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SOSTENIBLE DE SISTEMAS FORESTALES

TESIS DOCTORAL

Insights into Mycosilviculture in Ethiopian Forests: Towards  
Sustainable Forestry and Food Security

**Perspectivas sobre Micoselvicultura en los bosques Etíopes:  
hacia la gestión forestal sostenible y la seguridad alimentaria**

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## Table of Contents

|  |           |
|--|-----------|
| Acknowledgment.....  | i         |
| Abstract.....  | vi        |
| Outline of the thesis.....   | xii       |
| List of original articles .....  | xiv       |
| <b>1. General introduction.....</b>  | <b>1</b>  |
| 1.1. Ethiopian vegetation, climate and topography.....   | 1         |
| 1.2. The forests of Ethiopia and their socio-ecological significance .....   | 2         |
| 1.3. The role of fungi in forest ecosystems .....  | 4         |
| 1.4. Key factors affecting fungal community dynamics.....  | 7         |
| 1.4.1. Effects of forest types and forest stands on fungal communities.....  | 8         |
| 1.4.2. Effects of climate on fungal communities.....   | 11        |
| 1.4.3. Effects of site characteristics on fungal communities .....   | 13        |
| 1.5. Gaps in knowledge .....   | 16        |
| 1.6. Need for this study .....   | 18        |
| 1.7. Scope of the Study .....  | 20        |
| <b>2. Objectives of the thesis .....</b>   | <b>22</b> |
| <b>3. Materials and methods .....</b>  | <b>25</b> |
| 3.1. The study area.....   | 25        |
| 3.2. Data sources .....  | 29        |
| 3.3. Field plots establishments (Studies I, II & III) .....  | 30        |
| 3.4. Sampling .....  | 31        |
| 3.4.1. Sporocarps sampling and species identification (Studies I & II) .....   | 31        |
| 3.4.2. Environmental variables sampling and analysis (Studies I, II, and III) .....  | 32        |
| 3.4.3. Sporocarps yield prediction and model development (Study II) .....  | 34        |
| 3.5. Molecular and bioinformatics analysis (Study III).....  | 34        |
| 3.6. Statistical analysis.....   | 35        |
| <b>4. Results.....</b>   | <b>40</b> |
| 4.1. Taxonomic identification of wild edible mushrooms (Studies I and II) and<br>arbuscular mycorrhizal fungi (Study III)..... | 40        |
| 4.2. Sporocarps production (Studies I and II) .....  | 41        |
| 4.3. Taxa composition and environmental variables (Studies I, II, and III).....  | 41        |

|  |           |
|--|-----------|
| 4.4. Predictive modeling of sporocarps yields (Study II).....  | 43        |
| 4.5. Synthesis of Ethiopian fungal biodiversity (Study IV) .....   | 43        |
| <b>5. Discussion.....</b>  | <b>48</b> |
| 5.1. Taxonomic identification of edible wild mushrooms (Studies I and II) and<br>arbuscular mycorrhizal fungi (Study III)..... | 48        |
| 5.2. Sporocarps production (Studies I and II).....   | 49        |
| 5.3. Taxa composition and environmental variables (Studies I, II, and III).....  | 51        |
| 5.4. Predictive modeling of sporocarps yields (Study II).....  | 57        |
| 5.5. Synthesis of Ethiopian fungal biodiversity (Study IV) .....   | 58        |
| <b>6. Conclusions.....</b>   | <b>63</b> |
| <b>7. Conclusiones .....</b>   | <b>66</b> |
| <b>8. References.....</b>  | <b>69</b> |
| <b>Original articles .....</b>   | <b>88</b> |

## Abstract

Ethiopian highlands harbor diverse forest resources covering a variety of ecosystems, yet these forests are increasingly threatened by land-use and land cover changes, including agricultural land expansion and deforestation. Despite their potential to support a wide range of non-timber forest products (NTFPs), such as edible wild mushrooms and soil fungi, limited studies have investigated mycological resources in these forests. The impacts of forest degradation and associated site-specific variables on macrofungal species and soil fungal communities remain poorly understood. Additionally, as native forests are replaced by monospecific plantation systems, the impact of these changes on macrofungal productivity, soil fungal community composition, and ecological interactions remains unknown. Therefore, this study aims to address these knowledge gaps by investigating the dynamics of fungal communities in Ethiopian forests, with implications for sustainable forestry practices, biodiversity conservation, and enhanced food security. Specifically, this thesis aimed to (a) assess the diversity of valuable macrofungal species across various areas of Ethiopia and compare the richness, sporocarps production, and community assemblages of edible macrofungi in native forests and non-native plantation forests, considering the influence of climatic and environmental factors (**study I**); (b) develop predictive yield classificatory models for wild edible mushrooms production in both forest systems (**study II**); (c) investigate the diversity and community composition of arbuscular mycorrhizal fungi (AMF) between both forest systems, as well as identify environmental variables that govern AMF community composition (**study III**); and (d) assess and provide a comprehensive synthesis of fungal biodiversity in Ethiopia, focusing on their distribution, threats, and conservation across various habitats and sites (**study IV**). For sporocarps sampling (**studies I and II**), 63 plots (100 m<sup>2</sup> each) were established across seven forest sites. Sporocarps (mushroom fruiting bodies) were sampled weekly during the main rainy season (July to August 2019) to assess abundance, species richness, and fresh weight. Composite soil samples were collected from each plot to analyze soil properties (e.g., organic matter, nitrogen, phosphorus), while climate data (e.g., temperature, rainfall) were recorded for each study area. Expert-guided field identification and morphological methods were used to identify the macrofungal species collected. For **study III**, soil fungal sampling was conducted in 45 plots (100 m<sup>2</sup> each) to investigate the composition of AMF communities and the site-specific variables influencing them. DNA metabarcoding of the ITS2 rDNA region was also employed to assess AMF communities. Predictive models were developed to estimate mushroom yield and identify key environmental variables influencing sporocarps production. Six alternative models were tested to optimize yield prediction. The findings from the study revealed that a total of 64 wild

edible fungal species, belonging to 31 genera and 21 families, were recorded. Species richness was significantly higher in natural forests (40 species) compared to plantation forests. Despite lower species richness, the sporocarps yield from plantation forests (2097.57 kg ha<sup>-1</sup> yr<sup>-1</sup>) was significantly greater than that from natural forests (731.18 kg ha<sup>-1</sup> yr<sup>-1</sup>). Saprotrophic fungi dominated the communities in both forest systems (92.19%), while ectomycorrhizal fungi accounted for only 6.25%. Economically and ecologically important species, including *Agaricus campestris*, *Tylopilus niger*, *Suillus luteus*, *Tricholoma portentosum*, and *Morchella americana*, were collected. Sporocarps production strongly correlated with soil organic matter, available phosphorus, available nitrogen, and daily minimum temperature. The composition of AMF communities showed significant variation between forest types, with a total of 193 AMF operational taxonomic units (OTUs) identified. Glomerales was the dominant order, comprising 67.9% of the AMF community. AMF community structure varied notably between natural and plantation forests, with species such as *Septoglomus fuscum*, *Diversispora insculpta*, and *Funneliformis mosseae* being particularly prevalent. In plantation forests, AMF community composition was influenced primarily by soil factors, including pH, organic carbon, available nitrogen, and phosphorus levels. In contrast, natural forest AMF communities were more strongly associated with rainfall and soil electrical conductivity. The findings indicate that promoting fungal species richness and sporocarps production enhances forest economic value and biodiversity, as edible wild mushrooms contribute to sustainable forestry practices and enhance food security. However, replacement of natural forests with plantations has marked impact on mushrooms productivity and AMF community composition. While plantation forests yield more sporocarps, they support lower fungal species richness and different AMF communities, which may affect long-term ecosystem health and nutrient cycling. Given the economic and ecological importance of wild mushrooms NTFPs, there is a need for forest management policies in Ethiopia that integrate mushroom production into broader conservation and management strategies. The predictive models developed in this study provide valuable tools for optimizing forest management in relation to climate, soil conditions, and forest type. In addition to the findings from the three **studies (I, II, and III)**, the synthesis of existing literature (**study IV**) revealed that Ethiopian forests hold vast potential for appreciated mycological resources across a wide geographical range in the country. However, land use land cover changes, agricultural land expansion, and limited integration of mycological resources as potential NTFPs pose significant threats to these resources. The recent Green Legacy initiatives in Ethiopia, through afforestation and reforestation programs, offer opportunities to promote mycosilviculture practices. The findings and implications of this study contribute

to Ethiopia's National Adaptation Plan, National Mitigation Plan, and National Determined Contributions, as well as the global Sustainable Development Goals (Agenda 2030), and Agenda 2063. These insights will help in promoting sustainable forestry practices, biodiversity conservation, and enhancing food security. Further studies are needed to investigate fungal responses to environmental factors across different forest systems and to enhance our understanding of fungal dynamics over space and time by establishing permanent study plots.

