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Fungal community succession and sporocarp production following fire occurrence in Dry Afromontane forests of Ethiopia

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ABSTRACT

Fire is among the main threats to forest ecosystems in Ethiopia and is affecting the forest biodiversity, including fungal communities. This study was aimed to examine the effects of fire on macrofungal taxa richness, diversity and sporocarp production in the Dry Afromontane forests in Ethiopia. Sporocarps were collected from nine plots (100 m^2) established in one- and ten-year-old burned stands, and in an unburned stands. The data were used to quantify fungal richness and sporocarp fresh weights. Morphological and molecular analyses were used to identify the fungi. Composite soil samples were also collected from each stand and used to determine main edaphic explanatory variables for taxa composition. A total of 61 fungal taxa, belonging to *Basidiomycota* division were reported, of which 22 were edible. Fungal diversity, richness and sporocarp production were affected just after the fire. Fungal community composition was significantly correlated with Organic matter, P and Ca. Generally, the result is encouraging from the point of view of fungal conservation. It provides novelty information about the macrofungal communities in Ethiopian dry Afromontane forests, likely including many taxa are still unknown to science as well as several edible species which could supply complementary incomes for the rural populations in the study area.

1. Introduction

The Ethiopian highlands cover more than 44% of the country's land area. Afromontane vegetation originally dominated these highlands, characterized by high-altitude natural forests classified as either Dry or Moist Afromontane forests (Friis et al., 2010). Of these two, the Dry Afromontane forests form the largest part and are distributed mainly in the Central, Northern and Western parts of Ethiopia (Eshete et al., 2011; Friis et al., 2010). The existence of high humidity with a variable rainfall pattern and a prolonged dry season characterize the Dry Afromontane forests making them complex and rich in biodiversity (Wassie et al., 2005). The main tree species found in these forests include *Juniperus procera*, *Podocarpus falcatus*, *Hagenia abyssinica* and *Olea africana*. These tree species serve as the main sources of timber to the country (Kassa et al., 2009). The Dry Afromontane forests also harbor various types of Non-Timber Forest Products (NTFPs) (Shumi, 2009), including edible fungi (Dejene et al., 2017).

Fungi are key components of the forest ecosystems (Lindahl et al., 2007), since they are responsible for the decomposition of organic materials and recycling of nutrients (Ferris et al., 2000). Fungi play a key role in the mobilization, uptake and translocation of nutrients in forest soils. They can also improve plant water uptake and resistance to abiotic stresses; thereby influencing plant diversity, productivity and ecosystem functions (Pietras et al., 2013; Van Der Heijden et al., 2008). In addition to ecological functions, fungi have become a strategic component in the conservation and management of forest systems. This is because of their economic value, as during the last decade, there has been an increasing demand for wild edible fungi (Pettenella et al., 2007), which are becoming an important source of rural income (Boa, 2004). In fact, in some cases forest fungi may generate even higher economic benefits than timber production (Martín-Pinto et al., 2006).

Although reliable data on cover change is scarce, the forest history of Ethiopia indicates that forest land degradation and fragmentation is a continuous process, notably in the Dry Afromontane forests (Wassie et al., 2005). The ever-increasing demand for wood products as well as crop and grazing land expansion, stimulated by rapid population and livestock growth are factors aggravating the degradation of these forests in Ethiopia

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(Lemenih and Bekele, 2008). In addition, fire is also responsible for the loss of forest in the country, affecting the distribution, diversity and composition of forests resources (Lemenih and Bekele, 2008; Wassie et al., 2005). For instance, the most devastating wave of forest fires, which occurred in 2000 due to an extended drought, damaged over 150,000 ha (ha) of forested lands throughout the country (Teketay, 2001). This trend is more pronounced in the Dry Afromontane forests compared to other ecosystems, and has a direct implication on the loss of biological diversity of these forest ecosystems (Lemenih and Bekele, 2008).

As an ecological factor, fire is affecting forest fungal communities (Bastias et al., 2006). Differences in its return interval can modify the composition and diversity of fungi (Buscardo et al., 2010). A change in ecological conditions effects fungal growth and perpetuation depending on the intensity and duration of fire in the forests (Hart et al., 2005). Furthermore, fire produces direct effects on fungal communities by affecting belowground organisms (Buscardo et al., 2012). Thus, the subsequent structure of fungal communities following succession patterns will be affected, mainly driven by the dynamics of post-fire plant communities (Cairney and Bastias, 2007). On the other hand, some fungi might also benefit from fire since they fruit as a result of fire (Hart et al., 2005). Hence, some level of fire in the ecosystem could provide higher abundance of fire-loving fungal species. Also, fungal communities are closely influenced by other biotic and abiotic factors such as soil characteristics. Indeed, fungal species composition in the forest tends to be correlated with edaphic variables (Straatsma et al., 2001), especially saprotrophic fungi which are more dependent upon their respective substrates than mycorrhizal fungi (Reverchon et al., 2010).

A recent review work on the effects of forest fire on fungal association reveal that fungal-fire relations studies were mostly located in temperate and Mediterranean forest ecosystems (Taudière et al., 2017). The tropical forests are yet understudied, and comprehensive studies are recommended to improve understanding of the fungi–fire relationships with current global scale changes. Despite their ecological and economic importance, fungal communities are the most neglected components of Ethiopian forest systems, mainly of the Dry Afromontane forests (Dejene et al., 2017). This poor knowledge is worrying as fungi are highly sensitive towards anthropogenic threats like human induced fire, which are common in the Dry Afromontane forest ecosystems (IBC, 2014). Off course, the influence of fire on the diversity and sporocarp production of fungi remains understudied in the country overall. Thus, a close examination of fungal ecology in relation to fire factor may facilitate the diversity conservation and production of economically important fungal species in our study area.

This pioneering work was designed to provide baseline information about macrofungi assemblage, diversity and sporocarp production in the Dry Afromontane forests which helps to derive benefits through management strategies, and also to supplement the current knowledge about the fungal community in Ethiopia. The specific objectives included; (i) to analyze fungal richness after fire, (ii) to analyze the total and edible sporocarp yields after fire and (iii) to relate taxa composition to explanatory edaphic variables.

