



AperTO - Archivio Istituzionale Open Access dell'Università di Torino

Soil fungal communities under slash-and-burn system in Mozambique: A metataxonomic approach

This is the author's manuscript				
Original Citation:				
Availability:				
This version is available http://hdl.handle.net/2318/2031348 since 2024-11-20T16:07:06Z				
Published version:				
DOI:10.1111/sum.13062				
Terms of use:				
Open Access				
Anyone can freely access the full text of works made available as "Open Access". Works made available under a Creative Commons license can be used according to the terms and conditions of said license. Use of all other works requires consent of the right holder (author or publisher) if not exempted from copyright protection by the applicable law.				

(Article begins on next page)

- Soil fungal communities under slash-and-burn system in Mozambique: A metataxonomic
 approach

4	Dominique Serrani ^a , Ilario Ferrocino ^b , Cristiana Garofalo ^a , Andrea Osimani ^a , Maria Rita Corvaglia ^b ,
5	Vesna Milanović ^a , Lucia Aquilanti ^a , Valeria Cardelli ^{*a} , Andrea Salvucci ^a , Stefania Cocco ^a , Alves
6	Rafael Rogerio Borguete ^c , Giuseppe Corti ^{ad}
7	
8	^a Department of Agriculture, Food and Environmental Sciences – D3A; Polytechnic University of
9	Marche, 60131 Ancona, Italy.
10	^b Department of Agriculture, Forest and Food Sciences, University of Turin, 10095 Grugliasco, Italy.
11	^c Department of Rural Engineering, Soil Science Division; Faculty of Agronomy and Forestry
12	Engineering, University Eduardo Mondlane. Av. Julius Nyerere, No. 3435, P. Box 257, University
13	Campus, Building #1, Maputo, Mozambique.
14	^d CREA - Council for Agricultural Research and Analysis of the Agricultural Economy; Centre of
15	Agricultural and Environmental Research, 50125 Firenze, Italy.
16	
17	
18	*Corresponding author: Department of Agriculture, Food and Environmental Sciences - D3A;
19	Polytechnic University of Marche, 60131 Ancona, Italy. v.cardelli@univpm.it (V. Cardelli).
20	
21	
22	
23	
24	
25	
26	

27 Abstract

28 This study provides a metataxonomic analysis of the fungal communities in soils under slashand-burn agroforestry system and offers new insights into the relationships between fungal 29 populations and soil physicochemical features such as pH, the particle size distribution, easily 30 oxidizable organic carbon, total nitrogen, available phosphorus, and the mineralogical composition. 31 Soils from three locations in central Mozambique-Vanduzi, Sussundenga, and Macate-that are 32 subjected to slash and burn were considered to assess the effects of the forest fallow length (temporal 33 variation) and of the land use (charcoal kiln, crop field, and forest; meaning horizontal variation) on 34 the fungal community. The fungi of the genetic horizons (vertical variation) were also considered. 35

Most of the detected fungi were decomposers, antagonists of plant pathogens, and plant-growth 36 promoters; they were differently distributed in relation to the soil's physicochemical properties and 37 the soil use. The variations in the fungi distribution among the locations and between the horizons 38 39 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 40 improve soil fertility and induce changes in the fungal community. The pedological approach used to 41 identify and sample soil horizons allowed us to clearly distinguish the fungal community of the A 42 horizons, those richest in organics and nutrients, and that of the Bo horizons, which have poor fertility. 43

44

45

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

48 1. Introduction

Slash and burn is a rotational agroforestry system that is widespread in the tropical and 49 subtropical regions of the world (Mertz et al., 2009), where poorly fertile soils such as Oxisols occur 50 (Soil Survey Staff, 2015). In rural areas, farmers use the slash-and-burn approach to a segment of 51 52 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 53 charcoal production produce ashes as a byproduct; these are roughly distributed across the field. Such 54 55 distribution has the effect of temporarily increasing soil fertility and boosting microbial activity (Gaydes-Combes et al., 2017). After two to four years of cultivation, when crop production is insufficient 56 to maintain family supplies, the field is abandoned and natural reforestation is allowed to occur for 57 58 decades until the land is cultivated again. Due to the absence of chemical fertilization (Rafael et al., 59 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 60 61 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 62 socio-economic changes that occurred in the second half of the 20th century shortened this period by 63 a significant amount (Chowdhury et al., 2020; Nath et al., 2016), also reducing the ecosystem services 64 provided by forests (Wood et al., 2016). Indeed, studies have established that gradual soil degradation 65 66 (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 67 triggered by the intense deforestation caused by the intensification of the slash-and-burn practice 68 (Curtis et al., 2018). 69

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 73 74 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 75 soil properties such as the SOM content and fertility level (Shah et al., 2016; Spurgeon et al., 2013; 76 Oehl et al., 2017). Important soil fungi, such as saprotrophic varieties, are fundamentally important 77 decomposers of lignocellulosic remnants (Clocchiatti et al., 2020, van der Wal et al., 2013), while 78 79 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, 80 but few consider fungi in soils submitted to slash and burn. To the best of our knowledge, only 81 82 Aguilar-Fernández et al. (2009), Adenivi (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 83 focused on the arbuscular mycorrhizal fungi (AMF) community, a group of fungi that have obligate 84 85 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 86 our knowledge of soil fungal diversity would allow us to understand the complexity of specific 87 ecosystems and their responses to slash-and-burn practice. 88

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.

97 2. Materials and methods

98 2.1. Locations and morphological description of the studied areas

99 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 100 selected locations all fall into the Agro-Ecological Zone R4, which includes areas between 200 and 101 1000 m above sea level (Maria and Yost, 2006), with the mean annual rainfall ranging from 1000 to 102 1200 mm and the mean annual air temperature around 21°C (Climate Data, 2019). The geology of 103 104 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 105 order of Oxisols, which is characterized by primary low fertility and strong erosion due to the 106 107 topography of the terrain (Maria and Yost, 2006). Furthermore, the soils were recognized as having 108 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 109 110 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 111 Julbernardia globiflora (Benth.) with a more or less thick grass understorey of Themeda triandra 112 Forssk., Panicum maximum Jacq., Hyparrhenia filipendula (Hochst.) Stapf, and Andropogon gayanus 113 114 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 pedogenichorizon were collected (vertical variation).

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

126

127 2.2. Sampling campaigns and soil characteristics

After a brief geomorphological and soil survey was conducted in March 2017, the sampling 128 sites were selected in a relatively flat area (plateau) with a gentle slope (2–4%), featuring mostly 129 Oxisols (Soil Survey Staff, 2014) developed from similar metamorphic parent rocks (Chaúque et al., 130 131 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 132 sampling campaign was run in March 2017 (autumn) and the second one in November 2017 (spring). 133 134 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 135 profiles were opened in approximately the middle of their extension, while those in the *miombo* were 136 opened at ≈ 1 m from the trunk of one of the biggest *Brachystegia spiciformis* trees. Once excavated, 137 each profile was described according to Schoeneberger et al. (2012) and sampled according to genetic 138 139 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 140 redoximorphic feature, indicating good drainage and, consequently, a low water-holding capacity 141 (e.g., Agrawal 1991; Suzuki et al., 2007) (see Table S1 of Supplementary Materials in Serrani et al., 142 2023). About 4 kg of samples were collected from each horizon and stored inside a portable fridge 143 144 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. 145

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.

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 K α 1 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

152

Total microbial DNA was extracted from 250 mg of each soil sample using the E.Z.N.A. ® Soil DNA 153 Kit (Omega Bio-Tek, Inc., Georgia, USA), following the manufacturer's instructions. The extracted 154 DNA was quantified using a Qubit dsDNA assay kit (Life Technologies, Milan, Italy) and 155 standardized to 5 ng μ L⁻¹. Then, 2.5 μ L were used as a template to amplify the D1 domain of the 26S 156 rDNA gene by using the primers and the protocol described by Mota-Gutierrez et al. (2019); a 157 158 negative control was included in the PCR reactions by replacing the DNA solution with water. The 26S gene region provides a higher alpha diversity index and greater fungal rRNA taxonomic depth 159 and robustness results compared with ITS2 (Mota-Gutierrez et al., 2019). The PCR amplicons were 160

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.

164

165 2.4. Bioinformatic analysis

After sequencing, reads were analyzed using the Quantitative Insights into Microbial Ecology 166 QIIME2 (Bolyen et al., 2019). Primers and adapters were trimmed using Cutadapter and then filtered 167 for quality using the DADA2 algorithm (Callahan et al., 2016), removing low-quality bases and 168 chimeric sequences with the DADA2 denoise-paired plug-in of QIIME2. A total of 3.820.038 clean 169 170 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-171 classifier plug-in against the SILVA-implemented database for fungi (Mota-Gutierrez et al., 2019). 172 173 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 174 tools. The QIIME2 diversity script was used to perform alpha diversity analysis. The data generated 175 by sequencing were deposited in the NCBI Sequence Read Archive (SRA) and are available under 176 the Bioprojects Accession Number PRJNA631872: biosample accession numbers from 177 178 SAMN14895437 to SAMN14895491 and from SAMN14895517 to SAMN14895548.