**Keywords:** *Ethiopia, forest types, mushroom, arbuscular mycorrhizal fungi, fungal diversity, natural forest, plantation forest.*

## Resumen

Las tierras altas de Etiopía albergan diversos recursos forestales que cubren diversos ecosistemas, pero estos bosques se ven cada vez más amenazados por los cambios en el uso y la cobertura del suelo, incluida la expansión de las tierras agrícolas y la deforestación. A pesar de su potencial para sustentar una amplia gama de productos forestales no madereros (PFNM), como hongos silvestres comestibles y hongos del suelo, se han realizado estudios limitados que examinaron los recursos micológicos habitados en estos bosques. Los impactos de la degradación forestal y las variables específicas del sitio asociadas sobre las especies de macrohongos y las comunidades de hongos del suelo siguen siendo poco conocidos. Además, a medida que los bosques nativos son reemplazados por sistemas de plantaciones monoespecíficas, el impacto de estos cambios en la productividad de los macrohongos, la composición de la comunidad de hongos del suelo y las interacciones ecológicas sigue siendo desconocido. Por lo tanto, este estudio tiene como objetivo abordar estas lagunas de conocimiento explorando la dinámica de las comunidades de hongos en los bosques Etíopes, con implicaciones para las prácticas forestales sostenibles, la conservación de la biodiversidad y la mejora de la seguridad alimentaria. Específicamente, esta tesis tuvo como objetivo (a) evaluar la diversidad de especies valiosas de macrohongos en varias áreas de Etiopía y comparar la riqueza, la producción de esporocarpos y los ensamblajes comunitarios de macrohongos comestibles en bosques nativos y bosques de plantación no nativos, considerando la influencia de factores climáticos y ambientales (**estudio I**); (b) desarrollar modelos predictivos de clasificación de rendimiento para la producción de hongos comestibles silvestres en ambos sistemas forestales (**estudio II**); (c) investigar la diversidad y la composición de la comunidad de hongos micorrízicos arbusculares (HMA) entre ambos sistemas forestales, así como identificar variables ambientales que gobiernan la composición de la comunidad de HMA (**estudio III**); y (d) evaluar y proporcionar una síntesis integral de la biodiversidad de hongos en Etiopía, centrándose en su distribución, amenazas y conservación en varios hábitats y sitios (**estudio IV**). Para el muestreo de esporocarpos (**estudios I y II**), se establecieron 63 parcelas (100 m<sup>2</sup> cada una) en siete sitios forestales. Los esporocarpos (cuerpos fructíferos de los hongos) se muestrearon semanalmente durante la principal temporada de lluvias (julio a agosto de 2019) para evaluar la abundancia, la riqueza de especies y el peso fresco. Se recolectaron muestras de suelo compuestas de cada parcela para analizar las propiedades del suelo (por ejemplo, materia orgánica, nitrógeno, fósforo), mientras que se registraron datos climáticos (por ejemplo, temperatura, lluvia) para cada área de estudio. Se utilizaron métodos de identificación de campo y morfológicos guiados por expertos para identificar las especies de

macrohongos recolectadas. Para el estudio III, se realizó un muestreo de hongos del suelo en 45 parcelas (100m<sup>2</sup> cada una) para investigar la composición de las comunidades de AMF y las variables específicas del sitio que las influyen. También se empleó la codificación de barras de ADN de la región del ADNr ITS2 para evaluar las comunidades de AMF. Se desarrollaron modelos predictivos para estimar el rendimiento de los hongos e identificar las variables ambientales clave que influyen en la producción de esporocarpos. Se probaron seis modelos alternativos para optimizar la predicción del rendimiento. Los hallazgos del estudio revelaron que se registraron un total de 64 especies de hongos comestibles silvestres, pertenecientes a 31 géneros y 21 familias. La riqueza de especies fue significativamente mayor en los bosques naturales (40 especies) en comparación con los bosques de plantación. A pesar de la menor riqueza de especies, el rendimiento de esporocarpos de los bosques de plantación (2097,57 kg ha<sup>-1</sup> año<sup>-1</sup>) fue significativamente mayor que el de los bosques naturales (731,18 kg ha<sup>-1</sup> año<sup>-1</sup>). Los hongos saprotróficos dominaron las comunidades en ambos sistemas forestales (92,19%), mientras que los hongos ectomicorrícicos representaron solo el 6,25%. Se recolectaron especies económica y ecológicamente importantes, incluidas *Agaricus campestris*, *Tylopilus niger*, *Suillus luteus*, *Tricholoma portentosum* y *Morchella americana*. La producción de esporocarpos se correlacionó fuertemente con la materia orgánica del suelo, el fósforo disponible, el nitrógeno disponible y la temperatura mínima diaria. La composición de las comunidades de AMF mostró una variación significativa entre los tipos de bosque, con un total de 193 unidades taxonómicas operativas (OTU) de AMF identificadas. Glomerales fue el orden dominante, que comprendía el 67,9% de la comunidad de AMF. La estructura de la comunidad de AMF varió notablemente entre los bosques naturales y las plantaciones, con especies como *Septoglomus fuscum*, *Diversispora insculpta* y *Funneliformis mosseae* siendo particularmente prevalentes. En los bosques de plantaciones, la composición de la comunidad de AMF estuvo influenciada principalmente por factores del suelo, incluidos el pH, el carbono orgánico, el nitrógeno disponible y los niveles de fósforo. En contraste, las comunidades de AMF de los bosques naturales estaban más fuertemente asociadas con la lluvia y la conductividad eléctrica del suelo. Los hallazgos indican que fomentar la riqueza de especies de hongos y la producción de esporocarpos mejora el valor económico y la biodiversidad de los bosques, ya que los hongos silvestres comestibles contribuyen a las prácticas forestales sostenibles y mejoran la seguridad alimentaria. Sin embargo, el reemplazo de los bosques naturales con plantaciones ha marcado el impacto en la productividad de los hongos y la composición de la comunidad de AMF. Si bien los bosques de plantación producen más esporocarpos, sustentan una menor riqueza de especies de

hongos y diferentes comunidades de AMF, lo que puede afectar la salud del ecosistema a largo plazo y el ciclo de nutrientes. Dada la importancia económica y ecológica de los PFNM de los hongos silvestres, existe la necesidad de políticas de gestión forestal en Etiopía que integren la producción de hongos en estrategias más amplias de conservación y gestión. Los modelos predictivos desarrollados en este estudio proporcionan herramientas valiosas para optimizar la gestión forestal en relación con el clima, las condiciones del suelo y el tipo de bosque. Además de los hallazgos de los tres estudios (I, II y III), la síntesis de la literatura existente (estudio IV) reveló que los bosques etíopes tienen un gran potencial para recursos micológicos apreciados en una amplia gama geográfica en el país. Sin embargo, los cambios en la cobertura del suelo, la expansión de las tierras agrícolas y la integración limitada de los recursos micológicos como posibles PFNM plantean amenazas importantes para estos recursos. Las recientes iniciativas de Legado Verde en Etiopía, a través de programas de forestación y reforestación, ofrecen oportunidades para promover prácticas de micosilvicultura. Los hallazgos e implicaciones de este estudio contribuyen al Plan Nacional de Adaptación, el Plan Nacional de Mitigación y las Contribuciones Determinadas Nacionales de Etiopía, así como a los Objetivos de Desarrollo Sostenible (Agenda 2030) y la Agenda 2063. Estos conocimientos ayudarán a promover prácticas forestales sostenibles, la conservación de la biodiversidad y la mejora de la seguridad alimentaria. Se necesitan más estudios para investigar las respuestas de los hongos a los factores ambientales en diferentes sistemas forestales y para mejorar nuestra comprensión de la dinámica de los hongos en el espacio y el tiempo mediante el establecimiento de parcelas de estudio permanentes.

**Palabras clave:** *Etiopía, tipos de bosques, hongos, hongos micorrícicos arbusculares, diversidad fúngica, bosque natural, plantación forestal.*

## Outline of the thesis

The thesis consists of four studies: **Study I** deals with investigating the production of wild edible mushrooms in natural and plantation forests, revealing significant effects of climate and soil factors on sporocarps production. A total of 64 fungal species were recorded, with natural forests displaying higher diversity, while plantation forests showed higher biomass production. This study emphasizes the potential for sustainable forest management to enhance both biodiversity and economic value. **Study II** deals with developing simple predictive models to estimate sporocarps yields based on environmental and climatic factors in natural and plantation forests. The results highlight the importance of wild mushrooms as non-timber forest products (NTFPs), providing supplementary income for rural communities. Understanding fungal productivity patterns is crucial for improving forest management, particularly in plantation settings. **Study III** focuses on arbuscular mycorrhizal fungi (AMF) and the impact of replacing natural forests with exotic tree plantations. AMF diversity and abundance were significantly higher in natural forests, indicating the importance of conserving these habitats to support plant health and ecosystem stability. **Study IV** deals with exploring and synthesizing findings from the current study and existent literature on Ethiopian fungal biodiversity, threats, and prospects, providing comprehensive information on fungal biodiversity, sustainable use, and conservation efforts.

The main goal of this thesis is to enhance the understanding of fungal biodiversity and its ecological roles in Ethiopian forest ecosystems in order to promote sustainable forestry practices that can support rural livelihoods, forest conservation, and biodiversity in a changing climate. This knowledge can contribute to conserving biodiversity, supporting ecosystem services such as soil health and plant growth, and providing rural communities with additional income through the sustainable harvesting of non-timber forest products. It also highlights the importance of preserving natural forests and optimizing plantation management to maintain ecosystem stability and resilience in the face of climate change and land-use land cover changes. The finding will imply the sustainable integration of mycological resources and forest management through a mycosilviculture approach that could

provide complementary income for the local communities in the study area and beyond. The conceptual map of the study including the four studies is illustrated in Figure 1.