2. Material and method

2.1. Study area

The study was conducted at Wondo Genet natural forest area, one of the remnant Dry Afromontane forests, located in Southern Ethiopia. Wondo Genet is found approximately 265 km from Addis Ababa, the capital city of Ethiopia (Fig. 1). It is located at 7°06′–7°07′N latitude and 38°37′–38°42′E longitudes with an altitudinal range between 1600 m and 2580 m above sea level (m.a.s.l.) (Belaynesh, 2002; Fenta, 2014). The climate of the study area is characterized by the Woyna Dega agro-climatic type, and the rainfall pattern is bi-modal, with minor rainfall during spring and the major rain season during summer. The average annual rainfall of the study area is 1210 mm, which peaks in July. The average annual temperature of the study area is 20 °C (Belay, 2016; Fenta, 2014).

The topography is slightly undulating and the soils are young and of volcanic origin, characterized by sandy loam (Eriksson and Stern, 1987) with a pH average value of 5.7 (Eshetu and Högberg, 2000). The soil physical and chemical properties of the study plots are presented in Table 1.

The study area covers about 797 ha of natural forests lands (Ango and Bewket, 2007; Belaynesh, 2002; Fenta, 2014) that are characterized by remnant Dry Afromontane forest patches, home to important fauna and flora. This forest also provides a variety of important ecosystem services that can be expressed in terms of watershed protection and carbon sequestration. *Juniperus procera*, *Albizia gummifera*, *Afrocarpus falcatus*, *Bersama abyssinica*, *Prunus africana*, *Podocarpus falcatus*, *Cordia africana*, *Croton macrostachys* and *Olea africana* tree species mainly characterize the natural forests of our study area (Ango and Bewket, 2007; Belay, 2016). Forest fire is a recurrent phenomenon, occurring yearly in small patches in the natural forest of the study area (Bekele et al., 2013).

We established our study plots in the natural forests in 2015, taking into consideration the similarity of the stands in terms of ecological conditions such as climate, altitude and soil. Information from the Department of Forest Management in Wondo Genet College of Forestry was used to find patches of forest stands with similar fire history. The control stand was patches of forest representative of the original natural forest not affected by fire at least in the last 40 years. Burned stands were patches of forests affected similarly by high fire severity, with canopy and understory burned, and the soil organic layer consumed (Rincón and Pueyo, 2010). Three stands could be clearly differentiated: (1) unburned natural forest stand, hereafter UB stand: no fire occurred previously since the inception of the nearby college of forestry (1976) where it is located, (2) one-year-old burned forest stand, hereafter B-1 stand: mainly characterized by different kind of shrubs species and burned standing trees and logs, (3) ten-year-old burned forest stand, hereafter B-10 stand which resembles the unburned stands in terms of vegetation composition but without reaching the maturity and complexity of the unburned stand. Within each of the selected stands, plots were established systematically about 250 m apart. Differences in fungal diversity and productivity among stands prior to fire were thus unlikely.

2.2. Sporocarps sampling

A total of nine sample plots, three per stand (UB, B-1 and B-10), were established as described in Gassibe et al. (2011) and Hernández-Rodríguez et al. (2013). Each plot covered an area of 100 m^2, with a rectangular shape (2 m × 50 m). All sporocarps found in the plots were fully harvested weekly during the major rainy season in July and August in 2015. Fresh weight measurements were carried out *in situ* and the data are given in kilograms per hectare per year (kg fw/ha/year). Also abundance data of each species was taken from each plot. Sample fruit bodies from each species were taken to the laboratory and dried. Herbaria specimens were used for molecular and microscopic taxa identification. Furthermore, in the field, specimens were photographed and their ecological characteristics were noted in order to assist and facilitate taxa identification processes. This work could be considered as a case

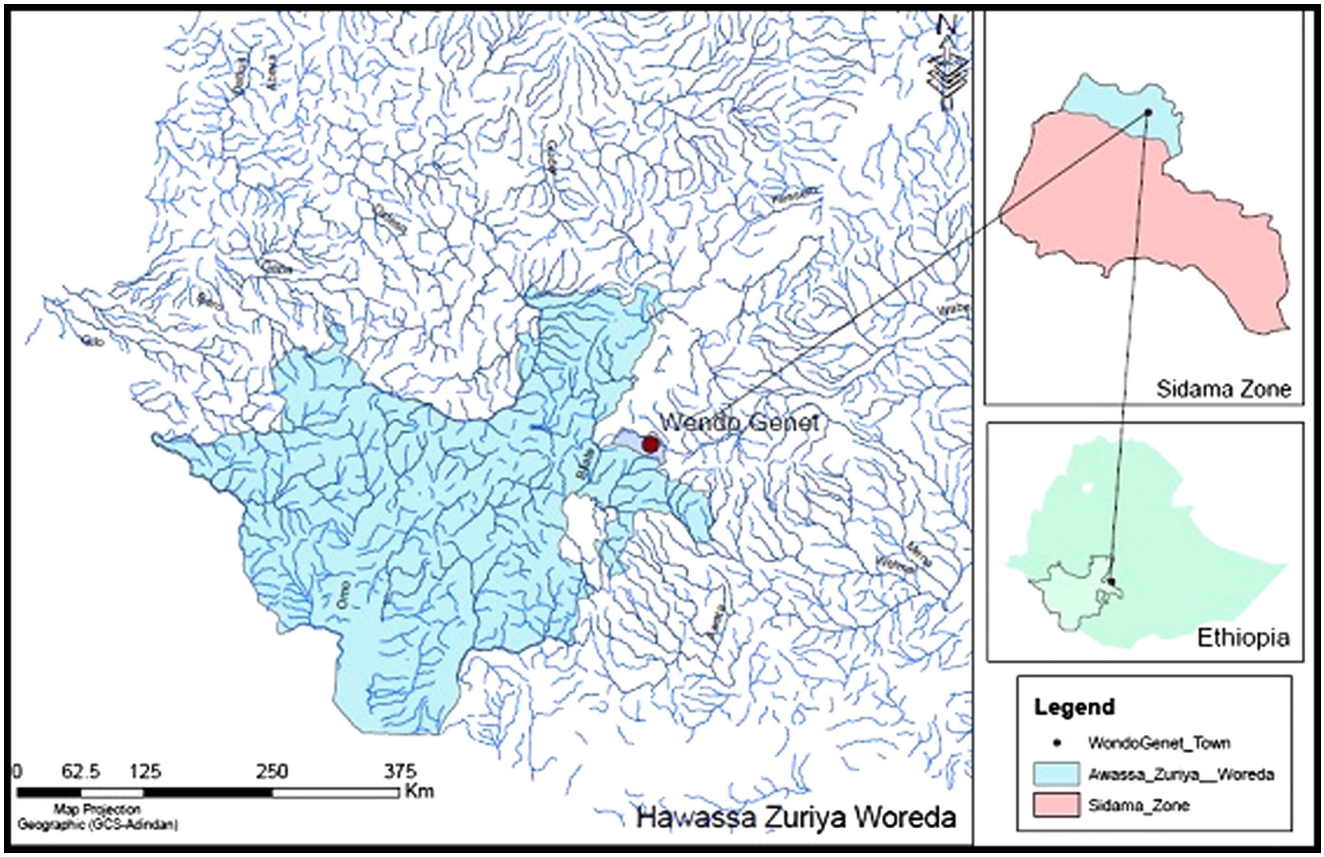

Fig. 1. Location map of the study area, Wondo Genet, Ethiopia.