179

180 *2.5. Statistical treatment of the data*

181 Statistical analyses of the soil's physicochemical properties are reported in Serrani et al. (2023) 182 and briefly reported below. Physicochemical soil data were statistically treated using the R program 183 (vv 1.3.1093) workspace. ANOVA was used to test the similarity of the two sampling campaigns for 184 physicochemical soil properties [pH, particle size distribution, easily oxidizable organic carbon 185 (EOOC), total N, and available P] (see Table S2 of Supplementary Materials in Serrani et al., 2023; 186 P > 0.05). Once it was confirmed that the samples collected in the two sampling campaigns were

replicates, ANOVA was run to test significative differences for sampling locations, land uses, and 187 188 horizons (see Table S3 of Supplementary Materials in Serrani et al., 2023; P > 0.05). The contrasted results of the whole profiles were obtained from the weighted mean of each outcome for the thickness 189 of the A and Bo horizons of each soil sample. To apply the parametric test, we verified the normal 190 distribution of the data using the Shapiro-Wilk statistical test (stats R package) and the equal 191 variances using Levene's test (car R package), both at a 5% of significance level. When the data were 192 193 non-normally distributed, each numerical variable was transformed using the Box-Cox procedure (Meloun et al., 2005). When the normality assumption was validated, a post hoc Tukey's Honest 194 Significant Difference (HSD) test with $P \le 0.05$ was used to compare the means; in contrast, the 195 196 Kruskal–Wallis non-parametric test was used to assess the significance of the differences. In the case of heteroscedasticity, the Welch one-way ANOVA test was used ($P \le 0.05$), while, in case of 197 heteroscedasticity and non-normality, the Friedman test (rstatix package) combined with Kendall's 198 199 W were used to measure the Friedman test effect size and pairwise Wilcoxon signed-rank tests.

Fungal α-diversity was assessed using the Chao1 index and the Shannon diversity index, calculated 200 using the diversity function of QIIME2 on an ASV table rarefied at the lowest feature count/sample. 201 A Bray–Curtis distance matrix was generated by QIIME2 and used to build the principal coordinate 202 analysis (PCoA) and to perform PERMANOVA as a function of location, land use, or horizon. 203 204 Variables that were not normally distributed were presented as the median (interquartile range). Variables were compared using the Mann–Whitney U test or the Kruskal–Wallis test, as appropriate. 205 An ASVs table was then imported in R to build the heatmap using the *made4* function. Spearman 206 correlation analysis between physicochemical properties and fungi was performed with 207 the *psych* package and *corrplot()* from corrplot R package. The *P* values were adjusted for multiple 208 testing using the Benjamini–Hochberg procedure, which assesses the false discovery rate (FDR). 209

The arithmetic means and relative standard deviations for physicochemical properties (see Tables S4,
S5, and S6 of the Supplementary Materials in Serrani et al., 2023) and ASVs were calculated for the

sampling locations (n=12), total land use (n=12), land use of each area (n=4), total horizons (n=18),
and the horizon of each site (n=6).

214

215 3. Results and discussion

216 3.1. Fungal diversity

Differences in fungal composition as a function of location, land use, and horizons were 217 examined at the highest taxonomic resolution reached, namely, at the genus or family level (Fig. 1). 218 219 ASVs were detected in the dataset and grouped into two main clusters: i) Cluster 1 was characterized by the highest frequency of Sarcinomyces, Catenulifera, Chaetomium, Zygoascus, Fusarium, 220 Trichoderma, and Chaetomiaceae and included most of the samples from the Macate and Vanduzi 221 222 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 of the samples from the Sussundenga soils and the Bo horizons. Toju et al. (2016) analyzed the fungal 224 225 network in a cool-temperate forest in Hokkaido (Japan) and found that, as in our case, Malassezia and *Cladosporium* had a strong preference for the B horizons. Elsewhere, Chen et al. (2019) found 226 an abundance of saprotroph fungi in organic soil and an abundance of symbiont fungi in the mineral 227 topsoil under a subtropical forest. 228

Analysing the alpha diversity values as a function of the locations, we observed the highest levels of 229 230 richness (the Shannon and Chao1 indices) and ASVs in the Macate soils (FDR<0.05, data not shown). Alpha diversity as a function of land use did not show significant differences, while the comparison 231 between horizons highlighted greater complexity in the A horizon than in the Bo horizon (FDR<0.05, 232 data not shown). The alpha diversity comparison referring to horizons showed the fungi to decrease 233 in both number and species from the A to the Bo horizons, that is, with increasing depth; this finding 234 235 was also reported by Warcup (1951) and Jumpponen et al. (2010). Some studies have reported that soils with high fungal richness and diversity showed a relatively large content of N (Mueller et al., 236

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).

244

245 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 252 are well-known as common endophytes (Bensch et al., 2012). Several bioactive molecules that are 253 254 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 255 in the control of plant pathogens (Yehia et al., 2020). Additionally, because of the generally higher N 256 content, the highest prevalence of *Cladosporium* is often associated with intensive cultivation 257 systems, but it has been also reported to be an important taxon of the phyllosphere microbial 258 community (Abdelfattah et al., 2016). Cladosporium is also involved in plant P absorption (Shi et al., 259 2020), and the highest frequency of these fungi were likely present in the Vanduzi soils due to the 260 highest content levels of available P in these soils (see Table S4 of Supplementary Materials in Serrani 261

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 264 been found to be associated with decaying wood and the fruit bodies of other fungi (Bogale et al., 265 2010; Hosoya et al., 2002). As far as we know, no information exists about the interaction between 266 *Catenulifera* requirements and soil properties; however, based on the correlation plot (Fig. 3), 267 268 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 269 prefer soil environments with acidophilic reactions and relatively high contents of silt and clay; 270 271 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 272 Catenulifera and these parameters was found (Fig. 3). 273

274 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 275 both macroconidia and ascospores may be favored by soil moisture conditions (Lemmens et al., 276 2004). In our soils, the positive correlation of *Fusarium* with total N and EOOC (Fig. 3), which 277 abounded in the Macate soils, was ascribed to the accumulation of decaying organic matter provided 278 279 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 280 level of soil moisture. 281

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 287 288 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 289 the frequency of Sarcinomyces was inversely correlated to available P and sand (Fig. 3). Given that 290 there are no specific indications for Sarcinomyces, since endophytic fungi are often isolated from 291 sandy soils as they produce growth-promoting metabolites that help the host plants to survive under 292 293 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). 294

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.

304 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 35 305 years, respectively. In the Macate soils, the different fungal compositions and the highest ASV 306 abundance were probably favored by the higher levels of nutrients, which are due to the pedogenic 307 conditions and soil management (mulching in the crop field, few disturbances in the forest), rather 308 309 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, 310 antagonists of plant pathogens, and plant-growth promoters. 311

	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				
Α	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

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 .

		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
Во	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

312

313 *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). 314 Comparing the different land uses, only 2 out of 37 fungi showed different ASV distributions, 315 Chaetomium and Penicillium, which showed the highest frequencies in both crop fields and forest 316 soils (Fig. 4, FDR < 0.05). Since the samples were small, the frequency of *Penicillium* for crop field 317 soils was slightly higher than that of the charcoal kiln soils, but this was not statistically different. 318 319 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 320 321 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 322 soils rich in cellulosic biomass because of the cellulose-degrading capabilities of this genus's 323 members (Ahmed et al., 2016). These characteristics effectively explain why the highest frequency 324 325 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 326 *Penicillium* distribution in the soils under forests (and crop fields) can be ascribed to their adaptability 327

to the low pH values that characterized these soils, as previously reported and as suggested by the 328 329 correlation analysis (Fig. 3).

Papiliotrema was the only taxon associated with the charcoal kiln soils of Macate (Fig. S3 of 330 Supplementary Materials, FDR<0.05). Few data are available for Papiliotrema, formerly 331 Cryptococcus. Members of this genus were found to be predominant in rice-storage granaries (Shi et 332 al., 2021) while, in soil, *Papiliotrema laurentii* was observed to develop a synergic interaction with 333 AMF to improve plants' uptake of N and P (Leguina et al., 2019) and the solubilization of scarcely 334 soluble forms of phosphate (apatites) and zinc (ZnO and ZnCO₃) (Kumla et al., 2020). The presence 335 of Papiliotrema in the charcoal kiln soils of Macate can be attributed to the possible presence of 336 337 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.

However, the low number of variations in the fungal composition between charcoal kilns, crop fields, 339 340 and forests indicate that the different land uses had little influence.

