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Survey of macrofungal diversity and analysis of edaphic factors influencing the fungal community of church forests in Dry Afromontane areas of Northern Ethiopia

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ABSTRACT

The Dry Afromontane forests in Northern Ethiopia have been cleared for agriculture and reduced to small and isolated fragments. Most of these forests are located around church territories and are they called church forests. The church forests are known to be biodiversity islands and provide key ecosystem services to local communities. However, to date, the fungal resources of these forests have not been assessed and, therefore, the contribution of fungi to their conservation value is unknown. In 2019, we investigated the fungal diversity of three Dry Afromontane church forests. In each forest, we established nine permanent plots (2 m × 50 m), which were surveyed weekly during the rainy season to quantify the fungal diversity and sporocarp production levels. Explanatory variables were also analyzed to determine their relationship with macrofungal species composition. We collected 13,736 sporocarps corresponding to 188 taxa. Of these, 81% were saprotrophic and 14% were ectomycorrhizal. Sixty-eight species were edible, including economically valuable species such as *Tricholoma* and *Termitomyces*. This suggests that these fragmented forest systems could be managed to provide valuable non-timber forest products such as mushrooms and socioeconomic benefits for local communities. Although many species were present in all three forests, some were only found in one forest, highlighting the importance of conserving individual forests. The correlation of the Shannon diversity indices of the two communities showed a positive trend in spite of the lack of correlation between their richness. Macrofungal communities as a whole were influenced by edaphic, spatial and climate variables. This study indicates that church forests support a wide diversity of fungi, including potentially novel fungal species, and highlights the need for forest managers to consider the importance of fungi in forest ecosystem management and to provide habitats that will maintain fungal diversity and sporocarp production when planning conservation strategies.

1. Introduction

The Ethiopian highlands constitute large parts of the Afromontane regions in Africa (Aynekulu et al., 2016; Nyssen et al., 2014). These highlands are dominated by Dry Afromontane forests and are mainly found in the Northern part of Ethiopia (Eshete et al., 2011; Friis et al., 2010a,b). Dry Afromontane forests are rich in biodiversity and are dominated by pioneers, shrubs, and high-quality trees (Abiyu et al., 2018; Lemenih et al., 2011) that are able to grow at high altitudes (Friis et al., 2010a,b). The main tree species that constitute the Dry Afromontane forests include *Juniperus procera*, *Podocarpus falcatus*, *Hagenia abyssinica* and *Olea africana* (Kassa et al., 2009). These trees serve as a vital source of timber to the country (Kassa et al., 2009) and thus an indication of a need for the sustainable management of these forests. The Dry Afromontane forests also produce several Non-Timber Forest Products (NTFPs) such as wild edible fruits and medicinal plants that are vital for the socioeconomics of the local communities (Shumi, 2009). Furthermore, edible mushrooms from the forest systems have been utilized as important sources of food and medicine by rural communities for their livelihoods in few specific regions in Ethiopia (Abate, 2008). However, high levels of historical human landscape alteration and land-use pressure have resulted in widespread deforestation and the degradation of forest land (Aerts et al., 2016; Aynekulu et al., 2016; Darbyshire et al., 2003; Nyssen et al., 2014). The ever-increasing demand for

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wood products as well as crop and grazing land expansion, stimulated by rapid population and livestock growth are also factors aggravating the degradation of the Dry Afromontane forests in the country (Bekele and Lemenih, 2008). As a result of the many physical and biological changes to the Dry Afromontane forests in Northern Ethiopia, natural forests have been reduced to small and isolated fragments, most of which belong to the church or are located around church forest territories (Aerts et al., 2016; Aynekulu et al., 2016; Wassie et al., 2009). These forest fragments have survived because of the cultural or religious values held by local communities, which have contributed to the conservation of their biodiversity. Owing to the small size of these forest fragments, there are variations in their biodiversity between forest fragments (Lemenih et al., 2011; Wassie et al., 2005) and probably of their fungal communities.

Fungal communities are an important component of forest ecosystems and have a broad range of functions (Song et al., 2019; Tedersoo et al., 2014a; Wagg et al., 2014). As decomposers, they are important for the degradation of organic matter and play a vital role in nutrient cycling (Chen et al., 2019; Ferris et al., 2000). Mycorrhizal fungi form symbiotic associations with higher plants, facilitating plant uptake of water and nutrients (Egli, 2011; Hall et al., 2003; Tedersoo et al., 2020). Fungi can also be used as bioindicators to assess the quality of forests (Egli, 2011; Van Bruggen and Semenov, 2000). In addition to their ecological roles, fungi have been used by humans for thousands of years in different ways (Boa, 2004; Oria-De-Rueda et al., 2008) and are sold in markets worldwide, providing an important source of rural income (Boa, 2004; Pettenella et al., 2007). Indeed, in some cases, forest fungi provide significant complimentary benefits to forest managers (Bonet et al., 2014; Martín-Pinto et al., 2006). Fungi also provide food and habitats for other organisms and, therefore, interactions between fungi and other organisms in forest systems cannot be overlooked (Jonsell and Nordlander, 2000). Pathogenic fungi also impact ecosystems, mainly by acting as natural population regulators, thereby influencing productivity, species diversity, and composition (Ruiz-Almenara et al., 2019). For all these reasons, fungi are considered a strategic component in the conservation and management of forest systems (Bonet et al., 2014).

Today, biodiverse remnants of the Dry Afromontane forests survive in the agricultural landscape and church areas as forest islands (Aynekulu et al., 2016). Several studies have evaluated the conservation value of these fragmented forests in the Northern landscapes of Ethiopia (Aerts et al., 2016; Aynekulu et al., 2016; Wassie et al., 2010, 2005; Nyssen et al., 2014). However, the ecology and conservation status of the macrofungi in these isolated and fragmented forest systems is unknown. Consequently, the fungal taxonomy and ecology are very poorly described and, hence, fungi are neglected when decisions need to be made regarding forest management and conservation actions. Recently, there has been an interest in surveying fungi in particular habitats (Alem et al., 2020), to describe and predict the extent of their diversity on a larger scale (Danielsen et al., 2005; Peay, 2014). This information is important to enable the integration of fragmented forests into global biodiversity conservation strategies (Hundera et al., 2013; Aerts et al., 2016; Aynekulu et al., 2016) and to understand what actions are required to conserve fragmented forests and their biological components, including fungi, which are known for their exceptionally high diversity levels (Burgess et al., 2006).

The practice of using plant communities as surrogates to predict fungal diversity has been reported by previous studies (McMullan-Fisher et al., 2010; Rudolf et al., 2013). Fungal communities have also been associated with essential ecosystem parameters such as edaphic variables (Chen et al., 2018), as well as other relevant drivers of fungal richness at a global level such as climate (Tedersoo et al., 2014b). Furthermore, fungal diversity is considered to reflect niche diversity given that reducing niche similarity drives species assemblage (Silvertown, 2004). The Dry Afromontane church forests in Ethiopia are reported to have high levels of plant species diversity (Mokria et al., 2015; Tsegaye et al., 2010). However, there is no evidence that the high level of plant diversity in the church Dry Afromontane forests system anticipates correspondingly high macrofungal diversity. In addition, as yet, the environmental variables that govern fungal communities in these fragmented forest systems have not been identified given that these forests vary in their status (size, density, species composition etc.), topography and altitude (Bongers and Tenngkeit, 2010). Thus, investigating the fungal community composition and how this community changes across sites in fragmented forests should help us to understand different aspects of fungal interaction within these systems and their function in the ecosystem (Genevieve et al., 2019). This information may also be a means to understand how to improve natural fungal richness and sporocarp production and also help us to facilitate the conservation of economically and ecologically important macrofungal species in these fragmented forest systems.

This study is the first attempt to provide baseline information about macrofungi assemblage, diversity, and sporocarp production in Dry Afromontane church forests with priority status in Northern Ethiopia. Priority forests are those that have been designated as reserves to give them additional protection. The information generated should help to guide management and conservation strategies for these priority forests and supplement our knowledge of macrofungal species in Ethiopia. Furthermore, determining whether edible mushrooms are produced in these forests could provide an opportunity for harvesting edible mushrooms for either subsistence or commercial use. Despite fragmentation, the forests in the study areas are suggested to be relatively rich in plant species (Aerts et al., 2016; Wassie et al., 2010). On average, there are 25 vascular tree species per forest patch (Aerts et al., 2016). The tree species composition of these forests also varied with their status, topography and altitude (Bongers and Tenngkeit, 2010), with a wide distribution over the landscapes (Aerts et al., 2016). Given that fungal diversity is related positively to plant richness (Tedersoo et al., 2014b), we hypothesized that the fungal diversity of the study plots in the church forests would be high in terms of total fungal species. In addition, the edaphic conditions, vascular plant richness and diversity would follow given the differences in climate and topography among the different fragmented forests, we also hypothesized that the composition of macrofungal communities would differ among the studied forests, resulting in an overall higher richness value for the study sites because fungi will be driven mainly by vegetation condition and site conditions such as soil fertility conditions (Castaño et al., 2018; Vašutová et al., 2017). Thus, our specific aims were to study three church forests in Dry Afromontane areas of Northern Ethiopia: (1) to describe fungal species richness, diversity, and sporocarp production; (2) to correlate the macrofungal and plant diversity of the three church forests; and (3) to determine whether the macrofungal community composition was governed by the soil fertility status of the three forest sites.