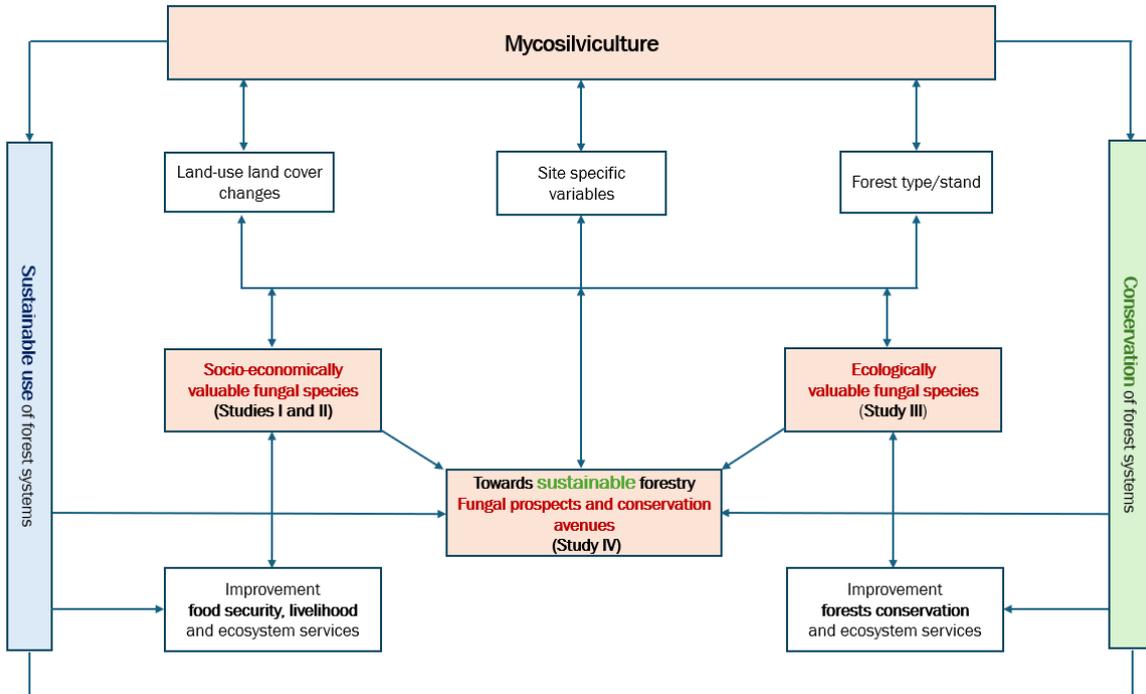


Figure 1. Conceptual map of the thesis including the four studies.

## List of original articles

The following articles have been generated from this thesis work. This thesis is based on four original works, which are referred to in the text with Roman numerals (I – IV). The fourth article is based on a synthesis of information from current studies and literature on fungal diversity, threats, and prospects in Ethiopian forests.

Detailed information related to each article is presented below:

**Gonfa Kewessa**, Tatek Dejene, Demelash Alem, Motuma Tolera, and Pablo Martín-Pinto, 2022. Forest Type and Site Conditions Influence the Diversity and Biomass of Edible Macrofungal Species in Ethiopia. *Journal of Fungi* 8, no. 10: 1023.  
<https://doi.org/10.3390/jof8101023>.

**Gonfa Kewessa**, Tatek Dejene, Pablo Martín-Pinto, 2023. Assessing the potential of forest stands for edible mushrooms productivity as a subsistence ecosystem service in Ethiopia. *Scientific African*, Volume 22, e01936.  
<https://doi.org/10.1016/j.sciaf.2023.e01936>.

**Gonfa Kewessa**, Tatek Dejene, Pablo Martín-Pinto, 2024. Untangling the effect that replacing Ethiopia's natural forests with exotic tree plantations has on arbuscular mycorrhizal fungi. *Science of The Total Environment*, Volume 942, 2024, 173718.  
<https://doi.org/10.1016/j.scitotenv.2024.173718>.

**Gonfa Kewessa**, Tatek Dejene, Wubalem Tadesse, and Pablo Martín-Pinto, 2024. Fungal Biodiversity in Ethiopia: Distribution, Threats and Prospects. *The Diversity of Fungal World* [Working Title]. IntechOpen.  
<http://dx.doi.org/10.5772/intechopen.1005910>.



## 1. General introduction

### 1.1. Ethiopian vegetation, climate and topography

Ethiopia, located in the Horn of Africa between latitudes 3° and 15°N and longitudes 33° and 48°E, covers an area of approximately 1.13 million km<sup>2</sup> with an altitudinal range from 125 m below sea level in the Afar Depression to 4,533 m above sea level at Ras Dashen in the Ethiopian Highlands (Bongers and Tenngkeit, 2010). This varied topography has fostered diverse ecosystems, from tropical lowland rainforests in the southwest to Afroalpine forests in the north and southeast. Rainfall ranges from 500 to 2,800 mm annually, and temperatures fluctuate between 10°C and 30°C (Demissew and Nordal, 2010), creating ideal conditions for unique vegetation and ecosystems (Asefa et al., 2020; Bongers and Tenngkeit, 2010; Friis et al., 2010).

Ethiopia's biodiversity is among the richest in Africa, hosting two major centers of endemism: the mesic Roof of Africa (Ethiopian Highlands) and the arid Horn of Africa (Fashing et al., 2022). These centers are part of the Eastern Afromontane and Horn of Africa biodiversity hotspots, designated as critical for global conservation. The country is home to between 6,500 and 7,000 vascular plant species, of which 12% are endemic (Gebre-Egziabher, 1991). The geomorphological history of the region has shaped this diversity, resulting in a heterogeneous landscape with high habitat and species diversity, particularly in the highlands.

Ethiopia's topography is divided by the Great East African Rift Valley into northwestern and southeastern highlands, each supporting distinct vegetation types. However, rapid population growth and habitat fragmentation are significant threats to the country's biodiversity. Natural vegetation, especially in the south, southwest, and northwest, is declining due to increasing demands on land and forest resources (Corlett, 2016; Tolessa et al., 2017). Additionally, Ethiopia is identified as a region with a high proportion of potentially threatened species (Stévant et al., 2019).

Despite these challenges, Ethiopia remains a vital area for biodiversity conservation, with eleven Afrotropical ecoregions and a Global 200 ecoregion

designation for its biodiversity importance (Olson and Dinerstein, 2002). However, the growing impacts of climate change and pressures from Africa's second-largest human population pose ongoing threats to its unique flora and fauna yet the least studied biodiversity (Fashing et al., 2022; Friis et al., 2010).

## 1.2. The forests of Ethiopia and their socio-ecological significance

Ethiopia's unique vegetation and ecosystems play a crucial role in supporting the country's biodiversity, regulating climate patterns, and providing water resources. These ecosystems are home to an abundance of flora and fauna, many of which are endemic to the region, making Ethiopia one of the world's biodiversity hotspots. As outlined by Friis et al. (2010), Ethiopia is home to 12 distinct vegetation types, along with a newly categorized intermediate evergreen Afromontane forest (EBC, 2022). These vegetation types include Desert and semi-desert shrubland; *Acacia-Commiphora* woodland and bushland; Wooded grassland of the western Gambela region; *Combretum-Terminalia* woodland and wooded grassland; Dry evergreen Afromontane forest and grassland complex; Moist evergreen Afromontane forest; Transition rain forest; Ericaceous belt; Afroalpine belt Riverine vegetation; Freshwater lakes, lake shores, marshes, swamps, and floodplain vegetation; Salt-water lakes, lake shores, salt marshes, and plain vegetation; and the Intermediate evergreen Afromontane forest. Each of these vegetation types provides essential services, such as timber and non-timber forest products, carbon sequestration, soil stabilization, and water regulation, while supporting diverse flora and fauna, many of which are unique to Ethiopia (Friis et al., 2010; EBC, 2022).

Historically, Ethiopia's highlands were covered by Afromontane forests, classified into dry Afromontane and moist Afromontane categories (Friis et al., 2010). Dry Afromontane forests, found mainly in the Central, Northern, and Western parts of the country, are characterized by high humidity, variable rainfall patterns, and a prolonged dry season, resulting in rich and complex biodiversity (Wassie et al., 2005), and creates various microhabitats suitable for variety of macrofungal species, including wild edible mushrooms (Dejene et al. 2017a; Agúndez et al. 2022). The dry Afromontane forests are dominated by tree species, such as *Juniperus procera*,

*Podocarpus falcatus*, *Hagenia abyssinica*, and *Olea africana*, which serve as key sources of timber for Ethiopia (Bekele et al., 2013; Kassa et al., 2009). In addition to timber, dry Afromontane forests provide non-timber forest products (NTFPs) like highland bamboo, mushrooms, coffee, and spices, which are vital to local livelihoods and the national economy.

In the early 1900s, Ethiopia's natural highland forests covered about 40% of the country's total land area, delivering critical social, ecological, and economic benefits, such as fuelwood, timber and other wooden products, watershed protection, and biodiversity conservation (Badege, 2001; Thomas and Bekele, 2003). However, by the mid-20<sup>th</sup> century, a combination of agricultural expansion, population growth, and unsustainable land use practices coupled with regime changes had led to a significant decline in forest cover (Lemenih and Bekele, 2008; Taddese, 2001). This deforestation resulted in fragmented and degraded forests, with many areas replaced by non-native tree plantations (Bekele, 2011; Moges et al., 2010; Tesfaye et al., 2016).