341

353

3.4. Effect of the horizon (vertical variation) on fungal diversity 342

As reported above, fungi tend to create distinct networks throughout the soil; indeed, a certain 343 degree of separation of fungi between the A and Bo horizons was highlighted by the PcoA (Fig. S4, 344 345 P < 0.001). The ASVs that were mainly associated with the A horizons were Aureobasidiaceae, Chaetomiaceae, Chaetomium, Meverozima, Mrakiaceae, Papiliotrema, Trichoderma, and Zygoascus 346 (Fig. 5, FDR<0.05), while the Bo horizons displayed the strongest association with 347 348 Debaryomycetaceae, Malassezia, Microascaceae, Pichia, and Saccharomyces (Fig. 5, FDR<0.05). For the A horizons, members of Aureobasidiaceae, Chaetomiaceae, and Chaetomium are endophytic 349

350 fungi that are particularly abundant in leaves and stems (Habtewold et al., 2020, Khan et al., 2016),

whereas Meyerozyma, Trichoderma, and Zygoascus were found to play a role in the soil in the 351

solubilization of phosphates (Gizaw et al., 2017; Kim et al., 2016; Saravanakumar et al., 2013). These 352 reports agree somewhat with the correlations we found, which highlighted the following positive

relations: i) Aureobasidiaceae and Trichoderma with EOOC and total N, ii) Chaetomiaceae with 354 355 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 et al., 2020) because of their ability to use nitrates and nitrites and to produce enzymes such as lipases, 357 amylases, proteases, pectinases, cellulases, and chitinases, and ligninolytic enzymes (Zhang et al., 358 2020b). The presence of *Mrakiaceae* in the A horizons of all the soils indicated that not all of the 359 360 members of this family are adapted to cold environments and that their ability to produce a broad spectrum of degradative enzymes enables these fungi to perform well where organic matter abounds. 361 Therefore, it appeared that the group of fungi associated with the A horizons was favored by the 362 363 abundance of organic matter and nutrients and, from an ecosystem/ecological point of view (Table 2), that they play the roles of decomposers, antagonists of plant pathogens, and plant-growth 364 promoters. 365

366 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. 367 Although little information is available for *Debaryomycetaceae*, this family of yeasts is involved in 368 the xylose fermentation of biomass with the potential to produce bioethanol (Hui et al., 2014; 369 370 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., Cheshire et al., 1990; Machinet et al., 2009) and which excrete exudates containing xylose (e.g., 372 Graystone and Campbell, 1996). For Saccharomyces, the wild species are commonly associated with 373 374 tree substrates (bark, leaves, exudates, and litter) and soil (Alsammar and Delneri, 2020), but they are also known as *i*) siderophore producers in both bulk and rhizosphere soils, and *ii*) being responsible 375 for various processes that are beneficial to plants (Das et al., 2021). Because of this, the presence of 376 Saccharomyces in the Bo horizons was ascribed to the conspicuous quantity of roots in the sub-377 surface horizons of several soils (those under the charcoal kilns of Sussundenga and Macate and the 378 forests of Vanduzi and Macate). Malassezia can colonize a wide range of extreme habitats (Amend, 379

2014), but Toju et al. (2016) found that Malassezia diffused in soil, especially in the Bo horizons, as 380 381 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 382 known to be able to produce siderophores and, similarly to Saccharomyces, to solubilize zinc and 383 phosphates (Kumla et al., 2020; Nakayan et al., 2009), thus explaining the inverse relation with 384 available P. In addition, the Pichia genus was recognized for its ability to ferment xylose and produce 385 bioethanol (Arumugam et al., 2020, Chamnipa et al., 2018; Pongcharoen et al., 2018), as was the case 386 for Debaryomycetaceae; because of this, their larger concentrations in the Bo horizons were 387 explained by the notable presence of roots. Microascaceae is a scarcely known fungi taxon that 388 389 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 390 parameters, but its abundance in the Bo horizons was explained by the large number of roots generally 391 392 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 393 oligotrophic conditions; it also appeared to be involved in xylose fermentation (Table 2). 394

No significant difference was observed for the vertical variation among land uses, while several 395 396 differences were observed between the fungi and soil horizons within each location. In Vanduzi, 397 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 398 Supplementary Materials, FDR<0.05). At Sussundenga, Trichoderma and Zygoascus prospered in 399 400 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, 401 Malassezia, and Microascaceae predominating in the Bo horizons (Fig. S7 of Supplementary 402 Materials, FDR<0.05). As mentioned before, Chaetomiaceae, Aureobasidiaceae, Meyerozyma, 403 Trichoderma, and Zygoascus were related to the presence of SOM and available nutrients, and their 404 abundance in the A horizons is explained by their relatively high contents of EOOC, total N, and 405

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

In addition to the above-mentioned correlations, Fig. 3 shows the other relationships between fungi and soil properties in the studied soils. Specifically, inverse relations were observed for *Acremonium* and pH, and for *Plectosphaerellaceae* and *Ogataea* with clay content (FDR<0.05), whereas *Aureobasidium* showed a negative relation with silt and a positive relation with clay content (FDR<0.05).

Members of the genus *Acremonium* include plant pathogens, wood saprotrophs, and mycoparasitic species (Nguyen et al., 2016), and they were found to be more abundant in N- and P-fertilized soils with an acidic pH (4.6 and 4.8) than in soils with a higher pH (Zhou et al., 2016). These findings agree with the results of our corrplot (Fig. 3).

The *Plectosphaerellaceae* family comprises numerous plant pathogen genera and soil-borne species that have been detected in sandy and loamy soils (Giraldo and Crous, 2019), thus explaining the inverse correlation between *Plectosphaerellaceae* and clay. The genus *Ogataea* is characterized by thermotolerant and nitrate-assimilating methylotrophic yeasts (Limtong et al., 2008; Suh and Zhou, 2010) that are probably more suited to coarse-textured soils where nitrate availability is higher than in clay-rich soils.

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

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

434

435 4. Conclusions

This study provides one of the first metataxonomic analyses of soil-associated fungi in soils 436 undergoing slash-and-burn practices and offers new insights into the relationship between fungal 437 populations and soil physicochemical properties. The results highlighted the separation of fungi into 438 439 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 440 441 differences were found among locations and between horizons. In the first case, the fungal 442 distribution was ascribed to genetic soil properties and soil management rather than to the different 443 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 444 445 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 446 findings indicate that temporal, horizontal, and vertical fungal distributions mainly depend on soil 447 genesis and management, and that forest fallow is ineffective in producing substantial changes in the 448 449 fungal community and, consequently, recovering soil biological fertility. Because of this, the fungi 450 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 451 method for characterizing fungi, we are aware of the limitations of our study. For example, the 452 extraction method is not equally efficient for the different forms of fungi (simple cell, hyphae, or 453 spore) and significant variation exists between methods. Thus, the metataxonomic technique may 454 lead to possible biases due to amplification and may produce over- or underestimations of ASVs. In 455 addition, sexual or asexual forms can produce different classifications in taxonomy. Because of this, 456

we believe that additional studies are needed to further disclose the role of fungi in various soil
horizons and the role of well-differentiated soil horizons in stimulating the proliferation of useful
fungi.

460

461 Acknowledgments

The authors are indebted to the Sussundenga Research Station (*Instituto de Investigação Agrária de Moçambique*). Grants were received through the Universidade Eduardo Mondlane by the Italian Cooperation and Development Agency for the project "Applied Research and Multi-sectorial Program" (No. 5.2.1), and by the project "PSA2017-Discovering "terra preta" in Mozambique: a model for sustainable agroforestry systems to preserve soil, forest, and wilderness areas", which was funded by the Polytechnic University of Marche (Italy). The findings, conclusions, and recommendations presented in this document do not necessarily reflect the views of the donors.

469

470 **References**

471 Abdelfattah, A., Wisniewski, M., Li Destri Nicosia, M. G., Cacciola, S. O., & Schena, L. (2016).

472 Metagenomic analysis of fungal diversity on strawberry plants and the effect of management

473 practices on the fungal community structure of aerial organs. *PloS ONE*, *11*, e0160470.

474 <u>https://doi:10.1371/journal.pone.0160470</u>

Adeniyi, A. S. (2010). Effects of slash and burning on soil microbial diversity and abundance in the
tropical rainforest ecosystem, Ondo State, Nigeria. *African Journal of Plant Science*, *4*, 322-329.