2. Materials and methods

2.1. Description of the study areas

The study was conducted in three church forests located in three different districts of the Amhara region, namely the Taragedam forest located in *Libokemkem* Woreda, the Alemsaga forest located in *Farta* Woreda, and the Banja forest located in *Banja* Woreda (Fig. 1). These forests are fragments of the remnant Dry Afromontane forests in Northern Ethiopia (Gebeyehu et al., 2019; Masresha et al., 2015; Zegeye et al., 2011). The Taragedam and Banja forests were designated as reserves in 1979 (Zegeye et al., 2011) and 1994 (Abere et al., 2017), respectively, to prevent any kind of encroachments. The Alemsaga forest was designated as a priority forest in 1978 to serve as a seed source, to conserve the remnant natural forest, and to rehabilitate the degraded area in Northern part of the country (Masresha et al., 2015). Comprehensive descriptions of the forests are provided in Table 1. Within each of the forests, plots were established systematically about 500 m apart in 2019. The plots were laid out randomly in the forests to avoid

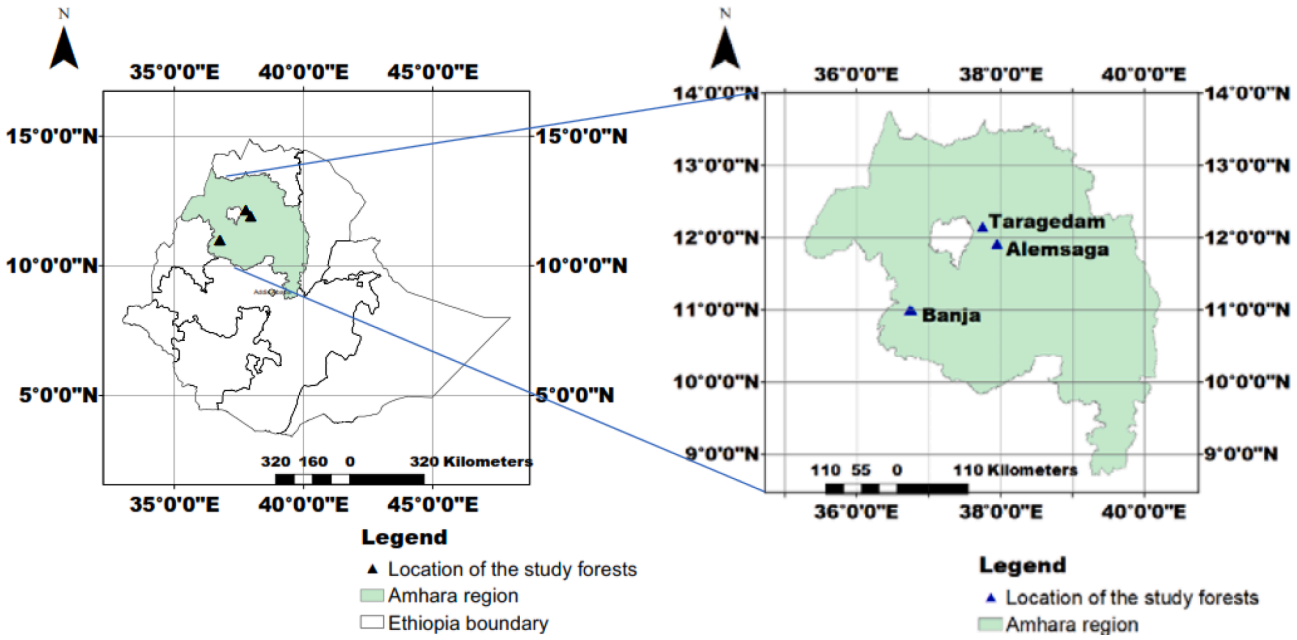

Fig. 1. Map of the Amhara region in Northern Ethiopia showing the location of the three church forests in which the study plots were located.

confounding spatial effects inherent to such a plot-based design (Hiiesalu et al., 2017; Rudolph et al., 2018). The plots were analyzed as independent samples as suggested by Ruiz-Almenara et al.(2019). However, the present study provides a starting place in broadening management objectives for NTFPs in the Dry Afromontane church forests. Thus, the result should be considered as a case study and as a preliminary indication and conclusions regarding other similar studies need to be taken with caution.

2.2. Sporocarp sampling

In total, 27 sample plots were established, nine in each of the three church forests, as described in Gassibe et al. (2011) and Hernández-Rodríguez et al. (2013). Each plot was rectangular in shape (2 m × 50 m) and covered an area of 100 m^2. Within each of the selected church forests, we studied three different blocks including three plots per block. The plots were established about a minimum distance of 500 m apart. All fungal fruit bodies found were harvested weekly during the major rainy season in July and August of 2019. Fresh weight measurements were taken *in situ* using a digital sensitive balance (SF-400) to determine fruit body production in kilograms per hectare per year. The number of sporocarps of each species in each plot was also recorded. Specimens were photographed in the field and their morphological features and ecological characteristics were noted to facilitate taxonomic identification processes in the laboratory (Adeniyi et al., 2018). Specimens of each macrofungus were taken to the laboratory and dried to preserve as herbaria specimens, and then used for morphological species identification.

2.3. Species identification

In the laboratory, the morphological features of the fruit bodies were examined using appropriate monographs, including Antonin (2007), Hama et al. (2010), Heinemann (1956), Hjortstam and Ryvarden (1996), Morris (1990), Pegler (1968, 1969, 1977), Rammeloo and Walleyn (1993), and Singer (1965), to determine the genus and species of the macrofungal specimens. Up-to-date fungal species names and authors' names were obtained from the Mycobank database (http://mycobank.org). Ecological functions at the genus level were identified using a FUNGuild (www.funguild.org) search and provided in Table 2. In addition, the edibility of the fruiting bodies collected from the study sites was assessed following the criteria used by Bonet et al. (2004). Species described in the literature as both non-edible and edible in the literature were classified as non-edible. Species described in the literature as having doubtful edibility were classified as non-edible. Only species classified as edible by a large majority of the literature consulted were classified as edible fungi (E).

2.4. Soil sampling and analysis

To relate macrofungal composition to edaphic variables, soil samples were collected from each of the sample plots established in the three forests. Composite samples were collected by grouping each plot into relatively homogeneous subsamples. After clearing and removing plant matter and debris from the soil surface, five soil cores were extracted from the center and the four corners of each plot using an auger (2 cm radius, 20 cm deep and 250 cm^3). Subsamples collected from each plot were mixed thoroughly and a composite sample of approximately 500 g was placed in a plastic bag for analysis. Soil samples were dried under a shed until a constant weight was obtained and ground to < 2 mm sieved soil is used in the analysis. The soil pH and electrical conductivity were determined by analyzing a soil:water (1:2.5) suspension and the supernatant from the same suspension with the aid of a pH meter and an electrical conductivity meter, respectively (Reeuwijk, 2002). The organic carbon content of the soil was determined using wet digestion (Walkley and Black, 1934). The Kjeldahl procedure was used to determine the total N content in soils (Kim et al., 2005). Sodium bicarbonate (0.5 M NaHCO3) was used as an extraction solution to determine the available phosphorus (P) (Kim, 1996). Available sodium (Na), potassium (K), calcium (Ca) and magnesium (Mg) were also determined. To assess soil particle size we used a hydrometer (Bouyoucos, 1951) and sodium hexametaphosphate (Calgon solution) was used as a dispersing agent. After calculating the proportions of sand, silt, and clay, the soil was assigned a textural class name using ASTM free software, Version 4, Available: http://www.astm.org. The results of the soil analysis are provided in Table 1. The soil analysis was conducted by the Amhara Design and Supervision Works Enterprise at Bahir Dar, Ethiopia.

Table 1
Characteristics of the study sites and selected edaphic properties.

Descriptions	Forests		
	Taragedam	Alemsaga	Banja
Geographical location	12°06′–12°07′ N 37°46′– 37°47′ E	11°54′–11°56′N 37°55′–37°57′E	10°57′–11° 03′N 36°39′– 36°48′E
Altitude range (m asl)	2142–2484	2180–2470	1870–2570
Mean annual precipitation (mm)	1098	1926	1884.3
Mean annual temperature (°C)	19.5	15.8	18.7
Forest area (ha)	875	814	897
Density of trees ha^{-1}	48.11	17.19	43.13
Sand (%)	58.89 ± 2.93b	51.78 ± 2.99b	68.67 ± 2.21a
Silt (%)	28.44 ± 2.38a	32.44 ± 2.13a	20.00 ± 1.76b
Clay (%)	12.67 ± 1.37a	15.78 ± 1.93a	11.33 ± 1.33a
pH H2O 1:2.5	7.04 ± 7.03a	5.85 ± 6.59b	5.60 ± 6.24c
EC (dS/m)	0.43 ± 0.05b	0.28 ± 0.03b	0.81 ± 0.14a
Ex.Ca (cmol (+)/kg)	13.95 ± 0.60a	9.19 ± 0.52b	13.55 ± 0.87a
Ex.Mg (cmol (+)/kg)	6.16 ± 0.10a	4.58 ± 0.15c	5.54 ± 0.20b
Ex.Na (cmol (+)/kg)	1.95 ± 0.05a	2.05 ± 0.10a	1.82 ± 0.12a
Ex.K (cmol (+)/kg)	0.73 ± 0.06a	0.61 ± 0.04a	0.77 ± 0.06a
CEC (cmol (+)/kg)	47.21 ± 1.36a	34.89 ± 0.92b	44.51 ± 1.96a
Organic matter (%)	4.46(0.60)a	3.35(1.34)b	4.87(0.10)a
Nitrogen (%)	0.23 ± 0.01a	0.17 ± 0.02b	0.26 ± 0.01a
P (ppm)	17.18 ± 5.72a	7.8 ± 0.73b	17.64 ± 6.05a
Dominant species in each plots	*Maytenus obscura*, *Carissa edulis*, *Olea* sp.	*Acacia abyssinica*, *Buddleja polystachya*, *Acacia nilotica*	*Albizia gummifera*, *Prunus africana*, *Brucea antidysenterica*
References	Gedefaw and Soromessa (2014), Zegeye et al. (2011), Zerihun et al. (2013)	Birhane et al. (2017), Masresha et al. (2015), Wubet et al. (2004)	Abere et al. (2017)

Note: Values shown are means; standard errors of the means are indicated in parentheses. Values with different lowercase letters are significantly different ($p < 0.05$). The mean annual precipitation and mean annual temperature are given based on nearby stations data of each study area by the year 2019. Abbreviations: EC, electrical conductivity; CEC, cation exchange capacity; m, meter; mm, millimeter; asl, above sea level. The references listed are related to the climatic and geographical descriptions of the study areas.

2.5. Vegetation sampling

To relate the vegetation characteristics to the macrofungal richness and diversity, vegetation inventories were conducted in the plots established for macrofungal species sampling as described above. Vascular plants identified in each plots were recorded using their vernacular names. For those species difficult to identify their scientific name in the field, specimens were collected and their taxonomic identification was conducted using published volume of the flora of Ethiopia and Eritrea (Hedberg and Sue, 1989). Large trees growing outside the plots were included in the survey if their crowns overhung the plots because tree crown projection areas can affect macrofungal occurrence (Collins et al., 2018). Furthermore, large trees create their own microhabitat and develop a large root system, providing more space for fungal associations (Schön et al., 2018). Then, the vascular plant species richness and diversity parameters were determined (Table 3). Plant parameters and their correlations were also used for further interpretation of macrofungal pattern from each study areas. The mycorrhizal status of the vascular tree species found in each of the studied plots were checked using freely accessible databases (Soudzilovskaia et al., 2020) and the data is provided (Table S1).