Recent reports from Ethiopian Forest Development and the Ministry of Agriculture (2023) indicate that Ethiopian forest cover has increased to 23.6% at the national level, reflecting progress in reforestation and afforestation efforts. Nevertheless, natural forests continue to face significant pressure from agricultural expansion (Figure 2), fuelwood collection, and urban development. These stresses not only threaten the health and diversity of forest ecosystems but also have a profound impact on fungi populations, which are vital for nutrient cycling, soil health, and forest regeneration. The loss or depletion of fungal diversity disrupts these ecological functions, leading to broader environmental consequences.



**Figure 2.** Forest encroachment for expansion of agricultural land adversely influences the macrofungi and diminishes their diversity and production in the central highlands of Ethiopia (Photo by: Gonfa Kewessa, March 2023)

Given these challenges, conservation and sustainable use of forest systems and resources are essential to balance conservation goals with the livelihood needs of rural communities dependent on forest resources. Toward this goal, mycosilviculture, which integrates fungi into forest management systems, offers a promising approach to addressing these socio-ecological challenges. By fostering the growth of fungi, particularly edible wild mushrooms, mycosilviculture can enhance forest regeneration, boost biodiversity, and support sustainable livelihoods. In Ethiopia's context of increasing plantation forests and ongoing forest cover transformation, integrating mycosilviculture into forest management offers a pathway toward a more resilient and sustainable ecosystem that meets both ecological and socioeconomic needs.

### 1.3. The role of fungi in forest ecosystems

Fungi are one of the most diverse groups of organisms found in terrestrial ecosystems, playing crucial roles in ecosystem development, functioning, and stability. They act as symbionts or saprotrophs in forest systems, depending on their relationship with other organisms. Fungi, being unable to produce their food, rely on external sources for sugars and carbohydrates. Mycorrhizal fungi establish symbiotic relationships with living trees and plants, forming intimate connections within and

around plant roots. In this relationship, fungi enhance the plant's ability to acquire nutrients and water and protect them from pathogens, while in return, they receive carbohydrates from the host (Brown et al., 2006; Ferris et al., 2000; Tedersoo et al., 2014a). On the other hand, saprotrophic fungi play vital roles in decomposing dead organic matter, thus contributing to nutrient cycling in forest ecosystems. This process significantly influences plant diversity, productivity, and overall ecosystem functions (Ferris et al., 2000; Van Der Heijden et al., 2008), as illustrated in Figure 3. Because of their importance in ecosystem processes, fungi are often used as indicators of ecological continuity or forest stability (Sverdrup-Thygeson and Lindenmayer, 2003).

Forest fungi provide numerous ecosystem services. They contribute to provisioning services, such as being a source of food (edible mushrooms), regulating services like soil carbon sequestration, cultural services (e.g., mushroom picking), and supporting services that maintain ecosystem processes like soil fertility and nutrient cycling (Leemans and De Groot, 2003). These ecosystem services are particularly crucial in tropical ecosystems, where fungi exhibit high biodiversity and help mitigate the effects of climate change (Tedersoo et al., 2014b). Fungi occupies multiple niches within forest ecosystems. Mycorrhizal fungi, for instance, enhance tree nutrient uptake by expanding the root system, while saprotrophic fungi drive global carbon cycles by breaking down organic material, releasing CO<sub>2</sub> in the process (Hawkins et al., 2023).

Beyond their functional roles, fungi interact with other organisms in forest ecosystems. For example, macrofungal species serve as food and habitat for invertebrates like fungus gnats, mollusks, and coleopterans (Santamaria et al., 2023), a relationship referred to as mycophagy or fungivory, which is the consumption of fungi by other organisms. Moreover, fungi are crucial for the broader ecosystem, functioning as ecosystem engineers by regulating the flow of energy and nutrients through their rhizomorphic and mycelial networks (Hawkins et al., 2023). Fungi also contribute significantly to the production of spores, which helps them reproduce and perpetuate their existence. The fruiting bodies or sporocarps of higher fungi are visible structures that aid in spore dispersal, often used in fungal ecological

studies (Mueller and Schmit, 2007). In recent years, technological advancements like molecular techniques have enhanced our understanding of fungal ecology by allowing researchers to analyze vegetative structures such as mycorrhizae and mycelia, expanding the scope of study beyond sporocarps (Blackwell, 2011).

Forest fungi are not only ecologically important but also hold economic and social value. Many forest fungi, especially wild mushrooms, are collected as non-timber forest products (NTFPs) and provide an essential source of income for rural communities. Their economic value has increased globally due to rising demand for edible mushrooms, which, in some cases, have even surpassed the value of timber (Boa, 2004; Bonet et al., 2014). In addition to food and income, fungi play a role in medicine and traditional livelihoods (Cai et al., 2011). Some studies from the Mediterranean regions stated that the economic value of wild mushrooms often surpasses that of timber, making them highly valuable non-wood forest products (NWFPs) (Bonet et al., 2014; Martínez de Aragón et al., 2011). For example, the economic impact of species like *Lactarius deliciosus* is significant in Spain, with mushrooms providing considerable income for local communities (Mumcu Kucuker and Baskent, 2019, 2015; Román and Boa, 2004). Mushroom picking is a popular recreational activity in many European countries, contributing to the cultural services provided by forest fungi. However, despite the high ecological and socioeconomic values of forest fungi in tropical regions in general and in Ethiopia in particular, their productivity, distribution, and community composition across a wide range of geographical locations largely remain unknown (Dejene et al., 2017b; Megersa et al., 2024).

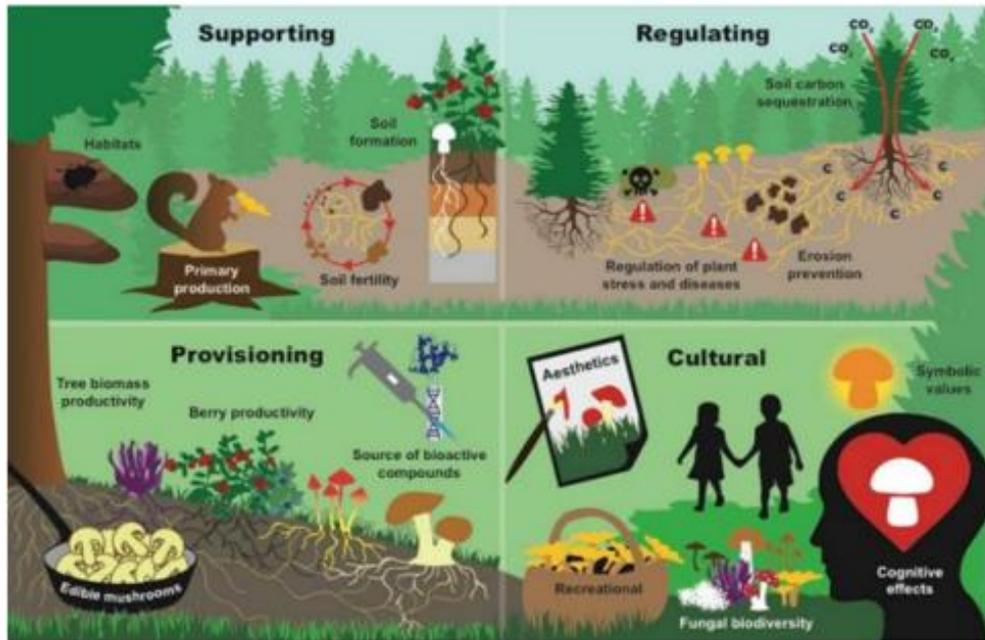
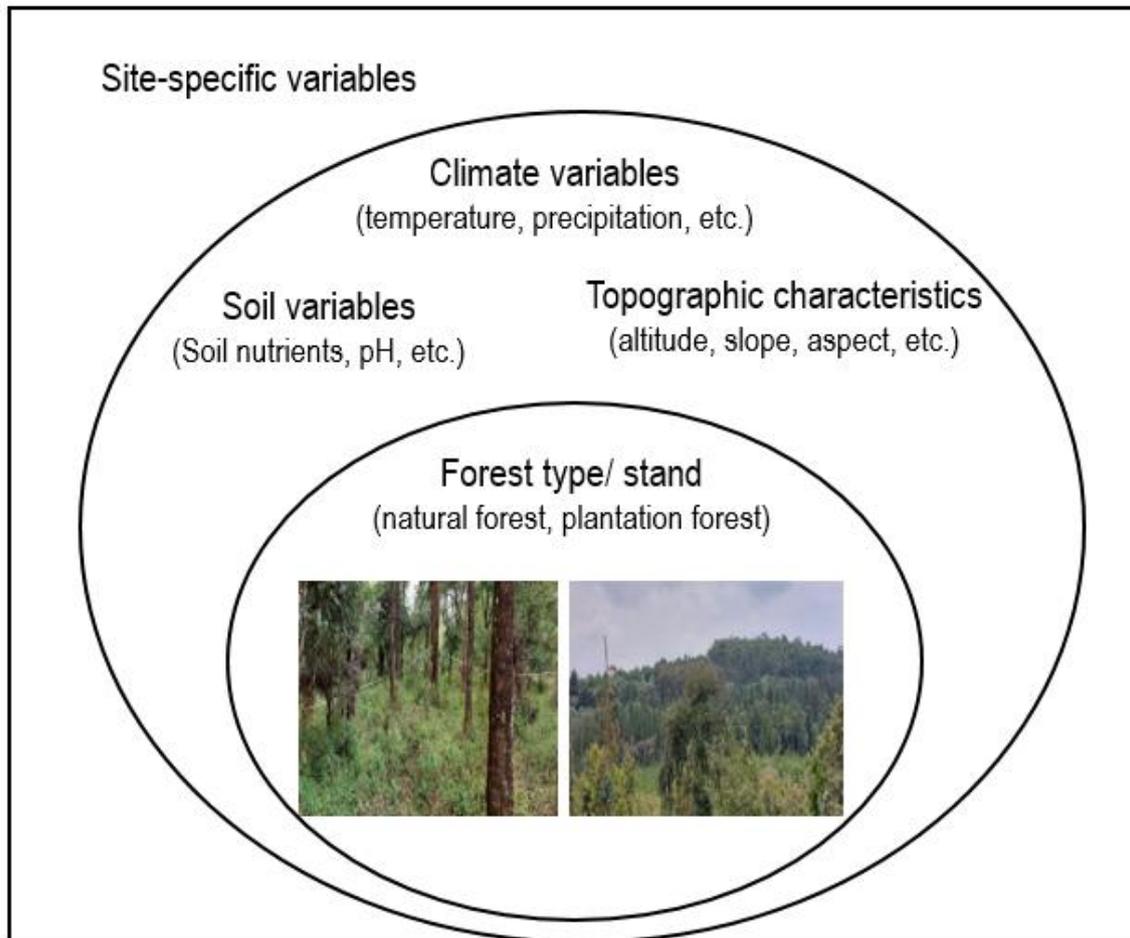