Table 1
Selected soil properties of the study plots in Dry Afromontane forest of Wondo Genet (Ethiopia).

Soil parameters	Plots		
	B-1	B-10	UB
Na (meg/100 gm soil)	1.00 (0.4)	0.99 (0.1)	0.83 (0.07)
K (meg/100 gm soil)	0.62 (0.35)	0.8 (0.08)	0.55 (0.12)
Ca (meg/100 gm soil)	20.85 (5.18)	24.15 (4.98)	28.43 (13.67)
Mg (meg/100 gm soil)	7.42 (1.42)	8.05 (1.5)	9.77 (5.18)
CEC (meg/100 gm soil)	43.97 (10.9)	42.66 (5.1)	52.44 (14.91)
Om (%)	2.93 (0.36)	5.08 (1.88)	6.05 (1.77)
N (%)	0.40 (0.06)	0.54 (0.11)	0.67 (0.17)
P (mg P_2O_5/kg soil)	28.89 (4.36)	32.59 (5.17)	43.33 (12.72)

Note: Numbers in parenthesis are standard deviation of the mean, B-1: one year old burned stand, B-10: ten year old burned stand, UB: unburned stand, CEC: Cations Exchange Capacity; and Om: organic matter.

study since the plots were established in a single stand for each treatment, and conclusions regarding other stands need to be taken with caution.

2.3. Soil sampling

To relate taxa composition to explanatory edaphic variables, soil samples were taken from each study plot. Composite soil samples, from the center and the four corners of each plot, were taken by clearing plant matter and debris from the surface. The soil was extracted to a depth of 20 cm with the aid of an auger and spade. Then the samples were mixed thoroughly, and approximately 500 g of soil was finally taken in a plastic bag for laboratory analysis. After air drying of the soil in shade, soil chemical properties such as Organic matter (OM), Cation Exchange Capacity, Sodium (Na), Potassium (K), Calcium (Ca), Magnesium (Mg), Nitrogen (N) and Phosphors (P) were determined using the test methods of Diethylen Triamine Penta Acetic acid (DTPA) extraction, KH_2PO_4 extraction, Olsen, Kjeldahl digestion Walklay Black, Ammonium Acetate and instrumental respectively. The analysis was conducted in Ethiopian Water Works Design and Supervision Enterprises, laboratory service subprocess, soil fertility section at Addis Ababa, Ethiopia.

2.4. Taxa identification and classification

Both morphological and molecular analyses were used for taxa identification. Morphological classification was aided by close microscopic examination of tissues and spores with an Optika B-350PL microscope. Small samples of dried specimens were rehydrated and mounted in 5% KOH. The following keys were mainly used for the purpose: Heinemann (1956), Singer (1965), Pegler (1968, 1969, 1977), Morris (1990), Rammeloo and Walleyn (1993), Ryvarden et al. (1994), Antonin (2007) and Hama et al. (2010). Specimens were deposited in the laboratory herbarium at the University of Valladolid. Up-to-date fungal taxa names and authors' names were obtained from Mycobank database (http://mycobank.org).

Molecular identification involved sequencing of the ITS region of the nuclear ribosomal genes (rDNA). For this, fungal DNA was extracted from dry sporocarps using an EZNA® Plant DNA kit (Omega Bio-Tek, USA) according to the manufacturer's instructions. Final elutions were done in a total volume of 100 μl. The internal transcribed spacer (nrITS) was amplified with primers ITS1F (Gardes and Bruns, 1993) and ITS4 (White et al., 1990). For PCR reactions, HotBegan™ Hot Start Taq DNA Polymerase (Canvax

Biotech, Cordoba, Spain) was used following manufacturer's instructions, adding 1 μl of genomic DNA to a final reaction volume of 25 μl. PCR conditions were: 5 min initial denaturation at 94 °C followed by 40 cycles of: 45 s denaturation at 94 °C, primer annealing at 56 °C for 30 s, and extension at 72 °C for 40 s, followed by a final extension step of 10 min at 72 °C. The PCR products were checked on a 2% agarose gel. Sequences were obtained in the laboratories of Macrogen (Amsterdam, Netherlands) using the primer ITS4 as a template.

Taxa edibility classification was accomplished by adapting the criteria used by Bonet et al. (2004). If the taxon is described in the literature as both non-edible and edible, we classified it as a non-edible. If the taxon is described in the literature as having doubtful edibility, we classified it as a non-edible. As edible (E) are classified all species that are listed as such in the large majority of the literature consulted.

2.5. Statistical analysis

Shannon's H′ diversity index (Shannon and Weaver, 1949) was estimated for each plot using the following formula, where p_i indicated the relative abundance of each macrofungal taxa. This index increases with both the number of species and the evenness of their distribution. It usually ranges between 1.5 and 3.5 and rarely exceeds 4.5 (Kent and Coker, 1992).

$$H = -\sum Pi(lnpi)$$

"Richness" (number of taxa), was defined as the total number of species found per plot.

Richness, Shannon index, and Fresh weight (for the edible and total taxa) estimates were subjected to one-way ANOVA analysis and a post hoc least square means difference test (LSD, $P \leq 0.05$) in order to test for differences among stands. Data were log-transformed when needed to achieve the parametric criteria of normality and homoscedasticity that ANOVA requires. All analyses were done with SAS software (SAS Institute Inc., 2012).