2.6. Statistical analysis

Data were transformed when needed to achieve the parametric criteria of normality and homoscedasticity. The macrofungi data were normalized by rarefying the abundance data to the smallest number of macrofungi per plot. Also, the data from soil variables were scaled using base R and used for subsequent statistical analyses. Shannon's H′ diversity index, $H' = -\Sigma pi\ (lnpi)$ (Shannon and Weaver, 1949), was estimated for each forest, where pi indicates the relative abundance of the species (Kent and Coker, 1993). Simpson's diversity, $D = 1 - \Sigma(pi2)$, where pi is the importance probability in element i; and the evenness, $J = H'/H'max$, where H′ is the number derived from the Shannon diversity index and the H′ max is the maximum possible value of H′ were also calculated (Magurran, 1988). In addition to species richness values, macrofungi biomass production levels in each forest were estimated and converted in to Kg bases. All diversity measures for macrofungi and vascular plants were analyzed using the Biodiversity R package (Kindt and Coe, 2005) in R version 4.0.3 (R Core Team, 2020). The difference in the soil, vegetation and sporocarps variables across forests were assessed by Linear Mixed Effects models (LME, Pinheiro et al., 2016), where block (a set of plots in a same site in each forest) was defined as random and forest was defined as fixed factor. The LME used to prevent the false positive associations due relatedness structure in the sampling. Tukey Test was later used to check significant differences ($p \leq 0.05$) between forests when needed.

Species accumulation curves were constructed to compare the rate at which new fungal species were found in the three forests and to provide an estimate of macrofungal species richness. Curves were generated using a sample-based estimator of EstimateS Version 9 (Colwell, 2013). The number of fungal species collected during each weekly visit to a plot within a forest constituted the sample. Curves were generated based on the total of the weekly sampling datasets. A Rényi diversity profile (Tóthmérész, 1995) was also used to depict the diversity curves of the three church forests. When parameter alpha = 0, this function gives the total species number and when alpha = 1, this gives an index proportional to the Shannon index.

The relationship of macrofungal composition with the edaphic, climate and location parameters was visualized using non-metric multidimensional scaling (NMDS), based on absence and presence species data matrix and environmental scaled data. A permutation-based nonparametric MANOVA (PerMANOVA) (Anderson, 2001) using Bray–Curtis distance was conducted to analyze differences in macrofungal communities across forests. The isolines of the elevation also plotted on the NMDS ordinations using the ordisurf function. The correlation of NMDS axes scores with explanatory variables was assessed using envfit function in R. To test the influence of categories of the edaphic, climate and location variables on the fungal community, we used Mantel Test (Bray-Curtis distance) on total species matrix and scaled environmental parameters. Also, an analysis of similarity percentages (SIMPER; Clarke, 1993) was performed to identify macrofungal species that were most responsible for the observed patterns and was also used to determine the percentage contribution of macrofungal species to significant dissimilarities between the three forests (Parravicini et al., 2010). The SIMPER analysis was performed using the sim function of the Vegan package in R (R Core Team, 2020).

3. Results

3.1. Macrofungal richness and diversity

In total, 13,736 sporocarps were collected from the three church

Table 2
Fungal sporocarps collected in July and August in three church forests in Northern Ethiopia.

Taxa	Order	Family	T	A	B	E	LM
Agaricus augustus Fr.	Agaricales	Agaricaceae		x		E	SS
Agaricus bitorquis (Quél.) Sacc.	Agaricales	Agaricaceae	x			E	SS
Agaricus campestris L.	Agaricales	Agaricaceae	x	x	x	E	SS
Agaricus cupreobrunneus (Jul.Schäffer & Steer ex F.H.Møller) Pilát	Agaricales	Agaricaceae		x	x	E	SS
Agaricus megalosporus J. Chen, R.L. Zhao, Karun. & K.D. Hyde	Agaricales	Agaricaceae	x	x	x	E	SS
Agaricus moelleri Wasser	Agaricales	Agaricaceae	x		x	E	SS
Agaricus murinaceus Bull.	Agaricales	Agaricaceae			x	E	SS
Amanita vaginata (Bull.) Lam.	Agaricales	Amanitaceae	x		x		EM
Amanita sp. Pers.	Agaricales	Amanitaceae	x		x	E	EM
Amanita verna (Bull.) Lam.	Agaricales	Amanitaceae	x	x	x	E	EM
Ampulloclitocybe clavipes (Pers.) Redhead, Lutzoni, Moncalvo & Vilgalys	Agaricales	Tricholomataceae		x	x	E	LS
Artomyces pyxidatus (Pers.) Jülich	Russulales	Amylostereaceae	x	x	x		WS
Auricularia auricula-judae (Bull.) Quél.	Auriculariales	Auriculariaceae	x			E	WS
Bisporella citrina (Batsch) Korf & S.E.Carp.	Helotiales	Helotiaceae			x		WS
Bjerkandera adusta (Willd.) P.Karst.	Polyporales	Meruliaceae	x		x		WS
Bolbitius sp. Fr.	Agaricales	Bolbitiaceae		x	x		DS
Bovista aestivalis (Bonord.) Demoulin	Agaricales	Agaricaceae	x		x		SS
Bovista plumbea Pers.	Agaricales	Agaricaceae		x			SS
Calvatia cyathiformis (Bosc) Morgan.	Agaricales	Agaricaceae		x	x	E	SS
Calvatia gigantea (Batsch) Lloyd	Agaricales	Agaricaceae	x			E	SS
Calvatia sp. Fr.	Agaricales	Agaricaceae			x	E	SS
Cantharellula umbonata (J.F.Gmel.) Singer	Agaricales	Tricholomataceae		x	x		LS
Cantharellus cinnabarinus (Schwein.) Schwein.	Cantharellales	Hydnaceae	x			E	EM
Chlorophyllum molybdites (G. Mey.) Massee	Agaricales	Agaricaceae	x	x	x	E	LS
Chlorophyllum rhacodes (Vittad.) Vellinga	Agaricales	Agaricaceae	x	x	x	E	LS
Clavaria falcata Pers.	Agaricales	Clavariaceae		x			SS
Climacodon septentrionalis (Fr.) P. Karst.	Polyporales	Phanerochaetaceae	x				WS
Clitocybe carolinensis H.E. Bigelow & Hesler	Agaricales	Tricholomataceae	x	x		E	LS
Clitocybe cistophila Bon & Contu	Agaricales	Tricholomataceae	x			E	LS
Clitocybe foetens Melot.	Agaricales	Tricholomataceae	x	x	x	E	LS
Clitocybe fragrans (With.) P.Kumm.	Agaricales	Tricholomataceae	x	x	x	E	LS
Clitocybe geotropa (Bull.ex DC.) Quél	Agaricales	Tricholomataceae		x		E	LS
Clitopilus hobsonii (Berk. & Broome) P.D. Orton	Agaricales	Entolomataceae	x	x	x		LS
Conocybe apala (Fr.) Arnolds	Agaricales	Bolbitiaceae			x		SS
Conocybe aurea (Jul.Schäff.) Hongo	Agaricales	Bolbitiaceae	x	x			SS
Conocybe dumetorum (Velen.) Svrcek	Agaricales	Bolbitiaceae		x	x		SS
Conocybe tenera (Schaeff.) Fayod	Agaricales	Bolbitiaceae	x	x	x		SS
Conocybe velutipes (Velen.) Hauskn. & Svrcek	Agaricales	Bolbitiaceae	x	x	x		SS
Coprinellus disseminatus (Pers.) J.E.Lange	Agaricales	Psathyrellaceae		x	x		SS
Coprinellus micaceus (Bull.) Vilgalys, Hopple & Jacq. Johnson	Agaricales	Psathyrellaceae	x	x	x		SS
Coprinopsis sp. P. Karst.	Agaricales	Coprinaceae	x		x		SS
Coprinus comatus (O.F.Müll.) Pers.	Agaricales	Coprinaceae	x	x	x	E	DS
Coprinus lagopus (Fr.) Fr.	Agaricales	Coprinaceae		x	x		DS
Coprinus micaceus (Bull.) Fr.	Agaricales	Coprinaceae	x			E	DS
Coprinus niveus (Pers.) Fr.	Agaricales	Coprinaceae	x	x	x	E	DS
Cortinarius rubellus Cooke	Agaricales	Cortinariaceae		x	x		EM
Craterellus ignicolor (R.H. Petersen) Dahlman, Danell & Spatafora	Cantharellales	Hydnaceae	x			E	EM
Crepidotus applanatus (Pers.) P. Kumm.	Agaricales	Inocybaceae	x	x	x	E	WS
Crepidotus mollis (Schaeff.) Staude	Agaricales	Inocybaceae	x	x	x	E	WS
Crucibulum laeve (Huds.) Kambly	Agaricales	Agaricaceae			x		LS
Cystodermella granulosa (Batsch) Harmaja	Agaricales	Agaricaceae	x		x		LS
Dacrymyces palmatus (Schwein.) Burt	Dacrymycetales	Dacrymycetaceae			x		WS
Daedaleopsis confragosa (Bolton) J.Schröt.	Polyporales	Polyporaceae	x		x		WS
Daldinia concentrica (Bolton) Ces. & De Not.	Xylariales	Hypoxylaceae			x		WS
Deconica montana (Pers.) P.D. Orton	Agaricales	Strophariaceae	x	x	x		LS
Entoloma asprellum (Fr.) Fayod.	Agaricales	Entolomataceae	x	x	x		SS
Entoloma olivaceohebes Noordel. & Hauskn.	Agaricales	Entolomataceae		x	x		SS
Entoloma poliopus (Romagn.) Noordel.	Agaricales	Entolomataceae		x	x		SS
Entoloma sp. Fr. ex P. Kumm.	Agaricales	Entolomataceae	x		x		SS
Entoloma undatum (Gillet) M.M. Moser	Agaricales	Entolomataceae		x	x		SS
Favolaschia calocera R. Heim	Agaricales	Marasmiaceae			x		WS
Galerina badipes (Pers.) Kühner.	Agaricales	Strophariaceae	x	x	x		WS
Geastrum triplex Jungh.	Geastrales	Geastraceae	x	x	x		LS
Geoglossum sp. Pers.	Geoglossales	Geoglossaceae	x	x			SS
Gymnopilus sp1. P.Karst.	Agaricales	Omphalotaceae		x	x		WS
Gymnopilus sp2. P.Karst.	Agaricales	Omphalotaceae	x		x		WS
Gymnopilus sp3. P.Karst.	Agaricales	Omphalotaceae	x				WS
Gymnopus dryophilus (Bull.) Murrill	Agaricales	Omphalotaceae	x	x	x		LS
Gymnopus luxurians (Peck) Murrill	Agaricales	Omphalotaceae	x				LS
Gymnopus putillus (Fr.) Antonín, Halling & Noordel.	Agaricales	Omphalotaceae		x	x		LS
Hebeloma eburneum Malençon	Agaricales	Strophariaceae			x		EM
Hemimycena delectabilis (Peck) Singer.	Agaricales	Tricholomataceae	x	x	x		LS
Hexagonia tenuis (Hook.) Fr.	Polyporales	Polyporaceae	x	x	x		WS
Hohenbuehelia petalodes (Bull.) Schulzer.	Agaricales	Pleurotaceae	x				WS