Figure 3. Ecosystem services provided by forest fungi (Varenius et al., 2017)

#### 1.4. Key factors affecting fungal community dynamics

Fungal community composition is largely determined by the combination of different factors (Figure 4): climate variability (e.g., temperature, precipitation), soil variables (e.g., soil nutrients, pH, etc.), topographic characteristics (e.g., aspect, altitude, slope), and forest stands (e.g., forest types, forest stands, tree species composition, etc.).



**Figure 4.** Factors involved in the fungal community composition. Adapted from Tomao et al. (2017)

#### 1.4.1. Effects of forest types and forest stands on fungal communities

Forest types and stand characteristics significantly influence fungal community dynamics by shaping key attributes such as age, canopy cover, stand density, and tree species composition (Collado et al., 2018; Tomao et al., 2020, 2017). These stand variables are central to how fungal communities establish, interact, and provide ecosystem services. Fungi often exhibit preferences for specific habitat niches within different forest types, influencing their distribution and abundance. For example, Figure 5 highlights various wild edible mushrooms identified in Ethiopian forest systems (Dejene et al., 2017b; Megersa et al., 2016). Forest type serves as a broad-scale determinant, setting the environmental conditions that govern fungal community composition (Megersa et al., 2024). Additionally, Wubet et al. (2003, 2009) reported that arbuscular mycorrhizal fungal

community structures vary among co-occurring tree species of dry Afromontane tropical forests, with seedlings showing potential to trap isolates suited for reforestation. However, significant gaps remain in understanding the specific impacts of habitats and associated factors on AMF communities across different forest ecosystems. Studying AMF community composition in diverse forest habitats is essential for a comprehensive understanding of ecological processes (Hazard et al., 2013).

Forest disturbances can indirectly affect fungi by modifying microclimatic conditions (Alvarez et al., 2016; Hernández-Rodríguez et al., 2013; Tomao et al., 2017), such as light, temperature, and soil moisture. Thinning, for instance, increases light penetration, which can raise soil temperatures and reduce moisture availability, altering the microhabitat where fungi thrive. These shifts in microclimate can impact both mycorrhizal fungi, which form symbiotic relationships with trees, and saprotrophic fungi, which decompose organic material and recycle nutrients. In contrast, heavy disturbances like clear-cutting, which drastically changes the forest structure, can lead to severe reductions in fungal biomass and diversity. For instance, low to moderate thinning intensities often promote fungal fruiting and increase mushroom production, while more intensive treatments like heavy thinning or clear-cutting tend to reduce mushroom yields and diminish fungal species richness (Sanz-Benito et al., 2022). This variation highlights how different levels of forest management intensity create contrasting responses in fungal communities. Studies have shown that ECM and saprotrophic fungi may respond positively to moderate thinning, but extreme disturbances lead to declines in fungal community richness (Dieler et al., 2017; Egli et al., 2010; Herrero et al., 2019).



**Figure 5.** Photographic representation of 17 selected mushroom species recorded in Ethiopia (Dejene et al., 2017b; Megersa et al., 2016). The images labeled A to Q correspond to the following species: (A) *Agaricus campestroides*, (B) *Agaricus subedulis*, (C) *Agrocybe pediades*, (D) *Armillaria heimii*, (E) *Calvatia rubroflava*, (F) *Coprinellus domesticus*, (G) *Coprinopsis nivea*, (H) *Coprinus pseudoplicatilis*, (I) *Hygrophoropsis aurantiaca*, (J) *Hymenagaricus fuscobrunneus*, (K) *Leucoagaricus holosericeus*, (L) *Leucoagaricus leucothites*, (M) *Leucoagaricus rubrotinctus*, (N) *Leucocoprinus birnbaumii*, (O) *Leucocoprinus cepistipes*, (P) *Lycoperdon perlatum*, and (Q) *Tylopilus niger*.

Forest management activities directly impact fungal dynamics by interfering with the carbon allocation between trees and fungi. Mycorrhizal fungi, in particular, rely on carbon transferred from their tree hosts, and disturbances that interrupt this carbon flow, such as deforestation or intense thinning, can severely affect fungal communities. In the absence of ECM fungi, saprotrophic fungi often take advantage of the disrupted carbon cycle to dominate the fungal community. While opportunistic non-ECM fungi can thrive in the aftermath of severe disturbances, the overall fungal

biomass may remain stable if host trees persist in the ecosystem. This suggests that the resilience of fungal networks depends largely on the presence of intact trees, even in disturbed stands. Some studies have demonstrated that belowground fungal networks can remain functional and maintain biomass after moderate disturbances if sufficient host trees are left untouched (Hawkins et al., 2023; Mediavilla et al., 2017; Parladé et al., 2019). Studies devoted to inspecting the influence of forest types and structures on overall fungal productivity, biomass, and compositions are extremely important to have a whole picture of the fungal dynamics. However, such studies are scant and only focused on specific species, with still non-conclusive results.

#### **1.4.2. Effects of climate on fungal communities**

Climate plays a crucial role in shaping fungal dynamics, influencing both the community composition and the overall productivity of fungal species across ecosystems. This influence manifests through interactions with temperature, precipitation, and seasonality, which collectively drive fungal growth, distribution, and fruiting patterns. Both mycorrhizal and saprotrophic fungi exhibit distinct preferences for specific climate conditions. For instance, in temperate and boreal ecosystems, the relative abundance of ectomycorrhizal (ECM) fungi increases during warmer seasons, such as summer and autumn, likely due to increased carbon allocation from host trees during their growth periods (Jumpponen et al., 2010; Parladé et al., 2017; Pickles et al., 2012; Santalahti et al., 2016). This pattern underscores the strong dependency of ECM fungi on tree phenology, which is, in turn, influenced by seasonal temperature fluctuations. In Mediterranean ecosystems, where drought is common, ECM fungal biomass fluctuates seasonally, with minimal mycelial production during extreme summer heat and winter cold (Castaño et al., 2017). Changes in precipitation and temperature across years can lead to shifts in fungal community composition. For instance, drier and colder conditions tend to favor ECM fungi, while wetter conditions increase the abundance of saprotrophic fungi (Castaño et al., 2018a). This change in climatic conditions exerts both direct and indirect pressures on fungal communities by altering the availability of moisture and carbon from tree roots.

The climate also dictates the seasonality of non-mycorrhizal fungi, such as litter-decomposing saprotrophs and molds, which tend to proliferate under cooler conditions (Fang et al., 2020; Jumpponen et al., 2010; Santalahti et al., 2016). These seasonal shifts in fungal composition highlight the adaptability of fungi to changing environmental conditions, with certain species exploiting specific temperature and moisture windows for growth and reproduction. Perhaps the most evident manifestation of climate influence on fungi is its control over sporocarps (mushroom) emergence and yield. Humid and warm conditions are generally ideal for fungal fruiting, with temperature acting as a limiting or promoting factor depending on the local environment (Alday et al., 2017; Andrew et al., 2018; Hernández-Rodríguez et al., 2015; Pinna et al., 2010). In temperate and boreal forests, mushroom production is closely tied to temperature, with higher yields typically observed in warmer seasons (Martínez-Ibarra et al., 2019; Ruiz-Almenara et al., 2019; Sato et al., 2012). Recent warming trends have further pushed mushroom fruiting seasons earlier in temperate regions, while in Mediterranean climates, where warming exacerbates drought, productivity has often been delayed or reduced (Boddy et al., 2014; Büntgen et al., 2015; Rick et al., 2020).