An ordination technique based on fungal fresh weight data was used in order to identify significant edaphic explanatory variables related to taxa composition. Firstly, the fresh weight data per taxa were subjected to a detrended correspondence analysis (DCA) (Ter Braak and Prentice, 1988). Since the length of the extracted gradient was less than 3 SD units, a redundancy analysis (RDA) (Ter Braak, 1986) was used to assess the correlation of edaphic variables and fungal taxa composition. Forward selection was used to select significant explanatory variables and only those significant at $P < 0.05$ levels were included in the models. The statistical significance of the Canonical axes was evaluated by Monte Carlo permutation tests (499 permutations). The analysis was conducted using CANOCO for Windows v.4.5 (Ter Braak and Šmilauer, 2002). The RDA result was displayed by ordination diagrams drawn with Cano Draw 4.1 (Ter Braak and Šmilauer, 2002).

3. Results

3.1. Fungal taxa richness and diversity

A total of 61 taxa were collected from the entire study forest area. All of the taxa were saprophytic, belonging to the *Basidiomycota* division (Table 2). No mycorrhizal taxa were found. Out of the total collected taxa, 28 (46%) were identified to species level, 29 (48%) to genus level and 4 (6%) were completely unidentified. The identified taxa were distributed in 13 families and 31 genera (Fig. 2). The families that contained the highest number of species were *Agaricaceae* (20) and *Psathyrellaceae* (12), which all together accounted for 52.5% of the total surveyed taxa (Fig. 2).

Fire had a significant effect on macrofungal taxa richness in the studied stand ($P < 0.0001$). The highest richness value was recorded for the unburned stand. The lowest value was recorded for the forest stand most recently affected by fire (B-1), showing significant differences with the other burned and unburned stands (Fig. 3A; $P < 0.001$). The B-10 and UB stands also showed significant difference in their richness values (Fig. 3A; $P = 0.003$). We also observed some taxa to be exclusive from some specific stands. For example, four taxa were exclusive for B-1, four species were solely found in B-10, and two *Psathyrella* spp. were found exclusively in the UB stand (Table 2).

Shannon's H′ diversity index also showed significant differences between fire affected stands ($P < 0.009$). The lowest Shannon's value was obtained from the stand most recently affected by fire (Fig. 3B). This value was significantly different from that of the ten-year-old burned stand ($P_{B\text{-}1} - P_{B\text{-}10} = 0.008$) and unburned stand ($P_{B\text{-}1} - P_{UB} = 0.005$). However, the B-10 and UB stands showed no significant difference in their Shannon's values (Fig. 3B; $P = 0.059$).

3.2. Sporocarp production

There was no significant difference in total sporocarp production among the three studied stands ($P = 0.214$, Fig. 4). We found an average sporocarp production of 26.16 kg ha^{-1} from the entire area. The lowest average fresh weight production (22.03 kg ha^{-1}) was obtained from the one-year-old burned stand while the highest (35.22 kg ha^{-1}) was from the B-10 stand.

A total of 22 edible taxa were identified (Table 2). The average fresh weight production of edible taxa was significant among the three studied stands (Fig. 4; $P = 0.028$). The highest average production, 7.42 kg ha^{-1}, was from B-10 stand. This value was significantly higher than that of the recently burned stand (B-1) ($P_{B\text{-}10} - P_{B\text{-}1} = 0.011$) but not that of unburned stand ($P_{B\text{-}10} - P_{UB} = 0.061$). The lowest production was collected from B-1 stand, with the average production amount of 3.46 kg ha^{-1} but the value was not significantly different from that of the unburned stand ($P_{B\text{-}1} - P_{UB} = 0.136$).

3.3. Taxa composition

Fungal community assemblies among the three studied stands can be analyzed from the results obtained in the Detrended Correspondence Analysis (DCA) (Table 4). The results are displayed in ordination bi-plots (Fig. 5). Axis-1 separated recently burned stands (B-1) from B-10 and unburned (UB) stands. Axis-2 also showed further differences between B-10 and UB stands where there was a relative higher species overlap. Majority of the taxa in B-10 and UB stands tended to concentrate towards the middle, except some taxa which are dispersed towards the axis two. The taxa in B-1 stand were dispersed towards axis-1 (Fig. 5).

The eigenvalues indicated that the variability in terms of taxa composition, explained by the gradients associated with the first two axes is higher. They together explained about 50.7% of the accumulative variance of fungal taxa data, and an accumulative variance for the interaction between fungal taxa and environment of 89.8% (Table 3). The third and fourth ordination axes with eigenvalues less than 0.1 were less important in ecological terms and not considered further.

A total of three edaphic variables such as Organic matter, Ca and P were found to be significantly related to the saprophytic fungal taxa composition in the ordination ($P < 0.05$, Table 4). The model was significant according to Monte Carlo permutation test for the first axis ($P = 0.002$, $F = 3.372$) and for all canonical axes ($P = 0.002$, $F = 2.158$). In this case, axis one was negatively corre-

Table 2
Total taxa collected from the Dry Afromontane forest of the study area, Wondo Genet (Ethiopia).