(*continued on next page*)

Table 2 (*continued*)

Taxa	Order	Family	T	A	B	E	LM
Hygrocybe chlorophana (Fr.) Wünsche	Agaricales	Hygrophoraceae	x	x	x	E	SS
Hygrocybe chlorophana var. *aurantiaca* Bon.	Agaricales	Hygrophoraceae			x	E	SS
Hygrophoropsis aurantiaca (Wulfen) Maire	Boletales	Hygrophoropsidaceae	x	x	x		LS
Hygrophorus hypothejus Fr. (Fr.)	Agaricales	Hygrophoraceae	x	x	x	E	EM
Hymenagaricus sp1. Heinem.	Agaricales	Agaricaceae			x	E	SS
Hymenagaricus sp2. Heinem.	Agaricales	Agaricaceae	x				SS
Inocybe viridiumbonata Pegler	Agaricales	Inocybaceae			x		EM
Laccaria glabripes McNabb.	Agaricales	Hydnangiaceae	x				EM
Laccaria laccata (Scop.) Cooke	Agaricales	Hydnangiaceae		x			EM
Laetiporus sulphureus (Bull.) Murrill	Polyporales	Fomitopsidaceae	x	x	x	E	PP
Lentinellus cochleatus (Pers.) P. Karst.	Russulales	Auriscalpiaceae		x	x	E	WS
Lepiota cristata (Bolton) P.Kumm.	Agaricales	Agaricaceae			x		LS
Lepiota ermine (Fr.) P.Kumm.	Agaricales	Agaricaceae		x	x		LS
Lepiota himalayensis Khalid & Razaq	Agaricales	Agaricaceae	x	x			LS
Lepiota sp1. (Pers.) Gray	Agaricales	Agaricaceae			x		LS
Lepiota sp2. (Pers.) Gray	Agaricales	Agaricaceae	x				LS
Lepiota sp3. (Pers.) Gray	Agaricales	Agaricaceae		x	x		LS
Leptonia lampropus (Fr.) Quél.	Agaricales	Entolomataceae	x	x	x		SS
Leucoagaricus americanus (Peck) Vellinga.	Agaricales	Agaricaceae	x	x	x	E	SS
Leucoagaricus purpureolilacinus Huijsman	Agaricales	Agaricaceae	x	x	x	E	SS
Leucoagaricus sp1. Locq. ex Singer	Agaricales	Agaricaceae	x		x	E	SS
Leucoagaricus sp2. Locq. ex Singer	Agaricales	Agaricaceae			x		SS
Leucocoprinus cepaestipes (Sowerby) Pat.	Agaricales	Agaricaceae	x		x		SS
Leucocoprinus fragilissimus (Berk. & M.A.Curtis) Pat.	Agaricales	Agaricaceae			x		SS
Lyophyllum infumatum (Bres.) Kühner	Agaricales	Lyophyllaceae			x		EM
Macrolepiota procera (Scop.) Singer	Agaricales	Agaricaceae			x	E	LS
Macrolepiota sp. Singer	Agaricales	Agaricaceae	x			E	LS
Marasimus sp1. Fr.	Agaricales	Marasmiaceae	x			E	LS
Marasmiellus chamaecyparidis (Hongo) Hongo	Agaricales	Omphalotaceae			x		LS
Marasmius arborescens (Henn.) Beeli	Agaricales	Marasmiaceae	x	x			LS
Marasmius candidus Fr.	Agaricales	Marasmiaceae	x			E	LS
Marasmius guyanensis Mont.	Agaricales	Marasmiaceae	x	x	x	E	LS
Marasmius oreades (Bolton) Fr.	Agaricales	Marasmiaceae	x	x		E	LS
Marasmius purpureostriatus Hongo	Agaricales	Marasmiaceae	x	x	x	E	LS
Marasmius scorodonius (Fr.) Fr.	Agaricales	Marasmiaceae			x	E	LS
Marasmius siccus Schwein. ex Fr.	Agaricales	Marasmiaceae	x	x		E	LS
Marasmius sp2. Fr.	Agaricales	Marasmiaceae	x	x	x	E	LS
Marasmius sp3. Fr.	Agaricales	Marasmiaceae	x		x	E	LS
Marasmius undatus (Berk.) Fr.	Agaricales	Marasmiaceae	x	x	x	E	LS
Micropsalliota sp. Höhn.	Agaricales	Agaricaceae		x			SS
Mycena griseoviridis A.H. Sm.	Agaricales	Mycenaceae		x	x		LS
Mycena interrupta (Berk.) Sacc.	Agaricales	Mycenaceae			x		LS
Mycena rhenana Maas Geest. & Winterh.	Agaricales	Mycenaceae	x	x	x		LS
Mycena rosea Gramberg	Agaricales	Mycenaceae			x		LS
Mycena sp1. (Pers.) Roussel	Agaricales	Mycenaceae			x		LS
Mycena sp2. (Pers.) Roussel	Agaricales	Mycenaceae		x			LS
Mycena stipata Maas Geest. & Schwöbel	Agaricales	Mycenaceae	x	x	x		LS
Mycena tenerrima (Berk.) Quél.	Agaricales	Mycenaceae		x			LS
Neopaxillus plumbeus Singer & Lodge.	Boletales	Serpulaceae		x	x		SS
Onnia tomentosa (Fr.) P.Karst.	Hymenochaetales	Hymenochaetaceae	x	x			WS
Panaeolina foenisecii (Pers.) Maire	Agaricales	Psathyrellaceae	x	x	x		SS
Panaeolus fimicola (Fr.) Quél.	Agaricales	Psathyrellaceae		x			DS
Panaeolus papilionaceus (Bull.) Quél	Agaricales	Psathyrellaceae		x	x		DS
Panellus mitis (Pers.) Singer	Agaricales	Mycenaceae	x	x			WS
Phaeolus schweinitzii (Fr.) Pat.	Polyporales	Fomitopsidaceae		x	x		WS
Phellinus noxius (Corner) G. Cunn.	Hymenochaetales	Hymenochaetaceae	x	x			PP
Phellinus populicola Niemelä	Hymenochaetales	Hymenochaetaceae			x		PP
Pholiota aurivella (Batsch) P. Kumm.	Agaricales	Strophariaceae		x	x	E	WS
Pleurotus luteoalbus Beeli	Agaricales	Pleurotaceae	x	x	x	E	WS
Pleurotus populinus O.Hilber & O.K.Mill.	Agaricales	Pleurotaceae		x	x	E	WS
Pleurotus pulmonarius (Fr.) Quél.	Agaricales	Pleurotaceae	x	x		E	WS
Pluteus longistriatus (Peck) Peck	Agaricales	Pluteaceae			x		LS
Pluteus mammillatus (Longyear) Minnis, Sundb. & Methven.	Agaricales	Pluteaceae	x				LS
Pluteus umbrosus (Pers.) P. Kumm.	Agaricales	Pluteaceae	x	x	x		LS
Polyporus brumalis (Pers) Fr.	Polyporales	Polyporaceae	x	x	x		WS
Polyporus tenuiculus (P. Beauv.) Fr.	Polyporales	Polyporaceae	x		x		WS
Polyporus varius (Pers.) Fr.	Polyporales	Polyporaceae	x	x	x		WS
Psathyrella candolleana (Fr.) Maire	Agaricales	Psathyrellaceae	x	x	x		WS
Psathyrella corrugis (Pers.) Konrad & Maubl.	Agaricales	Psathyrellaceae	x	x			WS
Psathyrella multipedata (Peck) A.H. Sm.	Agaricales	Psathyrellaceae	x	x	x		WS
Psathyrella gracilis (Fr.) Quél.	Agaricales	Psathyrellaceae	x	x	x		WS
Psathyrella ammophila (Durieu & Lév.) P.D. Orton	Agaricales	Psathyrellaceae	x	x	x		WS
Psathyrella piluliformis (Bull.) P.D.Orton	Agaricales	Psathyrellaceae	x	x	x		WS
Psathyrella sp1. Fr. ex Quél.	Agaricales	Psathyrellaceae		x			WS
Psathyrella sp2. Fr. ex Quél.	Agaricales	Psathyrellaceae	x				WS
Psathyrella sp3. Fr. ex Quél.	Agaricales	Psathyrellaceae	x	x			WS

(*continued on next page*)

Table 2 (*continued*)