As climate change progresses, the effects on fungal dynamics are expected to be profound, particularly in drought-prone regions such as the Mediterranean. Key projections include: (i) *temperature rise*: Mediterranean temperatures are expected to increase by 1.4 to 5.1 °C by 2055 (Bravo et al., 2008). This rise will likely result in reduced fungal diversity and productivity, especially for species adapted to cooler, moist conditions; (ii) *decline in precipitation*: a potential decrease in annual rainfall, coupled with more extreme rainfall events, will reduce soil moisture and further stress fungal communities (Collado et al., 2019; Evans, 2009; García-Ruiz et al., 2011), and (iii) *soil moisture reduction*: higher evapotranspiration rates due to increased temperatures could exacerbate soil drying, directly limiting fungal growth and fruiting (Dai, 2013; Davies et al., 2021).

The interaction between precipitation and temperature is particularly crucial in regions where evapotranspiration exceeds water input, as it directly affects both forest growth and mushroom yields. For example, in Mediterranean forest stands,

studies have observed higher mushroom production due to extended fruiting seasons brought about by increased early-season rainfall and warmer late-season temperatures (Karavani et al., 2018). However, under more severe drought conditions, the evapotranspiration rates may outpace precipitation, reducing soil water availability and curbing fungal productivity (Boddy et al., 2016, 2014; Büntgen et al., 2015).

One important aspect of climate's influence on fungal dynamics is the lagged effects between climate variables and fungal responses. For example, precipitation has been shown to affect mushroom yields with a delay of up to one month, highlighting the complex interaction between moisture levels and fungal fruiting cycles (Karavani et al., 2018). Similar lagged responses have been observed between tree growth and fungal production, particularly in ECM fungi. Additionally, the interaction between temperature, water availability, and fungal community dynamics differs across fungal guilds. While both mycorrhizal and saprotrophic fungi are affected by these climatic factors, the specific timing and intensity of these effects can vary. According to Ágreda et al. (2015), both fungal guilds responded similarly to temperature and moisture changes, however, the exact periods when these factors had the greatest impact varied between mycorrhizal and saprotrophic fungi. Such findings emphasize the importance of understanding how different fungal communities interact with their environment under varying climatic conditions.

#### **1.4.3. Effects of site characteristics on fungal communities**

Site characteristics, including soil properties and topographical features, play a fundamental role in shaping fungal dynamics and influencing the composition, diversity, and productivity of fungal communities in forest ecosystems. These characteristics, which can remain stable over time or change due to anthropogenic disturbances, interact in complex ways to shape fungal communities through a combination of environmental stability and local ecosystem variations. The interplay of soil nutrients, pH, moisture retention, and topographical features like slope, aspect, and altitude creates a diverse range of microhabitats that fungi must adapt to survive and thrive.

Soil properties such as pH, carbon-to-nitrogen (C/N) ratio, and soil texture directly affect fungal community composition by altering the availability of nutrients and water, which are crucial for fungal growth and reproduction. For example, soil pH is a well-established driver of fungal diversity. Acidophilic fungi, particularly many ectomycorrhizal (ECM) species, thrive in acidic soils. When soil pH is altered, either by natural processes or anthropogenic activities such as liming, the fungal community composition shifts accordingly. Liming, which adds magnesium (Mg) and calcium (Ca) to the soil to improve tree nutrient uptake, has been shown to negatively impact acidophilic ECM fungi by reducing their abundance and altering root-tip colonization (Rineau et al., 2010). This highlights how minor shifts in soil chemistry can lead to large-scale changes in fungal community dynamics.

Similarly, nitrogen levels in forest soils play a critical role in determining fungal composition. Elevated nitrogen inputs, often from atmospheric deposition or fertilizer use, generally have a negative impact on ECM fungi, as the increased nitrogen reduces the tree's need to allocate carbon to its symbiotic fungal partners. Elevated nitrogen levels, common in disturbed or fertilized forests, reduce ECM fungal activity as nitrogen disrupts the carbon allocation to roots and fungi (Demoling et al., 2008). This reduction in carbon availability results in lower ECM biomass and sporocarps production (Gillet et al., 2010). In contrast, saprotrophic fungi, which decompose organic matter, are less affected by increased nitrogen levels and may even benefit from it (Clocchiatti et al., 2020). This divergence in response between mycorrhizal and saprotrophic fungi demonstrates how nutrient availability can cause shifts in the balance between fungal guilds, altering overall ecosystem functioning. In Ethiopia's tropical forests, where agricultural expansion and deforestation are common, nitrogen deposition could significantly shift fungal composition, favoring saprotrophic fungi over ECM species, but detailed studies on this impact are lacking.

Soil texture and moisture retention capacity are also key determinants of fungal dynamics. Fungi, especially in drought-prone ecosystems, are highly sensitive to soil moisture content. Fine-textured soils, such as sandy loams, have a higher water-holding capacity compared to coarser soils like loamy sands, which translates into better fungal survival and productivity during dry conditions (Moore, 2001). In

Mediterranean forest stands, for instance, higher production of the *Lactarius deliciosus* group has been observed in sandy-loam soils, where moisture retention supports sustained fungal growth despite the region's drought-prone nature (Taye et al., 2016). Soil texture thus not only influences water availability but also helps moderate the microclimatic conditions that are critical for fungal life cycles. In Ethiopia, particularly in semi-arid and montane forests, soil texture likely plays a similar role in shaping fungal dynamics, especially during dry seasons. However, research on the impact of soil texture on fungal biomass and productivity in Ethiopia remains sparse.

Topographical features, such as slope, aspect, and altitude, create varying microclimates that directly affect fungal fruiting patterns and community structure. These factors often shape localized conditions such as light availability, temperature, and moisture, all of which are critical for fungal development. For example, slope steepness affects water runoff and soil depth, with steeper slopes leading to higher runoff rates and thinner soils. This reduces the amount of available water and nutrients, creating less favorable conditions for fungal growth (Bonet et al., 2008). Fungal sporocarps production, therefore, tends to be lower on steep slopes due to the less stable and nutrient-poor soil conditions.

Aspect, or the direction that a slope faces influences the amount of sunlight and moisture a particular area receives. In the Northern Hemisphere, north-facing slopes generally receive less sunlight, which helps retain moisture and creates cooler, more humid conditions. These microclimates tend to support greater fungal diversity and higher sporocarps productivity, as fungi often prefer cooler, moister environments (Bonet et al., 2010). In Mediterranean and temperate regions, studies have found significantly higher fungal species richness and productivity on north-facing slopes compared to south-facing ones, where conditions are typically warmer and drier. On the other hand, steeper slopes can lead to faster water runoff and thinner soils, reducing fungal sporocarps production (Bonet et al., 2008). These patterns are likely relevant in Ethiopia's rugged highlands, but the lack of detailed studies on slope and aspect effects on fungal productivity highlights a significant research gap.

Altitude is another critical topographic factor that affects fungal dynamics by influencing temperature, moisture, and atmospheric pressure. As altitude increases, temperatures generally decrease, creating cooler and often more humid conditions that are conducive to fungal growth. However, the effect of altitude on fungal productivity is not uniform across different ecosystems. In coastal pine forests, for instance, higher sporocarps productions are found at greater altitudes, possibly due to more favorable microclimatic conditions such as cooler temperatures and increased moisture retention (de-Miguel et al., 2014). Conversely, in mountainous regions, such as the Spanish pre-Pyrenees, fungal diversity, and productivity have been found to peak at altitudes up to 1500 meters, beyond which harsher conditions may limit fungal development (Bonet et al., 2010), but there is limited research on the altitudinal gradients and their effects on fungal communities in Ethiopia's tropical and subtropical montane forests.

Human activities, such as agriculture, deforestation, and soil management practices (e.g., fertilization and liming), can dramatically alter the soil environment and, consequently, fungal communities. These activities often result in changes to soil properties such as pH, nutrient availability, and soil structure, all of which directly influence fungal community composition and function. For instance, forest liming to counteract soil acidification not only benefits tree growth by improving nutrient uptake but also reduces the abundance of acidophilic ECM fungi (Rineau et al., 2010). Similarly, nitrogen deposition from industrial activities has caused widespread declines in ECM fungal communities, as the increased nitrogen availability reduces the need for trees to allocate carbon to their mycorrhizal partners (Demoling et al., 2008). This leads to a shift in fungal community composition, favoring saprotrophic species that are less reliant on carbon from tree roots.

### **1.5. Gaps in knowledge**

Knowledge of the diversity and distribution of plants and fungi is paramount to developing effective conservation and restoration aims, assessing the impact of climate and anthropogenic changes, and delivering the targets of the Kunming-Montreal Global Biodiversity Framework (Conference of the Parties to the CBD,

2022). This is recognized in the proposed set of complementary actions related to plant conservation (CBD Secretariat., 2023), representing an update of the original Global Strategy for Plant Conservation 2011–2020 (Convention on Biological Diversity, 2023), to be adopted by the Parties to the Convention on Biological Diversity at COP 16. Although the targets of the Global Biodiversity Framework cover all biodiversity, including fungi, proposals to address fungal conservation concerns explicitly in overarching global strategies have not been successful so far (Antonelli et al., 2024).

Largely, the knowledge underpinning such policies and actions is derived from botanical and mycological reference collections, preserved plant and fungal specimens deposited in herbaria and fungaria, and living collections of plants (including seeds) and fungi (e.g., culture collections). It is from those reference specimens, collected for various purposes and through different sampling methodologies, ranging from taxonomic surveys to ecological studies, that new species can be scientifically described. The associated data reveal occurrence patterns across space and time (Antonelli et al., 2024), as is the case in the region of this study, where limited information is currently available.