Taxa name	Code	B-1	B-10	UB	Edibility
Agaricus aff. *Ampestroides* Heinem & Gooss.-Font.	*Agcam*		x	x	E
Agaricus sp_1. L.	$Agar_1$		x	x	
Agaricus sp_2. L.	$Agar_2$		x	x	
Agaricus sp_3. L.	$Agar_4$		x	x	
Agaricus sp_4. L.	$Agar_5$		x	x	
Agaricus sp_5. L.	$Agar_6$		x		
Agaricus subedulis Heinem.	*Agsub*		x		E
Agaricus aff. *trisulphuratus* Berk.	*Agtris*		x	x	
Agrocybe sp. Fayod.	*Agroc*		x	x	E
Amauroderma sp. Murrill.	*Amaur*		x		
Armillaria heimii Pegler.	*Armihe*	x	x	x	E
Armillaria sp. (Fr) Staude.	*Armisp*	x	x	x	E
Calvatia sp. Fr.	*Calva*		x	x	E
Collybia piperata (Beeli) Singer.	*Colpip*		x	x	
Conocybe sp. Fayod.	*Conoy*		x	x	
Coprinellus domesticus (Bolton) Vilgalys, Hopple & Jacq. Johnson.	*Copdm*		x	x	E
Coprinellus sp. P. Karst.	*Coprll*	x	x	x	E
Coprinopsis nivea (Pers.) Redhead, Vilgalys & Moncalvo	*Coprni*		x	x	E
Coprinopsis sp_1. P. Karst.	$Copr_1$		x	x	E
Coprinopsis sp_2. P. Karst.	$Copr_2$	x	x	x	E
Coprinus sp. Pers.	*Coprsp*	x	x	x	E
Crepidotus sp. (Fr.) Staude.	*Crepid*	x	x	x	
Cyptotrama asprata (Berk.) Redhead & Ginns.	*Cypas*		x	x	
Favolaschia calocera R. Heim.	*Favcal*	x			
Gerronema hungo (Henn.) Degreef & Eyi.	*Gerhug*	x	x	x	
Gymnopilus junonius (Fr.) P.D. Orton.	*Gymjun*	x	x	x	
Gymnopilus pampeanus (Speg.) Singer.	*Gympa*	x	x	x	
Hygrophoropsis aurantiaca (Wulfen) Maire.	*Hygau*	x			E
Hymenagaricus sp. Heinem.	*Hymsp*		x	x	E
Hypholoma fasciculare (Huds.) P. Kumm.	*Hyphfas*	x	x	x	
Lepiota aff. *cristata* (Bolton) P.Kumm.	*Lepcri*	x	x	x	
Leucoagaricus holosericeus (J.J. Planer) M.M. Moser.	*Leuhol*		x	x	E
Leucoagaricus leucothites (Vittad.) Wasser.	*Leuleu*		x		E
Leucoagaricus aff. *rubrotinctus* (Peck) Singer.	*Leurub*		x	x	E
Leucoagaricus sp_1. Locq. ex Singer.	$Leucoa_1$		x	x	E
Leucoagaricus sp_2. Locq. ex Singer	$Leucoa_2$	x	x	x	E
Leucocoprinus birnbaumii (Corda) Singer.	*Leucbir*		x	x	E
Leucocoprinus cepistipes (Sowerby) Pat.	*Leucep*		x	x	E
Lycoperdon sp. Pers.	*Lycoper*	x	x	x	E
Marasmius buzungolo Singer.	*Marbuz*	x	x		
Marasmius katangensis Singer.	*Markat*	x	x	x	
Marasmius aff. *Rotalis* Berk & Broome.	*Marrot*	x	x		
Marasmius sp_1. Fr.	*Marsp*	x	x	x	
Microporus sp .P. Beauv.	*Microsp*		x	x	
Parasola sp_1. Redhead, Vilgalys & Hopple.	$Paras_1$	x	x	x	
Parasola sp_2. Redhead, Vilgalys & Hopple.	$Paras_2$	x		x	
Polyporus aff. *badius* (Pers.) Schwein.	*Polbad*	x	x	x	
Psathyrella sp_1. Fr.ex Quél.	$Psath_1$			x	
Psathyrella sp_2. Fr.ex Quél.	$Psath_2$			x	
Psathyrella sp_3. Fr.ex Quél.	$Psath_3$		x	x	
Psathyrella sp_4. Fr.ex Quél.	$Psath_4$		x	x	
Psilocybe cyanescens Wakef.	*Psicya*		x	x	
Psilocybe merdaria (Fr.) Ricken.	*Psilmed*	x	x	x	
Psilocybe sp. (Fr.) P. Kumm.	*Psilsp*	x	x	x	
Trametes versicolor (L.) Lloyd.	*Traves*		x		
Tremella mesenterica (Schaeff.) Retz.	*Tremes*	x			
Undescribed sp_1.	$Unkn_1$	x	x	x	
Undescribed sp_2.	$Unkn_2$	x			
Undescribed sp_3.	$Unkn_3$	x	x	x	
Undescribed sp_4.	$Unkn_4$		x	x	
Xerula sp. Maire.	*Xerusp*		x		

Note: B-1 and B-10 = One and ten years old burned plots, UB = unburned plots, E = Edible.

lated with all the three edaphic variables while axis-2 was positively correlated with all of them (Fig. 5).

4. Discussion

4.1. Taxa richness and diversity

Reports on macrofungal species from Ethiopian forests are limited. This study is the first to explain fungal communities in the Dry Afromontane forest system in the country. The taxonomic classification in this study was particularly challenging, as from the collected taxa, about 48% could be identified only to the genus level. This was an indication of both the uniqueness of the Dry Afromontane forest ecosystems in terms of diversity of yet undescribed macrofungi species as well as the lack of scientific studies on the local fungal flora in the country. All of the taxa collected were saprophytic, i.e. no ectomycorrhizal species were found. This was not surprising as the majority of tropical woody tree species are

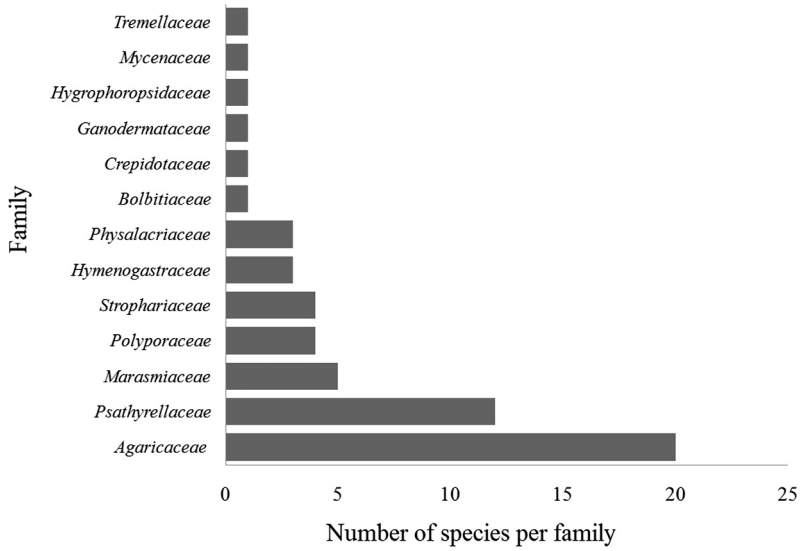

Fig. 2. Total number of fungal species per family encountered in the Dry Afromontane forest area of Wondo Genet (Ethiopia).

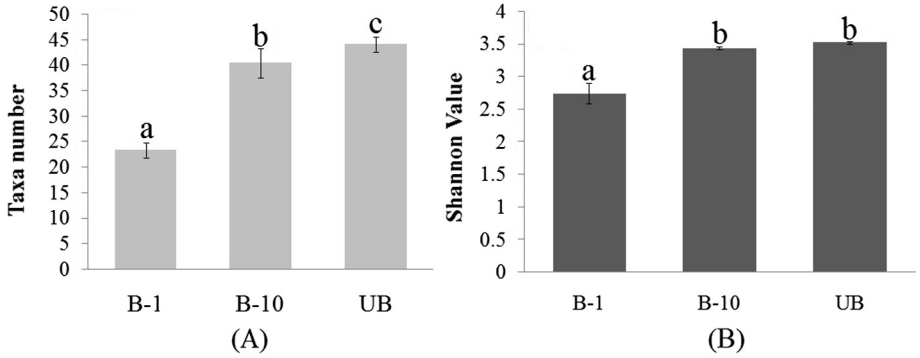

Fig. 3. Number of taxa (A) and the Shannon diversity index (B) in the Dry Afromontane forest area of Wondo Genet (Ethiopia). The data are mean results ± standard error of the mean. Values with the same letter are not significantly different.