Taxa	Order	Family	T	A	B	E	LM
Psathyrella sp4. Fr. ex Quél.	Agaricales	Psathyrellaceae	x				WS
Psathyrella sp5. Fr. ex Quél.	Agaricales	Psathyrellaceae	x	x	x		WS
Psathyrella sp6. Fr. ex Quél.	Agaricales	Psathyrellaceae			x		WS
Pseudoclitocybe cyathiformis (Bull.) Singer	Agaricales	Tricholomataceae	x				LS
Pseudohydnum gelatinosum (Scop.) P.Karst.	Auriculariales	Exidiaceae	x	x	x		WS
Pseudoomphalina pachyphylla (Fr.) Knudsen.	Agaricales	Tricholomataceae	x				LS
Psilocybe ovoideocystidiata Guzmán & Gaines	Agaricales	Strophariaceae	x		x		LS
Psilocybe samuiensis Guzmán, Bandala & J.W.Allen	Agaricales	Strophariaceae		x			LS
Ramaria stricta (Pers.) Quél.	Gomphales	Gomphaceae	x	x	x	E	EM
Rhizopogon luteolus Krombh.	Boletales	Rhizopogonaceae	x	x	x	E	EM
Rhizopogon pseudoroseolus A.H. Sm.	Boletales	Rhizopogonaceae	x			E	EM
Russula gracillima Jul. Schäff.	Russulales	Russulaceae			x		EM
Russula ochroleuca Pers.	Russulales	Russulaceae	x	x	x		EM
Sarcoscypha occidentalis (Schwein.) Sacc.	Pezizales	Sarcoscyphaceae	x	x	x		WS
Scleroderma areolatum Ehrenb.	Boletales	Sclerodermataceae			x		EM
Scleroderma aurantium (L.) Pers.	Boletales	Sclerodermataceae			x		EM
Sebacina concrescens (Schwein.) P. Roberts	Auriculariales	Exidiaceae			x		EM
Skeletocutis carneogrisea A.David	Polyporales	Polyporaceae		x	x		WS
Suillus luteus (L.) Roussel	Boletales	Suillaceae			x	E	EM
Suillus sp. Gray	Boletales	Suillaceae			x		EM
Terfezia leonis (Tul. & C.Tul.) Tul.	Pezizales	Terfeziaceae	x		x	E	EM
Termitomyces clypeatus R.Heim	Agaricales	Lyophyllaceae	x	x	x	E	LS
Termitomyces microcarpus (Berk. & Broome) R. Heim	Agaricales	Lyophyllaceae	x		x	E	LS
Termitomyces robustus (Beeli) R. Heim	Agaricales	Lyophyllaceae	x	x		E	LS
Termitomyces sp. R. Heim	Agaricales	Lyophyllaceae	x	x	x	E	LS
Termitomyces schimperi (Pat.) R.Heim	Agaricales	Lyophyllaceae	x	x	x	E	LS
Trichaptum biforme (Fr.) Ryvarden	Polyporales	Polyporaceae		x			WS
Tricholoma portentosum (Fr.) Quél.	Agaricales	Tricholomataceae			x	E	EM
Tricholoma saponaceum (Fr.) P.Kumm.	Agaricales	Tricholomataceae	x			E	EM
Tricholoma sp. (Fr.) Staude	Agaricales	Tricholomataceae	x			E	EM
Tricholomopsis rutilans (Schaeff.: Fr.) Sing.	Agaricales	Tricholomataceae	x	x	x		WS
Volvariella speciosa (Fr.) P.Kumm.	Agaricales	Pluteaceae	x		x		LS
Wilcoxina mikolae (Chin S. Yang & H.E. Wilcox) Chin S. Yang & Korf	Pezizales	Pyronemataceae	x		x	E	EM
Xeromphalina caulicinalis (Bull.) Kühner & Maire	Agaricales	Mycenaceae	x	x	x		WS
Xeromphalina tenuipes (Schwein.) A.H.Sm.	Agaricales	Mycenaceae	x	x	x		WS
Xerula radicata (Relhan) Dörfelt	Agaricales	Physalacriaceae	x	x			PP
Xylaria hypoxylon (L.) Grev.	Xylariales	Xylariaceae	x				WS
Xylaria scruposa (Fr.) Fr.	Xylariales	Xylariaceae	x		x		WS

Note: Abbreviations: T = the Taragedam forest group; A = the Alemsaga forest group; B = the Banja forest group; x = sporocarp production; E = edible; LM = mode of life; PP = Plant pathogen; EM = ectomycorrhizal, SS = Soil saprotroph, WS = Wood saprotroph, LS = Litter saprotroph, DS = Dung saprotroph.

Table 3
Macrofungal and vascular plant richness and diversity indices in three church forests in Northern Ethiopia.

Forest status	Banja forest	Taragedam forest	Alemsaga forest
All macrofungi			
Richness	22.56 ± 3.02a	18.44 ± 2.34a	22.67 ± 1.84a
Shannon	2.03 ± 0.23a	2.57 ± 0.13a	2.06 ± 0.20a
Simpson	0.73 ± 0.05b	0.88 ± 0.02a	0.77 ± 0.05ab
Evenness	0.38 ± 0.03c	0.60 ± 0.03a	0.47 ± 0.02b
Vascular plants			
Richness	5.78 ± 0.55c	16.89 ± 1.25a	12.67 ± 1.04b
Shannon	1.38 ± 0.12b	2.18 ± 0.08a	2.04 ± 0.07a
Simpson	0.67 ± 0.05b	0.83 ± 0.02a	0.82 ± 0.02a
Evenness	0.73 ± 0.04a	0.55 ± 0.03b	0.63 ± 0.03ab
Ectomycorrhizal fungi			
Richness	3.88 ± 0.64a	2.57 ± 0.3a	2.67 ± 0.21a
Shannon	1.09 ± 0.1a	0.80 ± 0.06a	0.90 ± 0.07a
Simpson	0.61 ± 0.03a	0.53 ± 0.02a	0.57 ± 0.02a
Evenness	0.85 ± 0.05a	0.91 ± 0.05a	0.94 ± 0.03a

Note: Values shown are means ± the SE of the mean. Different lowercase letters indicate a significant difference ($p < 0.05$) in richness or diversity between forests.

forests and classified into 258 fungal taxa (Table 2). Although identification of sporocarps down to species level was not possible, out of the total taxa collected, 155 (60%) were identified to species level, 33 (13%) to genus level and further 69 (27%) were completely unidentified. The unidentified sporocarps were excluded from further analysis. The Basidiomycota was the dominant phylum and was represented by 10 orders, 62 families, 90 genera, and 180 species. Ascomycota was represented by three orders, seven families, seven genera, and eight species (Table 2).

Among the taxa identified, the Agaricaceae was the most diverse family with 58 different taxa, followed by Psathyrellaceae (26), Tricholomataceae (22), and Mycenaceae (20), which together accounted for 33.6% of the total collected taxa (Table 2). The most abundant genera were *Termitomyces*, *Psathyrella*, *Leucoagaricus*, *Marasmius*, and *Mycena*. The proportions of macrofungal taxa at the genus level are provided (Fig. 2A). The Agaricales was the most prevalent order in the three forests (77.66%). Since many Agaricales are conspicuous macrofungi, it is not surprising to find a higher abundance during sampling. The family to genus and genus to species ratios were 0.70 and 0.50, respectively. Total numbers of fungal taxa per family encountered in the three studied forests are provided (Fig. 2B). In terms of the trophic groups, the majority of species were saprophytic (81%) followed by ectomycorrhizal (14%) and parasitic taxa (4%).

The accumulation curves (Fig. 3A) generated for the taxa identified in the three forests show that the saturation of macrofungal richness was not reached during the survey given that the curves showed a steady increase with additional samplings. Although there was no significant difference in species richness between the three forests ($p > 0.05$), the taxa accumulation curve for Banja forest showed a relatively steeper rising slope and yielded higher macrofungal richness values than the other forests. The highest macrofungal diversity values were obtained for Taragedam forest; however, diversity was not significantly different to that of the other two forests (Fig. 3B). The occurrence of macrofungi was more uneven in Banja forest than in the other forests (Table 3), with no fungal species found at all sampling events and certain macrofungal

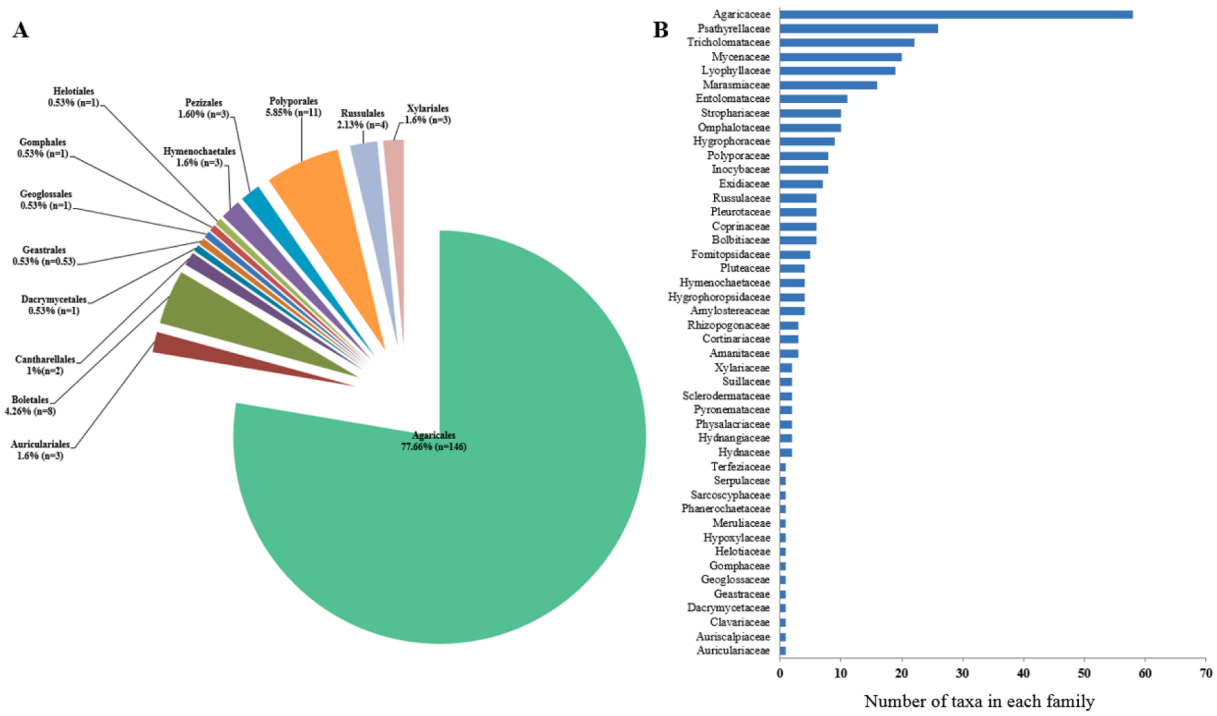

Fig. 2. (A) The proportions of macrofungal taxa at the genus level (name of genus; the number of species; percentage); and (B) total numbers of fungal taxa per family encountered in the three studied forests.