Agrawal, R. P. (1991). Water and nutrient management in sandy soils by compaction. *Soil & Tillage Research*, *19(2)*, 121-130. https://doi.org/10.1016/0167-1987(91)90081-8

Research, 17(2), 121 150. <u>https://doi.org/10.1010/010/11/00010</u>

479 Aguilar-Fernández, M., Jaramillo, V. J., Varela-Fregoso, L., & Gavito, M. E. (2009). Short-term

480 consequences of slash-and-burn practices on the arbuscular mycorrhizal fungi of a tropical dry

481 forest. *Mycorrhiza*, *19*, 179–186. <u>https://doi.org/10.1007/s00572-009-0229-2</u>

- 482 Ahmed, S. A., Khan, Z., Wang, X. -W., Moussa, T. A., Al-Zahrani, H. S., Almaghrabi, O. A., Sutton,
- 483 D. A., Ahmad, S., Groenewald, J. Z., Alastruey-Izquierdo, A., van Diepeningen, A., Menken, S.
- B. J., Najafzadeh, M. J., Crous, P. W., Cornely, O., Hamprecht, A., Vehreschild, M. J. G. T.,
- 485 Kindo, A. J., & de Hoog, G. S. (2016). Chaetomium-like fungi causing opportunistic infections
- 486 in humans: a possible role for extremotolerance. *Fungal Diversity*, 76, 11-26.
 487 <u>https://doi.org/10.1007/s13225-015-0338-5</u>
- Alsammar, H., & Delneri, D. (2020). An update on the diversity, ecology and biogeography of the
 Saccharomyces genus. FEMS Yeast Research, 20, 1-12. <u>https://doi.org/10.1093/femsyr/foaa013</u>
- 490 Altaf, M. M., Imran, M., Abulreesh, H. H., Khan, M. S. S., & Ahmad, I. (2018). Diversity and
- 491 applications of *Penicillium* in plant-growth promotion. In V. K. Gupta, & S. Rodriguez-Couto
- (Eds.), New and Future Developments in Microbial Biotechnology and Bioengineering:
 Penicillium system properties and applications (pp. 261-276). Elsevier.
 http://dx.doi.org/10.1016/B978-0-444-63501-3.00015-6
- Amend, A. (2014). From Dandruff to Deep-Sea Vents: *Malassezia*-like fungi are ecologically hyper diverse. *PloS Pathogens*, *10*. <u>https://doi.org/10.1371/journal.ppat.1004277</u>
- 497 Andriamananjara, A., Hewson, J., Razakamanarivoa, H., Andrisoa, R. H., Ranaivosona, N.,
- 498 Ramboatiana, N., Razafindrakoto, M., Ramifehiarivo, N., Razafimanantsoa, M. -P., Rabeharisoa,
- 499 L., Ramananantoandro, T., Rasolohery, A., Rabetokotany, N., & Razafimbelo, T. (2020). Land
- 500 cover impacts on aboveground and soil carbon stocks in Malagasy rainforest. *Agriculture*,
- 501 *Ecosystem & Environment*, 233, 1-15. <u>http://dx.doi.org/10.1016/j.agee.2016.08.030</u>
- 502 Arévalo-Gardini, E., Canto, M., Alegre, J., Arévalo-Hernández, C. O., Loli, O., Julca, A., Baligar, V.
- 503 (2020). Cacao agroforestry management systems effects on soil fungi diversity in the Peruvian
- 504 Amazon. Ecological Indicators, 115, 106404. <u>https://doi.org/10.1016/j.ecolind.2020.106404</u>
- 505 Arumugam, N., Boobalan, T., Saravanan, S., Jothi Basu, M., Arun, A., Suganya Devi, T., Kavitha,
- 506 T. (2020). In *silico* and in *vitro* comparison of nicotinamide adenine dinucleotide phosphate

- 507 dependent xylose reductase rossmaan fold in *Debaryomycetaceae* yeast family. *Biocatalysis and*
- 508 *Agricultural Biotechnology*, 24, 101508. <u>https://doi.org/10.1016/j.bcab.2020.101508</u>
- 509 Barraclough, A. D., Olsson, P. A. (2018). Slash-and-burn practices decrease arbuscular mycorrhizal
- 510 fungi abundance in soil and the roots of *Didierea madagascariensis* in the dry tropical forest of
- 511 Madagascar. *Fire*, *1(3)*, 37. <u>https://doi.org/10.3390/fire1030037</u>
- Bensch, K., Braun, U., Groenewald, J. Z., Crous, P. W. (2012). The genus *Cladosporium. Studies in Mycology*, 72, 1-401. https://doi.org/10.3114/sim0003
- 514 Bogale, M., Orr, M. -J., O'Hara, M. J., Untereiner, W. A., 2010. Systematics of Catenulifera
- 515 (anamorphic *Hyaloscyphaceae*) with an assessment of the phylogenetic position of *Phialophora*
- 516 *hyaline. Fungal Biology*, 114, 369-409. <u>https://doi.org/10.1016/j.funbio.2010.02.006</u>
- 517 Bolyen, E., Rideout, J. R., Dillon, M. R., Bokulich, N. A., Abnet, C., Al-Ghalith, G. A., Alexander,
- 518 H., Alm, E. J., Arumugam, M., Asnicar, F., Bai, Y., Bisanz, J. E., Bittinger, K., Brejnrod, A.,
- 519 Brislawn, C. J., Brown, C. T., Callahan, B. J., Caraballo-Rodríguez, A. M., Chase, J., Cope, E.
- 520 K., Da Silva, R., Diener, C., Dorrestein, P. C., Douglas, G. M., Durall, D. M., Duvallet, C.,
- 521 Edwardson, C. F., Ernst, M., Estaki, M., Fouquier, J., Gauglitz, J. M., Gibbons, S. M., Gibson,
- 522 D. L., Gonzalez, A., Gorlick, K., Guo, J., Hillmann, B., Holmes, S., Holste, H., Huttenhower, C.,
- 523 Huttley, G. A., Janssen, S., Jarmusch, A. K., Jiang, L., Kaehler, B. D., Kang, K. B., Keefe, C. R.,
- 524 Keim, P., Kelley, S. T., Knights, D., Koester, I., Kosciolek, T., Kreps, J., Langille, M. G. I., Lee,
- 525 J., Ley, R., Liu, Y. -X., Loftfield, E., Lozupone, C., Maher, M., Marotz, C., Martin, B. D.,
- 526 McDonald, D., McIver, L. J., Melnik, A. V., Metcalf, J. L., Morgan, S. C., Morton, J. T., Naimey,
- 527 A. T., Navas-Molina, J. A., Nothias, L. F., Orchanian, S. B., Pearson, T., Peoples, S. L., Petras,
- 528 D., Preuss, M. L., Pruesse, E., Rasmussen, L. B., Rivers, A., Robeson, M. S., Rosenthal, P.,
- 529 Segata, N., Shaffer, M., Shiffer, A., Sinha, R., Song, S. J., Spear, J. R., Swafford, A. D.,
- 530 Thompson, L. R., Torres, P. J., Trinh, P., Tripathi, A., Turnbaugh, P. J., Ul-Hasan, S., van der
- Hooft, J. J. J., Vargas, F., Vázquez-Baeza, Y., Vogtmann, E., von Hippel, M., Walters, W., Wan,
- 532 Y., Wang, M., Warren, J., Weber, K. C., Williamson, C. H. D., Willis, A. D., Xu, Z. Z., Zaneveld,

- J. R., Zhang, Y., Zhu, Q., Knight, R., & Caporaso, J. G. (2019). Reproducible, interactive,
 scalable and extensible microbiome data science using QIIME 2. *Nature Biotechnology*, *37*, 852857. <u>https://doi.org/10.1038/s41587-019-0209-9</u>
- Bozoudi, D., & Tsaltas, D. (2018). The multiple and versatile roles of *Aureobasidium pullulans* in
 the vitivinicultural sector. *Fermentation*, 4(4), 85. https://doi.org/10.3390/fermentation4040085
- 538 Bremmer, J. M. (1996). Nitrogen total. In D. Sparks, A. Page, P. Helmke, R. Loeppert, P. N.
- 539 Soltanpour, M. A. Tabatabai, C. T. Johnston, & M. E. Sumner (Eds.), Methods of soil analysis,
- 540 Part 3. Chemical Methods SSSA Book Series No 5 (pp. 1085-1121). SSSA and ASA, Madison,

541 WI. <u>https://doi.org/10.2136/sssabookser5.3.c37</u>

- Brindley, G.W., & Brown, G. (1980). Crystal structures of clay minerals and their X-ray
 identification. *Mineralogic Society Monograph No. 5*. Mineral. Soc. of Great Britain and Ireland,
 London. https://doi.org/10.1180/mono-5
- 545 Callahan, B. J., McMurdie, P. J., Rosen, M. J., Han, A. W., Johnson, A. J. A., & Holmes, S. P. (2016).
- 546 DADA2: High-resolution sample inference from Illumina amplicon data. *Nature Methods*, 13,