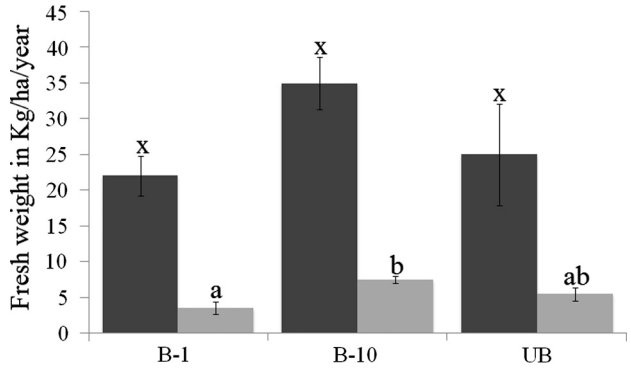

Fig. 4. Production of sporocarps according to total taxa (Dark colour) and edibility (Gray colour), in kg ha^{-1}collected from the dry Afromontane forest area of Wondo Genet (Ethiopia). The data are mean results ± standard error of the mean. Values with the same letter are not significantly different.

unable to form associations with ectomycorrhizal fungi (Brundrett, 2009), particularly those tree species of our study area.

The present study revealed occurrence of 61 macrofungal species considering fire-affected and unburned stands together. The number of fungal taxa reported here is the highest among the literature in Ethiopian natural forest areas. For example, Hjortstam and Ryvarden (1996) reported 15 taxa, Alemu (2013) reported seven taxa, and Decock et al. (2005) reported four taxa from the highland forest areas in the country. There are no previous works studying fire-fungal relation in Ethiopia. However, research in the Mediterranean region where forest fire is a dominant factor, have characterized the fungal communities. Unlike our result, lower numbers of saprophytic taxa were reported by Martín-Pinto et al. (2006), Oria-de-Rueda et al. (2010) and Mediavilla et al. (2014). This difference might be due to the variation in ecological factors such as climate and soils, which are among the most important factors that could affect saprophytic fungal taxa richness (Oria-de-Rueda et al., 2010). In the Mediterranean region, for example, rainfall is much lower (≤600 mm) than that of the Afromontane region where we carried out this study in Ethiopia (≥1200 mm). This difference in rainfall likely had an impact on richness as saprophytic fungi are dependent on available moisture in the soil for their fructification (Høiland, 2012). Furthermore, the reason could also be explained by the type of litter coverage on the forest soil, and thus on the species composition of the stands. A reduction in plant species richness (substrate richness) has been found to influence the diversity and richness of saprophytic species (Reverchon et al., 2010) as they depend on the available substrates. This probably indicates that the richness and complexity of the Dry Afromontane forests supply diversified substrates for saprophytic fungi to occur, as compared to the monotypic *Quercus* forest and/