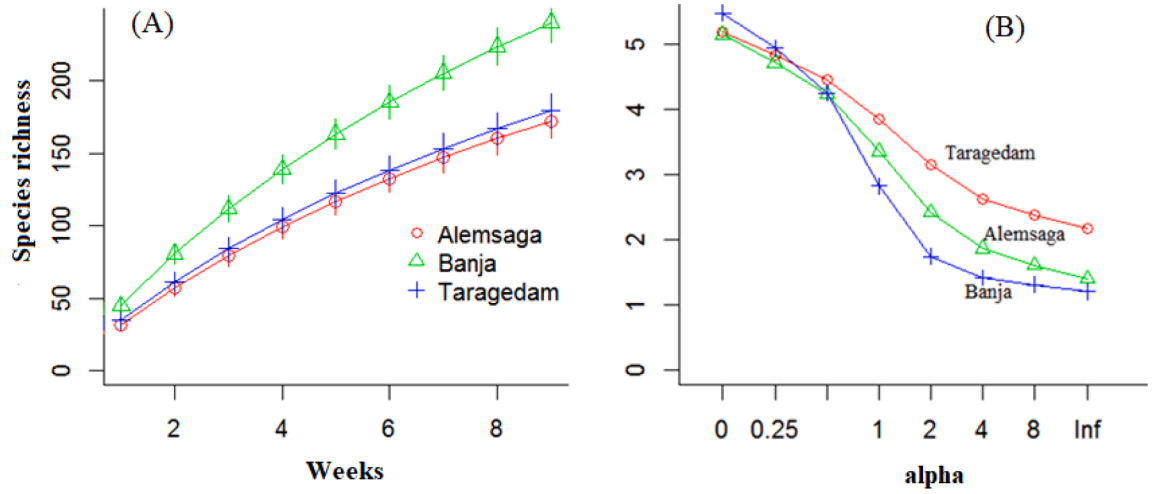

Fig. 3. Taxa accumulation curves generated for the fungal community found in the three studied forests using a rarefaction sample-based estimator (A) and Rényi diversity profiles (B).

species were more dominant in Banja forest than in the other two forests.

The Shannon index and richness for vascular plants were significantly correlated with Shannon and Simpson diversity indices for the fungal communities (Fig. 4). Interestingly, for all these variables, the highest values were found in Taragedam forests and the lowest values were observed in Banja forests (Table 3).

Although the three forests were not significantly different ($p > 0.05$; Table 3) in terms of measure of diversity of their ectomycorrhizal fungal species and richness, more ectomycorrhizal species were collected from Banja forest (20) than from Taragedam (15) or Alemsaga (7) forests (Table 2).

3.2. Sporocarp production

Taragedam forest produced the greatest quantity of sporocarps (25.4 kg ha^{-1}), although production levels were not significantly different ($p = 0.63$) to those of Alemsaga forest (21.6 kg ha^{-1}; Fig. 5). However, both of these forests produced significantly greater quantities of sporocarps than Banja forest ($p < 0.05$).

Sixty eight (36%) of the total macrofungi collected were deemed to be edible (Table 2). Banja forest produced the greatest quantity of edible fungi (mean fresh weight, 1.8 kg ha^{-1}) and Alemsaga forest produced the least (0.4 kg ha^{-1}); however, the production of edible species did not differ significantly among the three forests (Fig. 5; $p = 0.01$).

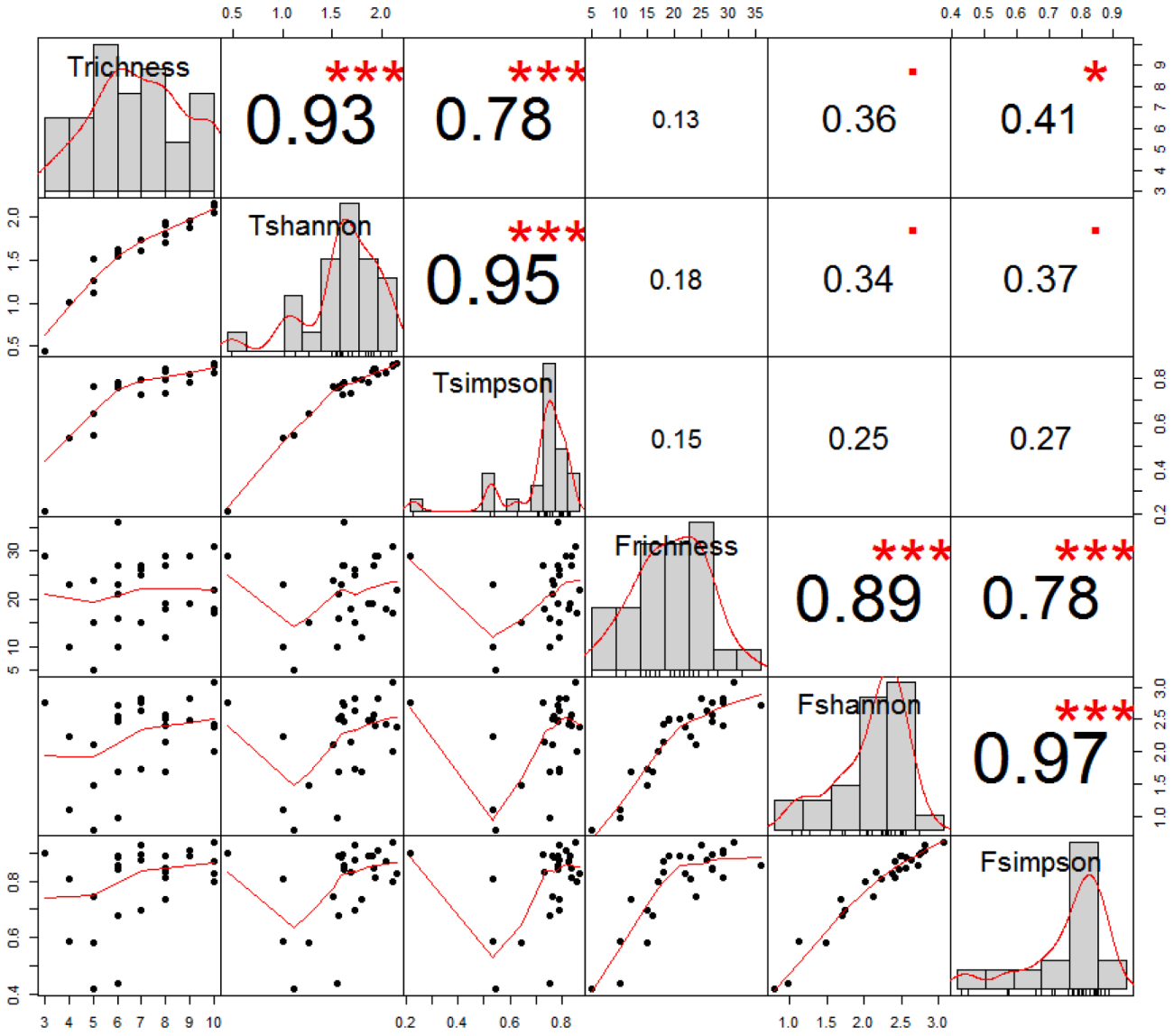

Fig. 4. Scatter plot matrices showing correlation coefficients between the entire tree and macrofungal variables and their significance levels. Abbreviations: T = tree, F = fungi. On the bottom of the diagonal, bi-variate scatter plots with a fitted line are displayed. On the top of the diagonal, the value of the correlation is shown, plus the significance level of the *p*-values, which are indicated by red asterisks. *p-values*: ***, <0.001; **, <0.01; and *, <0.05; *<0.1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.3. Macrofungal communities and edaphic variables

The perMANOVA analyses indicated the three church forests differed significantly in their macrofungal composition ($F = 2.05$, $R^2 = 0.14$, $p = 0.001$; Fig. 6). With respect to the explanatory variables, categorized edaphic, climate and location parameters were correlated to the macrofungal community composition ($p < 0.05$; Table 4). Of these, Mantel test confirmed that location variables aggregately had a strongly significant effect on macrofungal community structure ($p = 0.000$) than that of the climate ($p = 0.009$) and the edaphic variables ($p = 0.112$). The significance of each explanatory variable and their aggregated contribution to the difference of the macrofungal community compositions is provided (Table 4).

The SIMPER analysis also identified macrofungal species that distinguished between the three forests (Table 5). The overall between-group dissimilarity (Sørensen) was 88.73% for Taragedam and Alemsaga forests, 94.44% for Alemsaga and Banja forests, and 93.76% for Taragedam and Banja forests. In this regard, the *Coprinellus* species are found the most important in distinguishing all forest locations along with the others (Table 5). The cumulative contribution of the most influential macrofungal species for the dissimilarity between these forests is shown in Table 5.

4. Discussion

Although fragmentation poses major threats to forest ecosystems, the Dry Afromontane forests in the highland region of Ethiopia, including forest fragments owned by the church or located around church forest territories, are considered to be major reservoirs of biodiversity (Aerts et al., 2016; Aynekulu et al., 2016; Darbyshire et al., 2003; Nyssen et al., 2014). This study provides a comprehensive analysis of macrofungal communities and showed the differences in fungal community compositions of the fragmented forest systems in Northern Ethiopia. The difference in macrofungal species among the three forests might be due to the difference in vegetation composition or the variation in ecological factors such as soils, which are among the most important factors that could affect macrofungal species (Oria-de-Rueda et al., 2010). The availability of suitable substrates due to the difference in plant inputs on

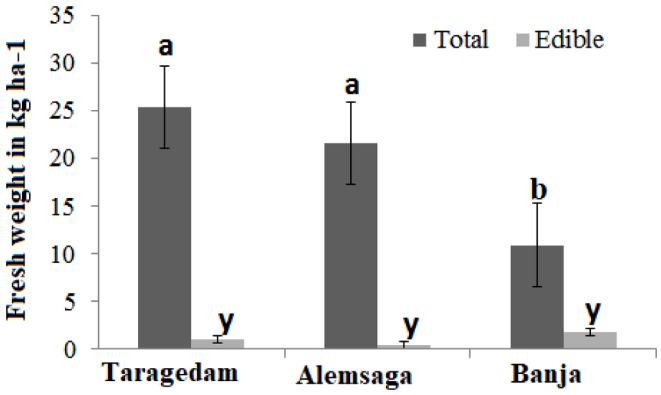

Fig. 5. Fresh weight of sporocarps collected from three forests in Northern Ethiopia. Dark-gray bars indicate the total fungal species collected; light-gray bars indicate edible fungal species. The data shown are means ± the SE of the mean. Values with different lowercase letters are significantly different ($p < 0.05$).

