-differentiated soil horizons in stimulating the proliferation of useful
459 fungi.
460
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469
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873 **Figure captions**

874

875 **Fig. 1.** Average-linkage clustering of soil samples based on fungal ASVs' relative abundance at the
876 highest taxonomical rank for locations, land use, and the A and Bo horizons. Manica province,
877 central Mozambique. The color scale represents the ASVs' abundance, denoted as the Z-score,
878 with brown indicating high abundance and blue indicating low abundance.

879 **Fig. 2.** Boxplots showing the differentially abundant fungal ASVs in the soils from Vanduzi,
880 Sussundenga, and Macate. Manica province, central Mozambique. Boxplots with different
881 letters significantly differ at FDR≤0.05.

882 **Fig. 3.** Correlation between fungi and soil physicochemical properties in the A and Bo horizons of
883 the soils under charcoal kilns, crop fields, and forests at Vanduzi, Sussundenga, and Macate.
884 Manica province, central Mozambique.

885 **Fig. 4.** Boxplots showing the differentially abundant fungi ASVs in the soils under charcoal kilns,
886 crop fields, and forests. Manica province, central Mozambique. Boxplots with different letters
887 significantly differ at FDR≤0.05.

888 **Fig. 5.** Boxplots showing the differentially abundant fungi ASVs between the A and Bo horizons.
889 Manica province, central Mozambique. Boxplots with different letters significantly differ at
890 FDR≤0.05.

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