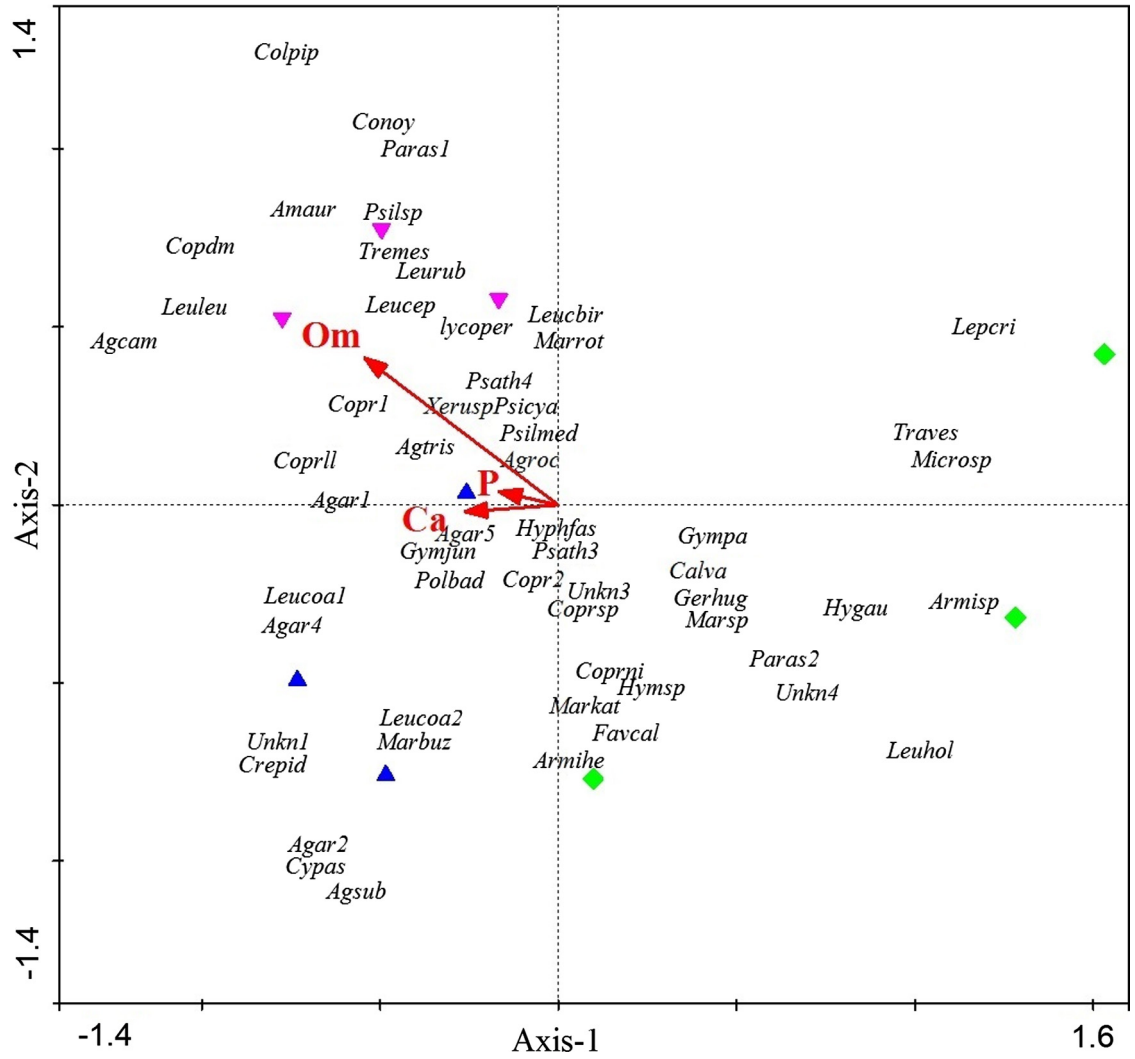

Fig. 5. RDA ordination bi-plots showing: fungal taxa abbreviated shown in Table 2, Plots in similar colour are in a group (Green triangle (B-1), Blue upward triangle (B-10), and Purple downward triangle (UB)) and environmental factors (arrows).

Table 3
Summary of constrained principal component analysis of fungal taxa presence and environmental factors for the study area, Wondo Genet (Ethiopia).

Axes	1	2
Eigenvalues	0.403	0.104
Taxa-environment correlations	0.925	0.892
Cumulative percentage variance of		
taxa data	40.3	50.7
taxa-environment relation	71.4	89.8

Table 4
Significant edaphic variables resulted from the forward selection process in Redundancy analysis (RDA).

Variables	*F*-ratio	*p*-value
OM	0.69	0.038
Ca	2.14	0.040
P	0.43	0.042

or *Pinus* plantation stands assessed by Martín-Pinto et al. (2006), Oria-de-Rueda et al. (2010) and Mediavilla et al. (2014) in the Mediterranean region.

High numbers of saprophytic taxa were also reported from studies in other eco-regions. For example, Tibuhwa et al. (2011) reported 91 taxa in Serengeti-Masai Mara ecosystem in Tanzania and Kenya, in Africa. Similarly, 72 saprophytic taxa were reported by Reverchon et al. (2010) from Mexico. O'Hanlon and Harrington (2012) also reported high numbers of saprophytic species from Atlantic region where rainfall is high. In all these cases, the sampling was done for extensive periods of time. Such systematic studies likely have a positive effect on macrofungal taxa numbers as fungi occurrence show considerable seasonal and yearly variation and in some cases individual taxa may not appear every year (Tibuhwa et al., 2011).

Forest fires typically have both short- and long-term effects on fungal communities. As a short-term effect, fire causes a reduction in richness (Kutorga et al., 2012; Oliver et al., 2015; Reazin et al., 2016) and as a long-term effect, fire also causes a shift in the presence or relative frequencies of fungal species in the forest system (Rincón and Pueyo, 2010; Smith et al., 2017). In this study, we also observed the least fungal taxa richness in the recently burned stand. This negative effect could be associated with the reduction of substrates in the forest floor after fire (Smith et al., 2008) and also due to the negative effect of fire on organic matter deposited

in the soil depending on fire intensity, leading to indirect effect on fungal growth and perpetuation (Kennedy et al., 2014). The loss of topsoil by erosion after fire could also reduce the infectivity of fungal propagules (Rashid et al., 1997), and thereby reduce taxa richness immediately following fire.

Fungal taxa richness was highest in UB stand (Fig. 3A). This is in line with Ratkowsky and Gates (2009) and Mediavilla et al. (2014) who noted succession of macrofungi related to time since fire in the *Eucalypt* and *Pinus* forests of Southern Tasmania and Spain respectively. Such increasing trend might be explained by the high soil humification and litter layer in relatively developed and canopy closed forest systems, which are particularly relevant for more saprophytic fungi occurrence. This assumption coincides with Dighton et al. (1986), Sysouphanthong et al. (2010) and Toivanen et al. (2012) who noted high fungal richness in matured stands with canopy closure.

When comparing diversity values among stands, the results were consistent with those from our richness analysis i.e. the lowest value was recorded at the one-year-old burned stands (Fig. 3B). The diversity value in early stage of fire might be due to the typical effects of fire to limit the type and number of fungal species appearing in an area. Thus, only a few fungi establish early in post-fire conditions, appearing adapted to the environment created after fire (Hansen et al., 2013; Reazin et al., 2016; Smith et al., 2017). In the following successional stage, however, the diversity values showed non-significant differences with the unburned stand (Fig. 3B). This might suggest that the environmental conditions in both stands are less likely to be hostile for a variety of fungal species. Thus, a large number of fungi are uniformly fruiting and distributed within any of these stands (Hernández-Rodríguez et al., 2013).

4.2. Sporocarp production

The negative effect of fire on sporocarp production has been investigated in previous studies by Hart et al. (2005), Bastias et al. (2006), Cairney and Bastias (2007), Hernández-Rodríguez et al. (2013); and Mediavilla et al. (2014) from multiple geographical areas. Post fire fruiting and the relative effects of fire on fungi fruiting, with a special emphasis on the saprophytic species are also deeply reviewed (Taudière et al., 2017). In the present study lower fungal production was also collected from recently burned stand. However, no significant differences were found. The absence of difference in sporocarp production between a recently burned and an unburned stands was previously reported by Mediavilla et al. (2014) who studied the effect of fire on saprophytic species associated to *Pinus nigra* stands in the Mediterranean. This could be explained by the existence of fungal species whose ephemeral fruit bodies may cover forest soil in recently burned areas (Hart et al., 2005; Taudière et al., 2017), taking advantage of the condition created (Bean et al., 2009). For example, *Armillaria* sp. fruited most abundantly in a recently burned stand as compared to other fungal species. This species might survive in the early stage of after fire and accumulate biomass either by persisting on remnant plant bodies or uses other organic matter after fire (Bonello et al., 1998). Furthermore, the quick recovery rates of some plant species like *Cordia africana*, an early colonizer in forest rehabilitation in the burned stand might also contribute to the quick accumulation of organic matter in the soil, which in turn benefits saprophytic fungi (Bonello et al., 1998).