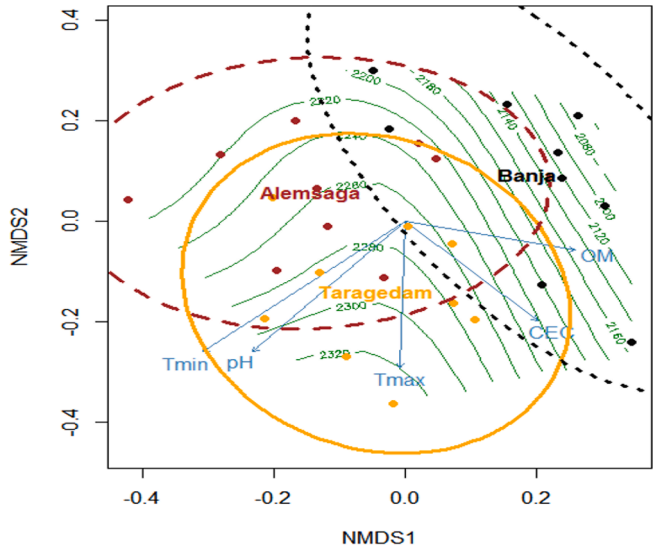

Fig. 6. Non-metric Multidimensional Scaling (NMDS) ordination graph with fitted explanatory variables based on dissimilarities calculated using the Bray–Curtis index of macrofungal communities compositions from plots in the three forests in Northern Ethiopia with altitude displayed as isolines. Arrows represent environmental variables that were most significantly ($p < 0.005$) related to ordination. Ellipses indicate forest groups with the names indicated. The explanatory variables are shown in blue color: CEC, cation exchange capacity; OM, organic matter; Tmax, maximum daily temperature; and Tmin, minimum daily temperature. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 4
Significance of the explanatory variables for macrofungal community compositions. Numbers in bold indicate a highly significant effects ($p < 0.001$).

Sources	Contribution%	Variables	pseudo-F	*p*
Edaphic variables	7.13%	pH	0.4358	**0.004**
		CEC	0.3191	0.010
		OM	0.2767	**0.017**
Climate	14.11%	Tmax	0.3441	0.004
		Tmin	0.6150	**0.001**
Spatial factors	33.92%	Latitude	0.6162	**0.001**

Note: the variables are: CEC, cation exchange capacity; OM, organic matter; Tmax, maximum daily temperature and Tmin, minimum daily temperature.

Table 5
Summary of similarity percentage (SIMPER) results showing the cumulative total contribution (50% cut-off) and the contribution (%) of the most influential species to the dissimilarity between stands in the three forests in Northern Ethiopia.

Species	Individual contribution to the dissimilarity	Cumulative contribution to the dissimilarity	Edibility status
Alemsaga and Banja forests			
Coprinellus disseminatus	13.07	13.07	
Coprinellus micaceus	10.37	23.44	
Coprinellus micaceus	6.49	29.93	
Geastrum triplex	5.35	35.27	
Marasmius guyanensis	4.19	39.46	edible
Psathyrella sp.	3.33	46.31	
Agaricus megalosporus	3.06	49.37	edible
Taragedam and Alemsaga forests			
Coprinellus micaceus	7.42	7.42	
Sarcoscypha occidentalis	6.02	13.44	
Geastrum triplex	5.36	18.80	
Psathyrella sp3.	3.83	30.81	
Psathyrella candollena	3.60	34.41	
Gymnopus dryophilus	3.14	37.55	
Marasmius guyanensis	2.92	40.47	edible
Phellinus noxius	2.74	43.20	
Termitomyces robustus	2.24	45.44	edible
Psathyrella sp.	2.04	47.49	
Marasmius guyanensis	1.71	49.19	edible
Polyporus varius	1.69	50.88	
Taragedam and Banja forests			
Coprinellus disseminatus	13.21	13.21	
Coprinellus micaceus	10.45	23.67	
Sarcoscypha occidentalis	5.68	29.34	
Marasmius guyanensis	3.90	33.24	edible
Geastrum triplex	3.50	40.63	
Agaricus megalosporus	3.08	43.71	edible
Crepidotus mollis	2.37	46.08	edible
Xylaria scruposa	1.96	48.04	
Crepidotus applanatus	1.85	49.89	edible
Psathyrella corrugis	0.93	67.45	
Psathyrella candollena	0.89	68.35	
Psathyrella candolleana	0.87	69.22	
Psathyrella sp.	0.84	70.05	

the forest floor could be also a factor explaining the variation in fungal species composition among the three forests. The retention of plant residues is thought to enhance fungal activity by promoting moisture retention and providing a source of organic carbon, which is important for fungal survival and growth (Blumfield and Xu, 2003). Thus, the differences in substrate richness among these three forests can influence the diversity and richness of macrofungal species (Reverchon et al., 2010). Besides, the variation in macrofungal species among the three forests probably reflect the heterogeneity of these habitats, resulting in

variations in microclimate and, hence, variations in moisture, temperature, and other factors among these different forest systems (Suggitt et al., 2011) that influence the richness and productivity of fungi (Gómez-Hernández and Williams-Linera, 2011). However, the characteristics of the macrofungi themselves could also explain the variation in fungal species among the three forests. Many macrofungal species are believed to fruit spontaneously, with no consistent pattern of occurrence at any time given favorable environmental conditions and suitable substrates (Piepenbring et al., 2012; Tibuhwa et al., 2011). Furthermore, fungal sporocarps are short-lived and may last only a few days before decomposing or being eaten and, therefore, may not have been observed during our weekly surveys (Maurice et al., 2021).

Habitat fragmentation can influence the fungal communities in forests (Sapsford et al., 2017). Lack of symbiotic fungal colonization in these systems may be a limiting factor for seedling establishment, which is the main regeneration ecological process in the studied forests. Thus, trees species more dependent on mycorrhizal fungi could potentially have a substantial decrease in recruitment, particularly in the rehabilitation or conservation scheme of the forests (Tonn and Ibáñez, 2017). Although, recently studies reported the availability of Ectomycorrhizal (ECM) hosts plant from the tropic regions (Tedersoo et al., 2010), the ECM associations has long been considered rare or absent from tropical forest ecosystems (Corrales et al., 2018), particularly of the African forests like that of Ethiopian. A previous study also reported the absence of ECM fungi in the Dry Afromontane forests of Ethiopia (Dejene et al., 2017a). Though the majority of the species collected in this study were saprophytic, about 14% were characterized as ectomycorrhizal. Species from the general of *Amanita, Entoloma, Geastrum, Laccaria, Russula* and *Rhizopogon* were reported from these studied forests. Although the mycorrhizal status of each tree species in the study area are unknown (Table S1), the existence of ECM species may be due to the diverse vegetation (Friis et al., 2010a,b) and, hence, there may be more trees present that can act as hosts for mycorrhizal fungi (Hailemariam et al., 2013; Wubet et al., 2003). Also, the existence of mycorrhizal species in the studied forests can be explained by the dispersion of mycorrhizal inocula from nearby plantation forests that are supposed to host trees. The plantations are constituted by *Eucalyptus camaldulensses*, *Eucalyptus globulus*, *Pinus patula* and other highland *Aacacia* species. Thus, the findings presented here may have important implication for the indigenous forest system for the maintenance of functional fungal diversity in Ethiopia (Dejene et al., 2017a). Besides, the coexistence of mycorrhizal fungi with natural forests has many practical advantages, such as the exchange of water and nutrients through hyphal networks (Brundrett, 2002; Brundrett, 2004). They are also commonly the key determinants of plant population and community dynamics in the forests systems (Tedersoo et al., 2020). This result presents an insight into the conservation of fungal functional groups in the forest system in the study areas as these functional groups are important for the rehabilitation and conservation of these fragmented forests as the fungi, particularly of the ECM, species could potentially have a substantial role in recruitments seedlings (Tonn and Ibáñez, 2017). Thus, further studies on tropical ectomycorrhizae are deeply needed, particularly in Africa where the vegetation resource is immense with significant livelihood and environmental benefits.

In Ethiopia, wild mushrooms have been used for their nutritional and medicinal properties (Abate, 2014; Dejene et al., 2017b; Tuno, 2001). Equally to other wild edibles, they have also been used as a coping food during food shortage periods (Alemu et al., 2012; Sitotaw et al., 2020). In some local markets mushrooms are also available where they are sold by the local people to earn some income to supplement the household economy (Abate, 2014). The sporocarp productions obtained in this study were not high. Although further research is needed to verify the claim, the lower biomass yield reported here could be explained by the single tone species and the species composition. Some of the species were collected in a single time during the collection period. Majority of the species were saprophytic fungi and are characterized by low biomass productions (Gassibe et al., 2011; Mediavilla et al., 2014). However, valuable edible macrofungal species belonging to the *Calvatia*, *Laetiporus*, *Pleurotus*, *Termitomyces* sp., and *Macrolepiota* genera were also collected in this study. Among these edible species, *Termitomyces* sp. is highly regarded by local people in southwest Ethiopia because of its good taste and aroma (Abate, 2014). Although the overall quantity of sporocarp biomass produced in the studied forests was low, the most productive species had biomass values of approximately 0.46 kg $ha^{-1}yr^{-1}$, which provides an insight into the potential production levels of valuable sporocarp species. This also provides a starting point in terms of broadening the management and conservation of fragmented forests for the production of non-timber forests products in Ethiopia. In addition, important ectomycorrhizal species such as *Tricholoma*, *Rhizopogon*, and *Suillus* were also found in this study. The presence of these species in the study areas may be due to the high level of plant diversity in church forests, which may provide ectomycorrhizal fungi with a very broad host range (Roy et al., 2008; Smith and Read, 2008) and, hence, there may be a number of trees that can act as hosts for mycorrhizal fungi (Hailemariam et al., 2013; Wubet et al., 2003). Interestingly, some of the fungi in the genera of *Trichoderma* could also function as biocontrol activity (Vinale et al., 2008) in the forests. In addition, the overall landscape connectivity of exotic tree plantations to nearby fragmented natural forests could also contribute to the presence of ectomycorrhizal fungi in the fungal community assembly (Boeraeve et al., 2018; Peay and Bruns, 2014; Vannette et al., 2016). In these kind of plantations, the local communities in Ethiopia are collecting edible mushrooms, particularly in the Southwest part of the country for their subsistence use or to generate income in some cases (Dejene et al., 2017c). However, this finding may have important implications for indigenous forest systems in terms of the maintenance of valuable macrofungal species for commercial production in Ethiopia (Dejene et al., 2017a). Thus, our survey of macrofungi provides an insight into the valuable fungal functional groups present in the fragmented Dry Afromontane forest system of Ethiopia, which may aid their conservation and management through increasing their economic outputs through NTFPs production in addition to other forests products.