Despite the recognized significance of fungi in forest ecosystems, fungi remain one of the least studied components of Ethiopian forest ecosystems. Existing research has highlighted a substantial gap in the understanding of fungal taxonomy and ecology, particularly when compared to other biodiversity components (Dejene et al., 2017a; Megersa et al., 2017; Rediet Sitotaw et al., 2015). While previous studies suggest that East Africa, including Ethiopia, is rich in fungal diversity (Pegler, 1977, 1969; Sileshi et al., 2023), a comprehensive assessment of fungal diversity in Ethiopian forests is lacking, leaving many species undocumented (IBC, 2014). This absence of comprehensive data extends to the neglect of fungi in national biodiversity databases, thereby undermining their ecological and economic significance in forest management and conservation strategies.

Without reliable data, the ecological significance of fungi and their responses to environmental changes cannot be adequately assessed. Additionally, the

economic and ecological importance of edible mushrooms and other NTFPs in forest management is often overlooked. This neglect contributes to unsustainable practices and threatens both biodiversity and local livelihoods. Furthermore, anthropogenic disturbances, such as agricultural expansion, deforestation, and forest degradation contribute to the degradation of forest resources and pose significant threats to fungal diversity (Lemenih and Bekele, 2008; Lemenih and Kassa, 2014; Wassie et al., 2005). The relationship between these disturbances and the dynamics of fungal communities remains poorly understood, highlighting the need for targeted research to document the impacts of habitat changes (both forest types and forest stands) on fungal species.

### 1.6. Need for this study

Globally, knowledge gaps regarding plant and fungal diversity hinder biodiversity conservation. It is estimated that over 90% of fungal species remain undescribed, limiting our ability to address biodiversity loss and develop protection strategies (Antonelli et al., 2024; Niskanen et al., 2023). The uneven and incomplete nature of biological collections, compounded by rising threats like habitat loss and climate change, exacerbates this challenge (Meyer et al., 2016). Addressing these gaps, particularly the lack of species descriptions and lack of distribution data is essential to ensure the conservation of fungi and the vital services they provide.

Sustainable conservation of fungal resources is a major challenge for developing countries like Ethiopia due to threats to forest resources that cause decline at an alarming rate due to factors such as high human and animal pressure and unsustainable use of forest resources (Gebru, 2016). Despite efforts like forest development initiatives and the establishment of protected forests like National Forest Priority Areas, the value of forest resources beyond timber, including non-timber forest products (NTFPs) like mushrooms, has been overlooked in management plans (Desalegn and Tadesse, 2004; Dejene et al., 2017). Therefore, alternative forest management approaches that integrate the economic and ecological benefits of NTFPs are critical for the sustainable management of Ethiopia's forest resources (Yadav and Mekonnen, 2013).

Plantation forests, particularly fast-growing species, were introduced in Ethiopia to meet demands for fuelwood and timber. And while these plantations offer economic benefits, they fail to account for NTFPs, such as wild mushrooms, which contribute to food security and ecological stability (Amma et al., 2018). The continued deforestation and degradation of forest resources have resulted in the decline of fungal resources and traditional mushroom consumption practices (Weldekiros et al., 2017). Degraded lands remain underutilized due to limited knowledge of effective restoration strategies involving fungal resources (Asmelash et al., 2019).

Existing literature highlights significant gaps in fungal studies in Ethiopia. Knowledge of fungal diversity, community composition, and productivity remains limited, despite their ecological and socio-economic importance (Abate 2014; Dejene et al., 2017a,b; Sitotaw et al., 2020; Tadesse et al., 2023). Without comprehensive information on fungi's resources including their distribution, composition, and productivity, it is challenging to develop effective conservation strategies or harness their potential benefits (Antonelli et al., 2024; Niskanen et al., 2023). Therefore, detailed studies are essential to assess fungal communities across different forest systems and explore fungal diversity, identify factors affecting their distribution, and integrate this knowledge into forest management plans for devising strategies to improve natural fungal richness, sustain sporocarps production, and facilitate the conservation of economically and ecologically important mycological species.

In Ethiopia, fungal resources are poorly studied despite their significant ecological and socio-economic roles. Wild edible mushrooms, for example, are vital for rural communities, offering nutrition, medicine, and income opportunities (Abate 2014; Agúndez et al., 2022; Dejene et al., 2017a,b). Rapid forest resource declines and the exclusion of NTFPs from forest management plans have further marginalized these resources (Dejene et al., 2017c). Therefore, this study seeks to conduct a comprehensive study of fungal diversity, distribution, and productivity over space in various forest ecosystems in Ethiopia. The findings and implications of this study will contribute to Ethiopia's National Adaptation Plan, National Mitigation Plan, and National Determined Contributions, as well as the global Sustainable Development Goals (Agenda 2030), and Agenda 2063. These insights will help in promoting

sustainable forestry practices, biodiversity conservation, and enhancing food security.

### 1.7. Scope of the Study

This study encompasses comprehensive investigations aimed at advancing the understanding of productivity, diversity, and distribution of valuable fungal species in Ethiopia's diverse forest ecosystems. The first component focuses on exploring and quantifying edible wild mushrooms by identifying and assessing the diversity and abundance of mushroom species across five distinct geographical conditions. By systematically recording these mushrooms, the study aims to fill the existing knowledge gap regarding their distribution and productivity, as well as ecological roles. The study also aims to model the various ecological and environmental factors that influence the composition and production of edible mushrooms. This includes examining the impacts of forest types and stands, soil characteristics, and climate variables on mushroom diversity and composition, thereby providing a comprehensive understanding of the factors that support or hinder their productivity and distribution. Additionally, the investigation of arbuscular mycorrhizal fungi (AMF) composition across four geographical regions under different forest stands will elucidate the relationships between AMF and forest management practices, unveiling their roles in promoting forest health and productivity.

This study also involves synthesizing information on fungal diversity, threats to their existence, conservation strategies, and prospects in Ethiopia. This included a comprehensive review of existing literature alongside findings from the current research, aimed at establishing a foundational understanding of fungal biodiversity in Ethiopia. This synthesis will serve as a reference for future studies and conservation efforts. The research will also highlight the ecological significance of fungi within forest ecosystems and their potential economic contributions, particularly in local communities reliant on mushroom harvesting. This includes identifying the most important and widely utilized species among rural populations.

Moreover, the study will address critical gaps in knowledge about the ecological dynamics of fungi in Ethiopian forests, particularly concerning how forest

conversion affects their diversity, distribution, and community composition. Overall, the study seeks to enhance the understanding of edible mushrooms and fungal biodiversity in Ethiopia, ultimately contributing to the sustainable management and conservation of forest resources in the region. This comprehensive approach will offer insights into fungal succession, diversity patterns, and the ecological roles of fungi within various forest ecosystems. It will provide essential data for policymakers, forest managers, and local communities, supporting the integration of mycosilviculture as a tool for sustainable forestry practice, biodiversity conservation, and enhancing food security.

## 2. Objectives of the thesis

The Ethiopian highlands are home to diverse forest resources encompassing a variety of ecosystems, yet these forests face growing threats from land-use land cover changes, such as agricultural expansion and deforestation. Despite their potential to support a wide range of NTFPs, such as edible wild mushrooms and soil fungi, limited studies have examined the mycological resources in these forests. The impacts of shift in land use types and associated site-specific variables on fungal communities remain poorly understood. In this thesis, we aim to address these knowledge gaps by investigating the dynamics of fungal communities in Ethiopian forests, with implications for sustainable forestry practices, biodiversity conservation, and food security. Understanding fungal communities across different forest systems and site conditions is crucial for developing species and ecosystem-specific strategies to conserve economically and ecologically important fungal species. The specific objectives of the thesis are:

- To assess the diversity of valuable macrofungal species across various areas of Ethiopia and compare the richness, sporocarp production, and community assemblages of edible macrofungi in native forests and non-native fast-growing plantation forests (**Study I**).
- To develop predictive yield classificatory models for wild edible mushrooms production in natural and plantation forests in Ethiopia (**Study II**). These models aim to identify the environmental variables that drive sporocarps productivity, providing an ecological perspective for optimizing mushroom yields.
- To investigate the diversity and community composition of arbuscular mycorrhizal fungi (AMF) between natural and plantation forests, as well as identify environmental variables that govern AMF community composition (**Study III**).
- To assess and provide a comprehensive synthesis of fungal biodiversity in Ethiopia, focusing on their distribution, threats, and conservation across various land uses and sites (**Study IV**).