Edible sporocarp production was also lower in B-1 stand (Fig. 4). However, only differences between B-10 and B-1 stands were observed. This result seems to contrast with those obtained for the total sporocarp production comparing B-10 and B-1 stands, where the total biomass production didn't significantly differ. An explanation for this apparent contradiction could be due to the existence of some exclusive taxa in B-10 that we characterized as higher biomass producer (e.g. *Agaricus subedulis*). This species accounted for up to 25% of the total edible sporocarp fresh biomass in B-10 stand of the study area. On the other hand, the p-value observed between B-10 and UB ($P = 0.06$) suggests a slight difference in sporocarp production. This should be ensured through further sampling efforts enough to detect practically existing differences between the two stands.

4.3. Taxa composition

We found the recently burned stand to have distinctive fungal communities (Fig. 5). The non-litter decomposer fungal species are more favored and exclusively found in this stand. This is likely the case for the species of *Favolaschia calocera* and *Hygrophoropsis aurantiaca*. These species are reported to commonly fruit in areas disturbed by human activities such as in burned forests (Smith and Read, 1997; Vizzini et al., 2009). Fungal species richness is lowest in the recently fire-impacted stand. This highlighted the perturbative effects that fire has on both the type and number of species, only those able to resist or adapt to the new conditions (Greeshma et al., 2016).

Similarities were found between B-10 and UB stands. Both are found on the right side of the ordination, characterized by high taxa richness. *Agaricus* spp. and most *Leucoagaricus* spp. were exclusively found in these stands. The possible explanation for such exclusive occurrence and high number of taxa in both stands could be due to the increased complexity of the forest system, featuring high soil humification and thickness of the litter layer (Toivanen et al., 2012; Mediavilla et al., 2014), particularly relevant for higher saprophytic fungi occurrence. Furthermore, the presence of a high number of taxa shared between B-10 and UB stands might be a reason for such occurrence. Some species occurring in the extreme points of the ordination axis are probably responding to specific ecological requirements of the species.

When analyzing saprotrophic taxa by family, we found *Agaricaceae*, *Psathyrellaceae*, and *Marasmiaceae* appearing in all three studied stands. The largest number of fungal taxa we found from the entire forest area was also represented by these families. The main reason for such wider representation might be the species in these families are able to fruit in different ecological conditions and have wide substrate requirements. Species such as *Armillaria heimii*, *Coprinellus* sp., *Coprinus* sp., *Crepidotus* sp., *Gerronema hungo*, *Gymnopilus junonius*, *Gymnopilus pampeanus*, *Hypholoma fasciculare*, *Lepiota cristata*, *Leucoagaricus* sp., *Lycoperdon* sp., *Marasmius buzungolo*, *Parasola* sp., *Psilocybe merdaria* were common to all study stands evaluated in this study. Interestingly, *Marasmius* sp. and *Lepiota* sp. were reported as common species in both fire affected and unburned stands by Greeshma et al. (2016).

It is well established that fungal communities as a whole are significantly influenced by edaphic variables (Straatsma et al., 2001; Zakaria and Boddy, 2002), although information about particular species is scarce. This is because soil nutrients have been shown to affect mycelial development and hence sporocarp occurrence (Zakaria and Boddy, 2002). In the present study, there seems to be a cumulative effect of edaphic variables on the composition and distribution of macrofungi in the studied forest stands. The soil OM, P and Ca were found to correlate significantly with the fungal taxa composition. Among these edaphic variables, OM appeared to be the most important factor related to saprophytic fungal composition (Fig. 5). This is likely because fungi typically extend their mycelia at the soil-litter interface (Boddy et al., 2009) and thereby the organic matter influences mycelia outgrowth and network formation (Zakaria and Boddy, 2002). Organic matter also influences the fungal community through its impact on water holding capac-

ity and nutrient availability in the soil (Harrington, 2003). Thus, OM may favor more saprophytic fungal assembly in an area.

Different fungal species seemed to have divergent responses to different soil factors. In this study we found that *Amauroderma* spp., *Agaricus campestroides*, *Coprinopsis* spp., *Psilocybe* spp., *Leucocoprinus birnbaumii*, *Leucoagaricus leucothites*, and *Parasola* spp., appeared to be in the higher end points of OM gradient in the ordination suggesting that the composition of these species could be highly associated with OM in the soil. Some of the species listed above (e.g. *L. birnbaumii*) are reported to be common in areas with abundant decayed plant matter (Dutta et al., 2011).

In this study we also found that the edaphic variables of P and Ca were correlated with saprophytic taxa composition. The result coincides with Gassibe et al. (2015) who noted the correlation of P with saprophytic taxa under *Pinus* stands in the Mediterranean. Cairney (2011) also noted the significant influence of P on soil fungal taxa assemblages. Such correlation might be due to the fact that P, among other elements, is essential for the growth and sporulation of fungal species (Nonzom and Sumbali, 2014), and thereby could influence sporocarp production. Likewise, Ca has been also been implicated as one of the major factors associated with fungal composition in the present study, as Ca is also crucial for fungal metabolism (Bindschedler et al., 2009) and growth (Griffin, 1994). Thus, some saprophytic species that are related to OM were also associated with the P and Ca in the ordination. In this sense, species such as *Agaricus campestroides*, *A. trisulphuratus, Psathyrella* sp., *Parasola* sp., *Psilocybe* sp., *Coprinellus* sp., and *Leucoagaricus* sp., were also closely related with P and Ca content of the soils in our study, indicating that their fructification is probably influenced by these elements. The fructification of these species was higher in UB and B-10 stands where the nutrients availability was higher. Some *Agaricus* and *Collybia* species were previously reported in unburned stands, where there was a higher availability of a pool of nutrients, when comparing to fire affected stands (Mediavilla et al., 2014).

5. Conclusion

This study represents the first systematic research providing noticeable contribution to the knowledge of fungal communities in the Dry Afromontane forests in Ethiopia and their relation with fire perturbation. The work provides a starting place in broadening management objectives for NTFPs in the Dry Afromontane forests. However, the results should be regarded as a preliminary indication due to sampling limitations.

The result indicated that an unburned mature natural stand provided high fungal richness as compared to the burned stand. The low fungal diversity was reported in the recently burned stands. An indication of differences in edible fungal yields was also observed among the studied stands. Finally, we also observed the noticeable presence of the edible species like *Agaricus subedulis* which could be potentially marketed in rural areas providing supplementary incomes. Taxa compositions in unburned and 10 years old stands were significantly explained by higher amounts of soil OM, Ca and P.

The results of this preliminarily case study are also encouraging from a conservation point of view. It provides novelty information about the diversity of macrofungal species in Ethiopian Dry Afromontane forests, likely including many taxa which are still unknown to science as well as several edible species which could supply complementary incomes for the rural populations in the study area.

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