547 581–583. <u>https://doi.org/10.1038/nmeth.3869</u>

- 548 Chamnipa, N., Thanonkeo, S., Klanrit, P., & Thanonkeo, P. (2018). The potential of the newly
- isolated thermotolerant yeast *Pichia kudriavzevii* RZ8-1 for high-temperature ethanol production.
- 550 *Brazilian Journal of Microbiology*, *49*, 378-391. <u>https://doi.org/10.1016/j.bjm.2017.09.002</u>
- 551 Chaúque, F. R., Cordani, U. G., & Jamal, D. L. (2019). Geochronological systematics for the
- 552 Chimoio-Macossa frontal nappe in central Mozambique: Implications for the tectonic evolution of
- the southern part of the Mozambique belt. Journal of African Earth Sciences, 150, 47-67.
- 554 https://doi.org/10.1016/j.jafrearsci.2018.10.013
- 555 Cheshire, M. V., Christensen, B. T., & Sorensen, L. H. (1990). Labelled and native sugars in particle-
- size fractions from soils incubated with ¹⁴C straw for 6 to 18 years. *European Journal of Soil*
- 557 *Science*, *41*, 29-39. <u>https://doi.org/10.1111/j.1365-2389.1990.tb00042.x</u>

- Chen, L., Xiang, W., Wu, H., Ouyang, S., Zhou, B., Zeng, Y., Chen, Y., & Kuzyakov, Y. (2019).
 Tree species identity surpasses richness in affecting soil microbial richness and community
 composition in subtropical forests. *Soil Biology and Biochemistry*, *130*, 113-121.
 <u>https://doi.org/10.1016/j.soilbio.2018.12.008</u>
- Chovanova, K., & Zámocký, M. (2016). Detection of the antibacterial effect of *Chaetomium cochliodes* Palliser CCM F-232 based on agar plugs and unprocessed fungal substances from
 cultivation media. *Biologia*, 71, 1204–1211. https://doi:10.1515/biolog-2016-0153
- 565 Chowdhury, F. I., Barua, I., Chowdhury, A. I., Resco de Dios, V., & Alam, M. S. (2020). Agroforestry
- shows higher potential than reforestation for soil restoration after slash-and-burn: a case study
- 567 from Bangladesh. Geology, Ecology, and Landscape, 6(1), 48-54.
 568 <u>https://doi.org/10.1080/24749508.2020.1743528</u>
- 569 Climate-data (2019). Retrieved from <u>https://en.climate-data.org/</u>.
- 570 Clocchiatti, A., Hannula, S. E., van den Berg, M., & Korthals, G. (2020). The hidden potential of
- 571 saprotrophic fungi in arable soil: Patterns of short-term stimulation by organic amendments.
- 572 *Applied Soil Ecology*, *147*, 103434. <u>https://doi.org/10.1016/j.apsoil.2019.103434</u>
- 573 Curtis, P. G., Slay, C. M., Harris, N. L., Tyukavina, A., & Hansen, M. C. (2018). Classifying drivers
 574 of global forest loss. *Science*, *361*, 1108-1111. https://doi.org/10.1126/science.aau3445
- 575 Das, S., Singh, S., Verma, J. P., & Mukherjee, A. (2021). Chapter 14 Fungi: A potential candidate
- for sustainable agriculture and agroecosystem. In V. Jay Prakash, C. Macdonald, V. Gupta, & A.
- 577 Appa Podile (Eds.), New and Future Developments in Microbial Biotechnology and
- 578 *Bioengineering* (pp. 159-164). Elsevier. <u>https://doi.org/810.1016/B978-0-444-64325-4.00014-6</u>
- 579 Deaver, N. R., Hesse, C., Kuske, C. R., & Porras-Alfaro, A. (2019). Presence and distribution of
 580 insect-associated and entomopathogenic fungi in a temperate pine forest soil: An integrated
- 581 approach. *Fungal Biology*, *123*, 864-874. <u>https://doi.org/10.1016/j.funbio.2019.09.006</u>

- Deveautour, C., Donn, S., Power, S. A., Bennett, A. E., & Powell, J. R. (2018). Experimentally altered
 rainfall regimes and host root traits affect grassland arbuscular mycorrhizal fungal communities.
 Molecular Ecology, 27, 2152-2163. https://doi.org/10.1111/mec.14536
- Diao, Y. Z., Chen, Q., Jiang, X. Z., Houbraken, J., Barbosa, R. N., Cai, L., & Wu, W. P. (2019). *Penicillium* section *Lanata-divaricata* from acidic soil. *Cladistics*, *35*, 514-249.
 https://doi.org/10.1111/cla.12365
- Dixon, J. B, & Schulze, S. G. (Eds.), 2002. Soil Mineralogy with Environmental Applications Num.
 7. In *Soil Science Society of America Book Series*. Soil Sci. Soc. Am. Inc., Madison, Wisconsin,
 USA.
- 591 Efthymiou, A., Grønlund, M., Müller-Stöver, D. S., & Jakobsen, I. (2018a). Augmentation of the
- 592 phosphorus fertilizer value of biochar by inoculation of wheat with selected *Penicillium* strains.
- 593 *Soil Biology and Biochemistry*, *116*, 139-147. <u>https://doi.org/10.1016/j.soilbio.2017.10.006</u>
- 594 Efthymiou, A., Jensen, B., & Jakobsen, I. (2018b). The roles of mycorrhiza and Penicillium
- inoculants in phosphorus uptake by biochar-amended wheat. *Soil Biology and Biochemistry*, 127,
- 596 168-177. <u>https://doi.org/10.1016/j.soilbio.2018.09.027</u>
- Frac, M., Hannula, S. E., Belka, M., & Jędryczka, M. (2018). Fungal biodiversity and their role in
 soil health. *Frontiers in Microbiology*, *9*, 1-19. https://doi.org/10.3389/fmicb.2018.00707
- 599 Gay-des-Combes, J. M., Sanz Carrillo, C., Jozef, B., Robroek, M., Jassey, V. E. J., Mills, R. T. E.,
- Arif, M. S., Falquet, L., Frossard, E., & Buttler, A. (2017). Tropical soils degraded by slash-and-
- burn cultivation can be recultivated when amended with ashes and compost. *Ecology and*
- 602 Evolution, 7, 5378-5388. <u>https://doi.org/10.1002/ece3.3104</u>
- Giraldo, A., & Crous, P. W. (2019). Inside *Plectosphaerellaceae*. *Studies in Mycology*, *92*, 227-286.
 https://doi.org/10.1016/j.simyco.2018.10.005
- Gizaw, B., Tsegay, Z., Tefera, G., Aynalem, E., Wassie, M., & Abatneh, E. (2017). Phosphate
- solubilizing fungi isolated and characterized from Teff rhizosphere soil collected from North

- 607 Showa zone, Ethiopia. *African Journal of Microbiology Research*, 11, 687-696.
 608 https://doi.org/10.5897/AJMR2017.8525
- 609 Gonçalves Lintemani, M., Loss, A., Sepulveda Mendes, C., & Fantini, A. C. (2019). Long fallows
- allow soil regeneration in slash-and-burn agriculture. *Journal of the Science of Food and*
- 611 *Agriculture*, *100*, 1142-1154. <u>https://doi.org/10.1002/jsfa.10123</u>
- 612 Goncharov, A., Glebova, A. A., & Tiunov, A. V. (2020). Trophic interactions between Fusarium
- species and soil fauna: A meta-analysis of experimental studies. *Applied Soil Ecology*, 145,
 103302. https://doi.org/10.1016/j.apsoil.2019.06.005
- Graystone, S. J., & Campbell, C. D., 1996. Functional biodiversity of microbial community in the
 rhizospheres of hybrid larch (*Larix europeis*) and Sitka spruce (*Picea sitchensis*). *Tree*
- 617 *Physiology*, *16*, 1031-1038. <u>https://doi.org/10.1093/treephys/16.11-12.1031</u>
- Habtewold, J. Z., Helgason, B. L., Yanni, S. F., Janzen, H., Ellert, B. H., & Gregorich, E. G. (2020).
- Litter composition has stronger influence on the structure of soil fungal than bacterial communities. *European Journal of Soil Biology*, 98, 103190. <u>https://doi.org/10.1016/j.ejsobi.2020.103190</u>
- Hamayun, M., Khan, S. A., Khan, A. L., Tang, D. -S., Hussain, J., Ahmad, B., Anwar, Y., & Lee, I.
- -J. (2010). Growth promotion of cucumber by pure cultures of gibberellin-producing *Phoma* sp.
- 624 GAH7. World Journal of Microbiology and Biotechnology, 26, 889-894.
 625 https://doi.org/10.1007/s11274-009-0248-3
- Hosoya, T. (2002). *Hyaloscyphaceae* in Japan (6)**: the genus *Hyphodiscus* in Japan and its
 anamorph *Catenulifera* gen. nov. *Mycoscience*, 43, 47-57.
 https://doi.org/10.1007/s102670200008
- Hui, F., Ren, Y., Chen, L., Li, Y., Zhang, L., & Niu, Q. (2014). Molecular phylogenetic analysis
- 630 reveals the new genus *Hemisphaericaspora* of the family Debaryomycetaceae. *PLoS ONE*, 9,
- 631 e103737. <u>https://doi:10.1371/journal.pone.0103737</u>