Vascular plants are often used as a surrogate for total biodiversity (Schmit et al., 2005; Sætersdal et al., 2004). Thus, the vascular plants have also been considered a useful indicator of fungal diversity in management programs based on the fact that a species-rich plant community assumed to have more ecological niches or microhabitats available for fungi than a species-poor community (Chiarucci et al., 2005). However, in this study reported a lack of congruence between the species richness of vascular plants and macrofungi in line with Rudolf et al. (2013) who indicted the negative correlation between the two communities regarding species richness. Such correlation might be due to the fact that higher species richness of vascular plants could cause variation of light availability for the ground species, including macrofungi, due to canopy (Härdtle et al., 2003). Thus, the fungal community and their species richness could be influenced by the amount and variation of light availability on the forest floor (Rudolph et al., 2018). The low correlation of species richness of vascular plant and fungi might be due to the fact that the pooled plant species richness not always maximize species richness of other organisms, including all macrofungi (Chiarucci et al., 2005). This is probably because of the special ecological requirements of the fungal that constitute the composition of the community, which are linked to substrate or other factors related to habitats such as edaphic variables (Liang et al., 2015; Rillig et al., 2015). In contrary to this, however, we found an indication of the positive correlation in the Shannon diversity index values of the two communities. Such association could suggests that the tree species identity can be used as a factor for macrofungal diversity (Otsing et al., 2021). Gabel and Gabel (2007) and McMullan-Fisher et al. (2010) also reported positive correlations between plant identities and fungal diversity based on abundance as a measure of diversity. This association is particularly evident for saprotrophic fungi because saprotrophic fungi increase their

community diversity through the provision of wider variety of substrates from the diverse vegetation to establish facilitative interactions in the systems (Gessner et al., 2010; Wu et al., 2019; Zhang et al., 2018), which in turn promote their higher levels of diversity (Ye et al., 2019). The observed correlation of plants and macrofungi diversity indices may suggest the influence of habitat microheterogeneity, causing a positive correlation between both plant diversity and macrofungal diversity (Rudolf et al., 2013). Thus, the promotion of vascular tree plantations in these fragmented forest systems, such as enrichment plantings or assisted natural regeneration systems, should offer suitable habitats with variable microclimates that would influence and/or assist the diversity and productivity of fungal species in the fragmented Dry Afromontane forests of Ethiopia.

Studies demonstrated that fungal community composition can be governed by various environmental variables and landscape heterogeneity (Bahram et al., 2015; Ferrari et al., 2016; Peay et al., 2010; Tedersoo et al., 2014b). Thus, evaluating the fungal communities in different ecosystems is essential to filter out the relative contributions of environmental factors to fungal diversity and composition in an ecosystem (Tian et al., 2018). In this study, the NMDS ordination against the environmental variables is shown distinct macrofungal pattern of the three studied forests. Of the categorized variables, the spatial factors contributed highly for driving the macrofungi assembly together with climate and edaphic variables. This may an indication that the climate, and soil characteristics together are vital in setting spatial variation (Chen et al., 2015), reflecting the combined effects of these variables on the vegetation and thus on macrofungal community (Li et al., 2020). Although the relative degree to which organisms can move is determined by multiple factors, Golan and Anne (2017) indicated that distances as a spatial factor could affect the dispersal of fungal propagules. This could affect the large scale connectively of the different fungal species to form similarity in community structure or morphology (Calhim et al., 2018). However, this needs further investigation to provide an ecological meaningful explanation from our study areas. Conversely, specific fungal species are likely to respond to environmental variables, mainly edaphic parameters, in different ways (Cozzolino et al., 2016; Koide et al., 2014), and, thus, in turn, the composition of the fungal community is directly correlated with edaphic variables (Cozzolino et al., 2016). In particular, pH is known to be the most critical soil characteristic affecting the composition and structure of fungal communities across different continents (Docherty et al., 2015; Fierer and Jackson, 2006; Zhang et al., 2016). Similarly in this study also, soil pH appeared to be correlated with fungal species composition. We found that the presence of greater numbers of macrofungal species was associated with lower pH values. A relatively lower pH values were found in the Alemsaga and Banja forests. This supports the findings of Puangsombat et al. (2010) and Zhang et al. (2016) who reported that higher pH levels negatively influenced fungal community structure, probably because a higher pH restrains the expansion of fungi and the production of sporocarps. However, the species from the Taragedam forests showed exceptional ordination towards a relatively higher end point of the pH gradient. This might be associated with their adaptability of the species to higher pH values in the soil. We also found that CEC and EC are explanatory factors for macrofungal composition. Although the exact role that the CEC and EC play in macrofungal composition and sporocarp production is not fully understood, Crabtree et al. (2010) observed that fungal species richness was low, particularly when the CEC was high. This is probably because the CEC and EC influence nutrient availability, soil pH, and soil reactions to other ameliorants in the soil (Ogeleka et al., 2017). The majority of species in our ordination were directed towards plots with low CEC and EC values. This is probably also because soils with a high CEC are less susceptible to the discharge of base saturation as base saturation is an important factor in the distribution of macrofungal species. Base saturation indicates the proportion of sites occupied by basic cations such as Ca^{2+}, Mg^{2+}, Na^{+}, and K^{+} (Zheng et al., 2019). These elements are vital in many physicochemical processes, such as photosynthesis (He et al., 2017) and, thus, can affect plant photosynthesis and, hence, the amount of carbon that is available to fungi in the soil (Shi et al., 2014).

Organic matter also appeared to be an important factor associated with the composition of macrofungi in the studied forests. This is likely because fungi typically extend their mycelia at the soil–litter interface (Boddy et al., 2009) and, thereby, organic matter influences mycelial outgrowth and network formation (Zakaria and Boddy, 2002). Organic matter also influences the fungal community through its impact on the water-holding capacity of soil and nutrient availability (Harrington, 2003). Thus, a high level of organic matter accumulation implies a high level of macrofungal assembly, particularly of saprophytic species. However, the accumulation of organic matter in some cases may also attract the ectomycorrhizal fungi as some of the ECM species can be benefit from organic matter decomposition in a similar manner to free-living saprotrophs; that is, as a source of reduced C compounds to support metabolism (Lindahl and Tunlid, 2015). Nitrogen was also correlated with the composition of fungal species. This finding is in line with those of Kranabetter et al. (2009) and Reverchon et al. (2010), who reported that fungi assembly increased along soil N gradients. This is because nitrogen can influence the formation of mycelium in the soil and play a role in sporocarp formation (Trudell and Edmonds, 2004). Furthermore, many fungal species can adapt to more nitrogen-rich sites (Kranabetter et al., 2009; Toljander et al., 2006). In addition to the edaphic variables, the analysis also showed a significant role of max and minimum temperature on the composition of macrofungal composition. This may be due to the fact that the mycelium of the fungal species is more readily affected by atmospheric changes (Salerni et al., 2002), being more superficial specifically for those saprotrophs species that constitute mainly the community composition of our studied forests. Furthermore, the temperature can play role in nutrient cycling process (Geng et al., 2017). An increase in temperature generally facilitates the decomposition organic matter in the soil and accelerates the availability of nutrients. Thus, the fungal species likely are responding to this condition and form distinct communities, particularly of the fungi that are soil dependet as a substrate (Nicolás et al., 2019).

5. Conclusions

We investigated the diversity and composition pattern of macrofungi in three church forests in Northern Ethiopia to help us to understand the strategies required for the management and conservation of these remnant Dry Afromontane forests and the crucial roles played by fungi in the management and protection of these forest systems. The diversity indexes and community composition of macrofungi in the study areas were influenced by site conditions, including vascular plant diversity and soil fertility gradients. From the analysis on fungi and plant diversity indices, we can see that the species richness of macrofungi is independent of the diversity and richness of vascular plant communities. In our analysis, no correlations were observed for richness, suggesting that richness of vascular plants cannot be used as a proxy for macrofungi richness. However, a positive correlation was found between the two communities for their diversity Shannon index, indicating the tree identity might be used as a factor for macrofungal diversity as there was a highest fungal diversity value in forests with the highest level of tree diversity values. Unsurprisingly, macrofungal communities as a whole were influenced by edaphic variables given that edaphic variables are the main factors affecting mycelial development and, hence, the production of sporocarps by different macrofungal species. Thus, the promotion of vascular tree diversity in fragmented forest systems by enrichment plantings or assisted natural regeneration management systems would offer suitable habitats with variable microclimates that should assist macrofungal species diversity and productivity in the fragmented Dry Afromontane forests of Ethiopia. In addition, the effects of the aforementioned management practices on soil fertility should be taken into consideration owing to the important relationship between

edaphic variables and macrofungal composition in these forests. Forests and sites showed a significant influence in the composition of the fungal communities associated. Therefore, conservation of a higher number of these fragmented forests, can lead to the conservation of a higher fugal richness in an overall landscape scale. Our survey also revealed the presence of valuable edible macrofungal species belonging to the *Tricholoma*, *Suillus*, and *Termitomyces* genera, which could potentially be marketed and, hence, could provide supplementary incomes to forest-dependent local people and forest managers. Thus, we suggest that the production of valuable non-timber forest products such as wild mushrooms should be incorporated into management and conservation strategies for these fragmented forest systems. Moreover, the application of the baseline information provided in this study could assist other countries that are facing similar forest conservation issues due to deforestation and forest fragmentation.

CRediT authorship contribution statement

Demelash Alem: Investigation, Data curation, Writing - original draft. **Tatek Dejene:** Supervision, Investigation, Writing - review & editing. **Juan Andrés Oria-de-Rueda:** Conceptualization, Methodology. **Pablo Martín-Pinto:** Supervision, Conceptualization, Methodology, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119391.

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