- Ji, S., Liu, Z., Liu, B., Wang, Y., Wang, J. (2020). The effect of *Trichoderma* biofertilizer on the
 quality of flowering Chinese cabbage and the soil environment. *Scientia Horticulturae*, *262*,
 109069. <u>https://doi.org/10.1016/j.scienta.2019.109069</u>
- Jumpponen, A., Jones, K. L., Blair, B. (2010). Vertical distribution of fungal communities in tallgrass
 prairie soil. *Mycologia*, 102, 1027-1041. <u>https://doi.org/10.3852/09-316</u>
- 637 Khan, A. L., Al-Harrasi, A., Al-Rawahi, A., Al-Farsi, Z., Al-Mamari, A., Waqas, M., Asaf, S.,
- Elyassi, A., Mabood, F., Shin, J. H., & Lee, I. J. (2016). Endophytic fungi from frankincense tree
- 639 improves host growth and produces extracellular enzymes and indole acetic acid. *PLoS ONE*, 11,
- 640 1-19. <u>https://doi.org/10.1371/journal.pone.0158207</u>
- 641 Khan, S. A., Hamayun, M., Khan, A. L., Lee, I. -J., Shinawari, Z. K., & Kom, J. -G. (2012). Isolation
- of plant growth promoting endophytic fungi from dicots inhabiting coastal sand dunes of Korea. *Pakistan Journal Botany*, *44*, 1453-1460.
- 644 Kim, J. S., Baek, J. H., Park, N. -H., & Kim, C. (2016). Complete genome sequence of halophilic
- 645 yeast *Meyerozyma caribbica* MG20W isolated from rhizosphere soil. *Genome Announcement*, 3,
- 646 e00127-15. <u>https://doi:10.1128/genomeA.00127-15</u>
- 647 Kumla, J., Nundaeng, S., Suwannarach, N., & Lumyong, S. (2020). Evaluation of multifarious plant
- growth promoting trials of yeast isolated from the soil of assam tea (*Camellia sinensis* var.
- assamica) plantations in Northern Thailand. *Microorganisms*, 8, 1-18.
 https://doi.org/10.3390/microorganisms8081168
- Lavkulich, L. M., & Wiens, J. H. (1970). Comparison of organic matter destruction by hydrogen
 peroxide and sodium hypochlorite and its effect on selected mineral constituents. *Soil Science Society of America Journal*, 34, 755-758.
- 654 <u>https://doi.org/10.2136/sssaj1970.03615995003400050025x</u>
- Leguina, A. C. del V., Barrios, A. C., del M. Rosales Soro, M., Lacosegliaz, M. J., Pajot, H. F.,
 Castellanos de Figueroa, L. I., & Nieto-Peñalver, C. G. (2019). Copper alters the physiology of

- tomato rhizospheric isolates of *Papiliotrema laurentii*. Scientia Horticulturae, 243, 376-384.
 https://doi.org/10.1016/j.scienta.2018.08.057
- 659 Lemmens, M., Buerstmayr, H., Krska, R., Schuhmacher, R., Grausgruber, H., & Ruckenbauer, P.
- 660 (2004). The effect of inoculation treatment and long-term application of moisture on *Fusarium*
- head blight symptoms and deoxynivalenol contamination in wheat grains. *European Journal of*
- 662 *Plant Pathology*, *110*, 299-308. <u>https://doi.org/10.1023/B:EJPP.0000019801.89902.2a</u>
- Li, X., Wang, J., Zhang, S., Wang, H., Li, X., Li, X., & Zhang, H. (2018). Distribution of fungal
 endophytes in roots of *Stipa krylovii* across six vegetation types in grassland of northern China. *Fungal Ecology*, *31*, 47-53. <u>https://doi.org/10.1016/j.funeco.2017.11.001</u>
- Limtong, S., Srisuk, N., Yongmanitchai, W., Yurimoto, H., & Nakase, T. (2008). *Ogataea chonburiensis* sp. nov. and *Ogataea nakhonphanomensis* sp. nov., thermotolerant,
 methylotrophic yeast species isolated in Thailand, and transfer of *Pichia siamensis* and *Pichia thermomethanolica* to the genus *Ogataea*. Int. J. Syst. Evol. Microb. 58, 302-307.
 https://doi.org/10.1099/ijs.0.65380-0
- Lueders, T., Kindler, R., Miltner, A., Friedrich, M. W., & Kaestner, M. (2006). Identification of
 bacterial micropredators distinctively active in a soil microbial food web. *Applied and Environmental Microbiology*, 72, 5342-5348. https://doi.org/10.1128/AEM.00400-06
- Machinet, G. E., Bertrand, I., Chabbert, B., & Recous, S. (2009). Decomposition in soil and chemical
 change of maize roots with genetic variations affecting cell wall quality. *European Journal of*
- 676 Soil Science, 60, 176-185. <u>https://doi.org/10.1111/j.1365-2389.2008.01109.x</u>
- 677 Makhuvele, R., Ncube, I., Jansen van Rensburg, E. L., & La Grange, D. C. (2017). Isolation of fungi
- from dung of wild herbivores for application in bioethanol production. *Brazilian Journal of Microbiology*, 48, 648-655. <u>https://doi.org/10.1016/j.bjm.2016.11.013</u>
- Maria, R. M., & Yost, R. (2006). A survey of soil fertility status of four agroecological zones of
 Mozambique. Soil Science, 171(11), 902-914.
- 682 https://doi.org/10.1097/01.ss.0000228058.38581.de

- Meloun, M., Sáňka, M., Němec, P., Křítková, S., & Kupka, K. (2005). The analysis of soil cores
 polluted with certain metals using the Box-Cox transformation. *Environmental Pollution*, *137*,
 273–280. https://doi.org/10.1016/j.envpol.2005.01.027
- 686 Mertz, O., Leisz, S. J., Heinimann, A., Rerkasem, K., Dressler, T., Dressler, W., Pham, V. C., Vu, K.
- 687 C., Schmidt-Vogt, D., Colfer, C. J. P., Epprecht, M., Padoch, C., & Potter, L. (2009). Who
- counts? Demography of swidden cultivators in Southeast Asia. *Human Ecology*, *37*, 281–289.
 https://doi.org/10.1007/s10745-009-9249-y
- 690 Mohammed, A., Kadhim, J. H., & Hasan, A. M. (2019). Laboratory evaluation of entomopathogenic
- fungi for the control of khapra beetle (*Coleoptera dermestidae*) and their effects on the beetles'
- fecundity and longevity. Journal of Agriculture and Urban Entomology, 35, 1–12.
 https://doi:10.3954/1523-5475-35.1.1
- Mota-Gutierrez, J., Ferrocino, I., Rantsiou, K., & Cocolin, L. (2019). Metataxonomic comparison
 between internal transcribed spacer and 26S ribosomal large subunit (LSU) rDNA gene.
 International Journal of Food Microbiology, 290, 132-140.
 https://doi.org/10.1016/j.ijfoodmicro.2018.10.010
- Mueller, R. C., Balasch, M., & Kuske, C. R. (2014). Contrasting soil fungal community responses to
 experimental nitrogen addition using the large subunit rRNA taxonomic marker and
 cellobiohydrolase I functional marker. *Molecular Ecology*, 23, 4406-4417.
 https://doi.org/10.1111/mec.12858
- Nakayan, P., Shen, F. -T., Hung, M. -H., & Youn, C. -C. (2009). Effectiveness of *Pichia* sp. CC1 in
 decreasing chemical fertilization requirements of garden lettuce in pot experiments. *Asian Journal of Food and Agro-Industry*, Special Issue, S66-S68.
- Nath, T. K., Jashimuddin, M., Hasan, Md. K., Shahjahan, Md., & Pretty, J. (2016). The sustainable
 intensification of agroforestry in shifting cultivation areas of Bangladesh. *Agroforestry Systems*,
- 707 90, 405-416. <u>https://doi.org/10.1007/s10457-015-9863-1</u>

- Nelson, D. W., & Sommers, L. E. (1996). Total Carbon, Organic Carbon, and Organic Matter. In D.
- L. Sparks, A. Page, P. Helmke, R. Loeppert, P. N. Soltanpour, M. A. Tabatabai, C. T. Johnston,
- 710 & M. E. Sumner (Eds.), Methods of Soil Analysis. Part 3. Chemical Methods, SSSA Book Series
- 711 *No.* 5 (pp. 961-1010). SSSA and ASA, Madison, WI.
- Nguyen, N. H., Song, Z., Bates, S. T., Branco, S., Tedersoo, L., Menke, J., Schilling, J. S., &
 Kennedy, P. G. (2016). FUNGuild: An open annotation tool for parsing fungal community
 datasets by ecological guild. *Fungal Ecology*, 20, 241-248.
 <u>https://doi.org/10.1016/j.funeco.2015.06.006</u>
- 716 Oehl, F., Laczko, E., Oberholzer, H. R., Jansa, J., & Egli, S. (2017). Diversity and biogeography of
- arbuscular mycorrhizal fungi in agricultural soils. *Biological Fertility of Soils*, 53, 777-797.
- 718 <u>https://doi.org/10.1007/s00374-017-1217-x</u>
- Olsen, S. R., Cole, C. V., Watanabe, F. S, & Dean, L. A. (1954). Estimation of available phosphorus
 in soils by extraction with sodium bicarbonate. *USDA circular 939*. U.S. Gov. Print. Office,
 Washington, D.C.
- 722 Oskiera, M., Szczech, M., Stępowska, A., Smolińska, U., Bartoszewski, G. (2017). Monitoring of
- 723 Trichoderma species in agricultural soil in response to application of biopreparations. *Biological*
- 724 *Control*, *113*, 65-72. <u>https://doi.org/10.1016/j.biocontrol.2017.07.005</u>
- Paula, F. S., Tatti, E., Thorn, C., Abram, F., Wilson, J., O'Flaherty, V. (2020). Soil prokaryotic
- community resilience, fungal colonisation and increased cross-domain co-occurrence in response
- to a plant-growth enhancing organic amendment. Soil Biology and Biochemistry, 149, 107937.
- 728 <u>https://doi.org/10.1016/j.soilbio.2020.107937</u>
- Pongcharoen, P., Chawneua, J., & Tawong, W. (2018). High temperature alcoholic fermentation by
- new thermotolerant yeast strains *Pichia kudriavzevii* isolated from sugarcane field soil.
- 731 *Agricultural and Natural Research*, *52*, 511-518. <u>https://doi.org/10.1016/j.anres.2018.11.017</u>
- 732 Procópio, L., & Barreto, C. (2021). The soil microbiomes of the Brazilian Cerrado. Journal of Soils
- 733 and Sediments, 21, 2327–2342. https://doi.org/10.1007/s11368-021-02936-9

Rafael, R. B. A., Fernández-Marcos, M. L., Cocco, S., Ruello, M. L., Weindorf, D. C., Cardelli, V.,
& Corti, G. (2018). Assessment of potential nutrient release from phosphate rock and dolostone
for application in acid soils. *Pedosphere*, *28*, 44-58. <u>https://doi:10.1016/S1002-0160(17)60437-</u>
<u>5</u>

Randriamalala, J. R., Randriarimalala, J., Hervé, D., & Carrière, S. M. (2019). Slow recovery of
 endangered xerophytic thickets vegetation after slash-and-burn cultivation in Madagascar.
 Biological Conservation, 233, 260-267. https://doi.org/10.1016/j.biocon.2019.03.006

741 Rożek, K., Rola, K., Błaszkowski, J., Leski, T., & Zubek, S. (2020). How do monocultures of fourteen

742forest tree species affect arbuscular mycorrhizal fungi abundance and species richness and743composition in soil?. Forest Ecology and Management, 465, 18091.

- 744 <u>https://doi.org/10.1016/j.foreco.2020.118091</u>
- 745 Saliou Sarr, P., Sugiyama, A., Boyogueno Begoude, A. D., Yazakia, K., Araki, S., & Nawata, E.

746 (2019). Diversity and distribution of Arbuscular Mycorrhizal Fungi in cassava (Manihot

esculenta Crantz) croplands in Cameroon as revealed by Illumina MiSeq. *Rhizosphere*, *10*, 100-

748 147. <u>https://doi.org/10.1016/j.rhisph.2019.100147</u>

- 749 Sandoval-Denis, M., Guarro, J., Cano-Lira, J. F., Sutton, D. A., Wiederhold, N. P., de Hoog, G. S.,
- Abbott, S. P., Decock, C., Sigler, L., & Gené, J. (2016). Phylogeny and taxonomic revision of

Microascaceae with emphasis on synnematous fungi. *Studies in Mycology*, *83*, 193-233.
 https://doi.org/10.1016/j.simyco.2016.07.002

753 Sannino, C., Borruso, L., Smiraglia, C., Bani, A., Mezzasoma, A., Brusetti, L., Turchetti, B., &

- Buzzini, P. (2020). Dynamics of *in situ* growth and taxonomic structure of fungal communities
 in Alpine supraglacial debris. *Fungal Ecology*, 44, 100891.
 https://doi.org/10.1016/j.funeco.2019.100891
- 757 Saravanakumar, K., Shanmuga Arasu, V., & Kathiresan, K. (2013). Effect of Trichoderma on soil
- phosphate solubilization and growth improvement of *Avicennia marina*. Aquatic Botany, 104,
- 759 101-105. <u>https://doi.org/10.1016/j.aquabot.2012.09.001</u>

- Schoeneberger, P. J., Wysocki, D. A., Benham, E. C., & Soil Survey Staff (2012). Field book for
 describing and sampling soils Version 3.0. Natural Resources Conservation Service, National
 Soil Survey Center, Lincoln, NE.
- 763 Serrani, D., Ferrocino, I., Garofalo, C., Osimani, A., Corvaglia, M. R., Milanović, V., Aquilanti, L.,
- Cocco, S., Cardelli, V., Alves Rafael, R. B., Franciosi, E., Tuohy, K., Clementi, F., & Corti, G.
- 765 (2023). Soil bacteria communities under slash and burn in Mozambique as revealed by
 766 metataxonomic approach. *Pedosphere*, 33, 508-520.
 767 https://doi.org/10.1016/j.pedsph.2022.06.053
- Shah, F., Nicolás, C., Bentzer, J., Ellström, M., Smits, M., Rineau, F., Canbäck, B., Floudas, D.,
- 769 Carleer, R., Lackner, G., Braesel, J., Hoffmeister, D., Henrissat, B., Ahrén, D., Johansson, T.,
- Hibbett, D. S., Martin, F., Persson, P., & Tunlid, A. (2016). Ectomycorrhizal fungi decompose
- soil organic matter using oxidative mechanisms adapted from saprotrophic ancestors. *New Phytologist*, *209*, 1705-1719.
- Sharmah, D., & Jha, D. K. (2014). Diversity of arbuscular mycorrhizal fungi in undisturbed forest,
 slash-and-burn field, and monoculture forest of Indo-Burma megadiverse region. *Brazilian*
- 775 *Journal of Botany*, 37, 339-351. <u>https://doi.org/10.1007/s40415-014-0075-0</u>
- Shi, J., Zhang, T., Geng, S., Liang, F., & Wang, T. (2021). Effect of accumulated temperature on
 flavour and microbial diversity of japonica rice during storage. *Journal of Stored Products Research*, 92, 101779. https://doi.org/10.1016/j.jspr.2021.101779
- Shi, Q., Liu, Y., Shi, A., Cai, Z., Nian, H., Hartmann, M., & Lian, T. (2020). Rhizosphere soil fungal
 communities of aluminum-tolerant and -sensitive soybean genotypes respond differently to
- aluminum stress in an acid soil. *Frontiers in Microbiology*, 11, 1177.
 https://doi:10.3389/fmicb.2020.01177
- 783 Silva-Forsberg, M. C., & Fearnside, P. M. (1997). Brazilian Amazonian caboclo agriculture: effect
- of fallow period on maize yield. Forest Ecology and Management, 97, 283-291.
- 785 <u>https://doi.org/10.1016/S0378-1127(97)00070-4</u>

- Sitoe, A. (2004). Miombo woodlands and HIV/AIDS interactions Mozambique country report
 forestry working paper. Food and Agriculture Organization of the United Nations, Rome, Italy.
- Soil Survey Staff (2014). Keys to Soil Taxonomy, 12th ed. United States Department in Agriculture
 Natural Resources Conservation Service, Washington, DC.
- Soil Survey Staff (2015). Illustrated guide to soil taxonomy, version 2. U.S. Department of
 Agriculture, Natural Resources Conservation Service, National Soil Survey Center, Lincoln,
 Nebraska.
- Soytong, K., Kanokmedhakul, S., Kukongviriyapa, V., & Isobe, M. (2001). Application of
 Chaetomium species (*Ketomium*®) spectrum biological review article fungicide. *Fungal Diversity*, 7, 1-15.
- Spurgeon, D. J., Keith, A. M., Schmidt, O., Lammertsma, D. R., & Faber, J. H. (2013). Land-use and
 land-management change: relationships with earthworm and fungi communities and soil
 structural properties. *BMC Ecology*, *13*, 46. <u>https://doi.org/10.1186/1472-6785-13-46</u>
- Sterflinger, K. (2010). Fungi: Their role in deterioration of cultural heritage. *Fungal Biology Reviews*,
 24, 47-55. <u>https://doi.org/10.1016/j.fbr.2010.03.003</u>
- Sterflinger, K. (1998). Temperature and NaCl- tolerance of rock-inhabiting meristematic fungi.
 Antonie van Leeuwenhoek, Journal of Microbiology, 74, 271–281.
 <u>https://doi.org/10.1023/A:1001753131034</u>
- 804 Suh, S. O., & Zhou, J. (2010). Methylotrophic yeasts near Ogataea (Hansenula) polymorpha: A
- proposal of *Ogataea angusta* comb. nov. and *Candida parapolymorpha* sp. nov. *FEMS Yeast Research*, *10*, 631-638. https://doi.org/10.1111/j.1567-1364.2010.00634.x
- Suzuki, S., Noble, A. D., Ruaysoongnern, S., & Chinabut, N. (2007). Improvement in water-holding
 capacity and structural stability of a sandy soil in Northeast Thailand. Arid Land Res. Manag.
 21(1), 37-49. <u>https://doi.org/10.1080/15324980601087430</u>
- 810 Thomas, G. W. (1996). Soil pH and Soil Acidity. In D. L. Sparks, A. L. Page, P. A. Helmke, R. H.
- Loeppert, P. N. Soltanpour, M. A. Tabatabai, C. T. Johnston, M. E. Sumner (Eds). Methods of

- Soil Analysis. Part 3. Chemical Methods (pp. 475–490). Soil Science Society of America and
 American Society of Agronomy, Madison, WI.
- 814 Thomaz, E. L. (2013). Slash-and-burn agriculture: Establishing scenarios of runoff and soil loss for
- a five-year cycle. Agriculture, Ecosystems & Environment, 168, 1-6.
 https://doi.org/10.1016/j.agee.2013.01.008
- Toju, H., Kishida, O., Katayama, N., & Takagi, K. (2016). Networks depicting the fine-scale cooccurrences of fungi in soil horizons. *PLOS ONE*, *11*, e0165987.
 https://doi.org/10.1371/journal.pone.0165987
- van der Wal, A., Geydan, T. D., Kuyper, T. W., & de Boer, W. (2013). A thready affair: linking
- fungal diversity and community dynamics to terrestrial decomposition processes. *FEMS Microbiological Reviews*, *37*, 477–494. <u>https://doi.org/10.1111/1574-6976.12001</u>
- Vega, F.E. (2018). The use of fungal entomopathogens as endophytes in biological control: a review.
 Mycologia, *110*, 4-30. <u>https://doi.org/10.1080/00275514.2017.1418578</u>
- Volkmann, M., Whitehead, K., Rütters, H., Rullkötter, J., & Gorbushina, A. A. (2003). Mycosporine-
- glutamicol-glucoside: A natural UV-absorbing secondary metabolite of rock-inhabiting
 microcolonial fungi. *Rapid Communications in Mass Spectrometry*, *17*, 897-902.
 https://doi.org/10.1002/rcm.997
- Warcup, J. H. (1951). The ecology of soil fungi. *Transactions of the British Mycological Society*, *34*,
 376-399. <u>https://doi.org/10.1016/S0007-1536(51)80065-2</u>
- Weber, C. F., Vilgalys, R., & Kuske, C. R. (2013). Changes in fungal community composition in
 response to elevated atmospheric CO₂ and nitrogen fertilization varies with soil horizon.
 Frontiers in Microbiology, 4, 1-14. <u>https://doi.org/10.3389/fmicb.2013.00078</u>
- 834 Wijnhoud, J. D. (1997). Solos e outros recursos naturais da Estação Agrária de Sussundenga, vol. 1:
- Relatório. Série da Terra e Água do Instituto Nacional De Investigação Agrónomica,
 comunicação n°93.

- 837 Wood, S. L. R, Rhemtulla, J. M., & Coomes, O. T. (2016). Intensification of tropical fallow-based
- 838 agriculture: Trading-off ecosystem services for economic gain in shifting cultivation landscapes?
- 839
 Agriculture,
 Ecosystem
 and
 Environment,
 215,
 47–56.

 840
 http://dx.doi.org/10.1016/j.agee.2015.09.005
 http://dx.doi.org/10.1016/j.agee.2015.09.005
 http://dx.doi.org/10.1016/j.agee.2015.09.005
- 841 Yadav, M., Singh, A., Balan, V., Pareek, N., & Vivekanand, V. (2019). Biological treatment of
- 842 lignocellulosic biomass by *Chaetomium globosporum*: Process derivation and improved biogas
- production. International Journal of Biological Macromolecules, 128, 176-183.
 https://doi.org/10.1016/j.ijbiomac.2019.01.118
- 845 Yang, H., Yuan, Y., Zhang, Q., Tang, J., Liu, Y., & Chen, X. (2011). Changes in soil organic carbon,
- total nitrogen, and abundance of arbuscular mycorrhizal fungi along a large-scale aridity gradient.
- 847 *Catena*, 87, 70-77. <u>https://doi.org/10.1016/j.catena.2011.05.009</u>
- 848 Yehia, R. S., Osman, G. H., Assaggaf, H., Salem, R., & Mohamed, M. S. M. (2020). Isolation of
- 849 potential antimicrobial metabolites from endophytic fungus *Cladosporium cladosporioides* from
- endemic plant Zygophyllum mandavillei. South African Journal of Botany, 134, 296-302.
 https://doi.org/10.1016/j.sajb.2020.02.033
- Zalar, P., Gostinčar, C., de Hoog, G. S., Uršič, V., Sudhadham, M., & Gunde-Cimerman, N. (2008).
- Redefinition of *Aureobasidium pullulans* and its varieties. *Studies in Mycology*, *61*, 21-38.
 https://doi.org/10.3114/sim.2008.61.02
- Zhang, F., Xu, X., Wang, G., Wu, B., & Xiao, Y. (2020a). Medicago sativa and soil microbiome
- responses to *Trichoderma* as a biofertilizer in alkaline-saline soils. *Applied Soil Ecology*, 153,
- 857 103573. <u>https://doi.org/10.1016/j.apsoil.2020.103573</u>
- 858 Zhang, K. H., Shi, C. F., Chai, C. Y., & Hui, F. L. (2020b). Mrakia panshiensis sp. nov. A new
- 859 member of the *Cystofilobasidiales* from soil in China, and description of the teleomorphic-stage
- 860 of *M. Arctica. MycoKeys*, 74, 75-90. <u>https://doi.org/10.3897/mycokeys.74.53433</u>

- Zhang, Y., Hao, X., Alexander, T. W., Thomas, B. W., Shi, X., & Lupwayi, N. Z. (2018). Long-term
 and legacy effects of manure application on soil microbial community composition. *Biology and Fertility of Soils*, 54, 269-283. <u>https://doi.org/10.1007/s00374-017-1257-2</u>
- 864 Zhou, J., Jiang, X., Zhou, B., Zhao, B., Ma, M., Guan, D., Li, J., Sanfeng, C., Cao, F., Shen, D., &
- Jie, Q. (2016). Thirty-four years of nitrogen fertilization decreases fungal diversity and alters
- fungal community composition in black soil in northeast China. *Soil Biology and Biochemistry*,
- 867 95, 135-143. <u>https://doi.org/10.1016/j.soilbio.2015.12.012</u>
- 868 Zwartendijk, B. W., van Meerveld, H. J., Ghimire, C. P., Ravelona, M., Lahitiana, J., Bruijnzeel, L.
- A. (2020). Soil water- and overland flow dynamics in a tropical catchment subject to long-term
- 870 slash-and-burn agriculture. *Journal of Hydrology*, 582, 124287.
 871 <u>https://doi.org/10.1016/j.jhydrol.2019.124287</u>

873 Figure captions

874

- Fig. 1. Average-linkage clustering of soil samples based on fungal ASVs' relative abundance at the
 highest taxonomical rank for locations, land use, and the A and Bo horizons. Manica province,
 central Mozambique. The color scale represents the ASVs' abundance, denoted as the Z-score,
 with brown indicating high abundance and blue indicating low abundance.
- Fig. 2. Boxplots showing the differentially abundant fungal ASVs in the soils from Vanduzi,
 Sussundenga, and Macate. Manica province, central Mozambique. Boxplots with different
 letters significantly differ at FDR≤0.05.
- Fig. 3. Correlation between fungi and soil physicochemical properties in the A and Bo horizons of
 the soils under charcoal kilns, crop fields, and forests at Vanduzi, Sussundenga, and Macate.
 Manica province, central Mozambique.
- Fig. 4. Boxplots showing the differentially abundant fungi ASVs in the soils under charcoal kilns,
 crop fields, and forests. Manica province, central Mozambique. Boxplots with different letters
 significantly differ at FDR≤0.05.
- Fig. 5. Boxplots showing the differentially abundant fungi ASVs between the A and Bo horizons.
 Manica province, central Mozambique. Boxplots with different letters significantly differ at
 FDR≤0.05.