## Materials and methods

### 3. Materials and methods

#### 3.1. The study area

In this thesis, the research was conducted across five distinct dry Afromontane Forest areas in Ethiopia, namely Taragedam, Alemsaga, Banja, Wondo Genet, and Menagesha Suba forests (Figure 6 A and B; Table 1). **Studies I and II** covered all five forest areas, providing a comprehensive analysis of fungal diversity, productivity, and ecological roles under various natural and plantation forest conditions. However, in **study III**, the Menagesha Suba forest was not included, focusing instead on the remaining four sites (Taragedam, Alemsaga, Banja, and Wondo Genet). These areas represent a range of geographical, altitudinal, and climatic conditions, from natural stands to plantation environments, making them ideal for a comprehensive study on the diversity, productivity, and ecological roles of edible macrofungi and arbuscular mycorrhizal fungi (AMF) in Ethiopia. Finally, **study IV** took a broader approach by synthesizing existing literature on fungal ecology and management, incorporating findings from the current research in Ethiopia. The synthesis provided a comparative framework, combining existing knowledge with results obtained from the study areas to offer practical insights into the sustainable management of fungal biodiversity in Ethiopian forests. Detailed descriptions of each forest and study area are presented below;

*Taragedam forest:* is located in the South Gondar Zone within the Amhara National Regional State. Addis Zemen town is located at 12°06'59" N–12°07'25" N and 37°46'14" E–37°47'02" E, on the Addis Ababa Gondar main road, about 82 km north of Bahir Dar and 93 km south of Gondar town. The forest covers 875 hectares (Gedefaw and Soromessa, 2014). The main tree species, including *Olea europaea*, *Allophylus abyssinicus*, *Nuxia congesta*, *Premna schimperii*, and *Albizia schimperiana* characterize the Taragedam forest (Gedefaw and Soromessa, 2014). Taragedam forest lies at an altitude of 2062–2457 meters above sea level (masl). The area receives an average annual precipitation of 1300 mm and has a mean annual temperature of 20.4 °C (Worku, 2017). It is characterized by natural forests, providing an important habitat for studying fungal biodiversity under native vegetation conditions. This forest area is generally characterized by a moderate climate, locally

known as Woina Dega. The area has a mono-modal rainfall distribution and the rainy season is from June to August. The dry season extends from December to March. Climatic data obtained from the National Meteorological Services Agency for the study area showed that the mean annual maximum and minimum temperatures are 27.9°C and 11.1°C, respectively, and the mean annual rainfall is from 900 mm to 1,200 mm. Most of the areas are covered by volcanic rocks mainly basalt. The rocks are light dark, grey, whitish, reddish or brown. The fertility of the soils in the area deteriorated as a result of erosion and continuous cultivation. The vegetation of Taragedam consists of forests, bushlands, shrublands and mixed/enrichment plantations. There is dense natural forest just around the monastery. Taragedam forests consist of different trees and shrubs interspersed with climbers and herbs.

*Alemsaga forest:* is situated at 11°54'30"-11°56'00" N and 37°55'00"-37°57'00" E, with altitudes ranging from 2100 to 2470 masl. It experiences an average annual rainfall of 1484 mm and a cooler mean annual temperature of 16.4°C (Esubalew et al., 2019). This area is also covered by natural forests, offering a slightly wetter and cooler environment for the study of macrofungi.

*Banja forest:* Banja, located between 10°57'17"-11°03'05" N and 36°39'09"-36°48'25" E, sits at altitudes of 1870-2570 masl (Abera et al., 2017). This site receives approximately 1215.3 mm of rainfall annually, with a mean annual temperature of 17.7°C. Like Taragedam and Alemsaga, Banja is home to natural forests, providing additional context for studying the effects of elevation and climate on fungal dynamics.

*Wondo Genet forest:* located in Southern Ethiopia about 265 km from Addis Ababa, is geographically positioned between 7°06' - 7°07'N latitude and 38°37'-38°42'E longitude, with an altitudinal range between 1,600 - 2,580 m a.s.l. (Fenta, 2014). This area experiences a bi-modal rainfall pattern, with minor rainfall during spring and a major rainy season during summer. The average annual rainfall is 1210 mm, and a mean annual temperature of 20°C (Fenta, 2014; Kebede et al., 2013). The climate is classified under the Woina Dega-climatic zone. The area's topography is slightly undulating, and its soils are of volcanic origin, characterized by well-drained

loam or sandy loam (Eriksson and Stern, 1987), with an average pH of 5.7 (Zewdu and Högberg, 2000).

The natural forest, covering approximately 797 hectares (Fenta, 2014), is home to key dry Afromontane species, such as *Juniperus procera*, *Albizia gummifera*, *Podocarpus falcatus* (*Afrocarpus falcatus*), *Bersama abyssinica*, *Prunus africana*, *Cordia africana*, *Croton macrostachyus* and *Olea africana* (Bekele et al., 2013; Fenta, 2014; Kebede et al., 2013). However, this forest is threatened by human activities, shrinking from 16% to 2.8% of the catchment area over the past three decades due to agriculture, commercial farming, and logging (Kebede et al., 2013). Recurrent forest fires, mostly human-induced, further threaten biodiversity (Ango and Bewket, 2007; Bekele et al., 2013; Teshome, 2011).

Additionally, Wondo Genet includes about 100 hectares of plantation forests consisting primarily of exotic species, such as *Pinus patula*, *Eucalyptus grandis*, *Cupressus lusitanica*, and *Grevillea robusta* (Teshome, 2011). These plantation forests undergo common silvicultural practices, with *P. patula* and *E. grandis* selected for the study due to their dominance. These plantations are managed with a clear-cut and replacing approach, except for *Eucalyptus* species, which are managed through coppicing (Teshome, 2011). This site allows for investigation of how land-use changes and plantations impact fungal diversity and ecosystem services.

*Menagesha Suba forest:* The Menagesha Suba forest is located between 8° 56'–9° 03' N and 38° 28'–38° 36' E, at altitudes of 2200–3385 masl (Jemal and Getu, 2018). It receives about 1100 mm of rainfall per year, with a mean annual temperature of 16°C. The forest is dominated by *Pinus radiata* plantation forests, representing an entirely human-modified landscape for studying how non-native tree species affect the fungal community and productivity.

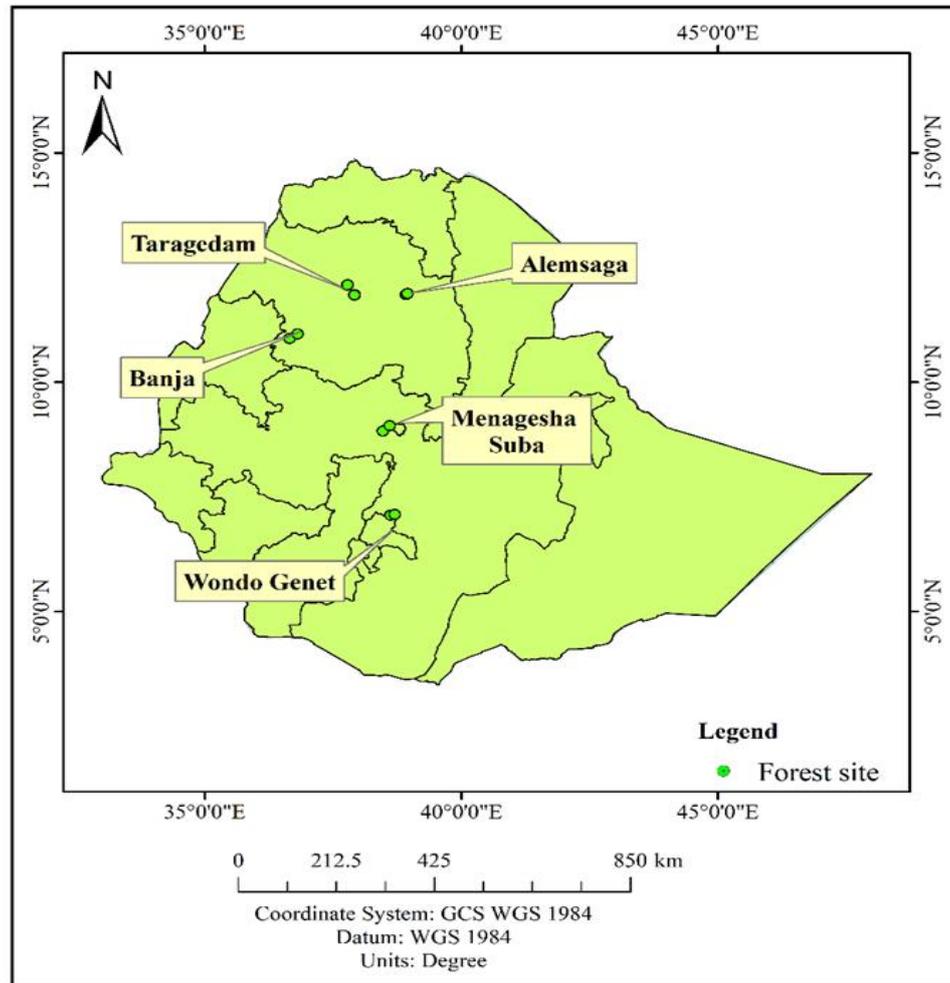


Figure 6. Map showing the locations of forests in which the study plots were located.

Table 1. Comprehensive descriptions of the forests and the study sites.

| Forests   | Geographical coordinates                          | Altitude (m asl) | MAP (mm) | MAT (°C) | Vegetation types | References              |
|-----------|---|------------------|----------|----------|------------------|-------------------------|
| Taragedam | 12°06'59"–12°07'25" N and 37°46'14" – 37°47'02" E | 2062–2457        | 1300     | 20.4     | Natural forests  | (Worku, 2017)           |
| Alemsaga  | 11°54'30"–11°56'00" N and 37°55'00"–37°57'00" E   | 2100–2470        | 1484     | 16.4     | Natural forests  | (Esubalew et al., 2019) |
| Banja     | 10°57'17"–11°03'05" N and 36°39'09"–36°48'25" E   | 1870–2570        | 1215.3   | 17.7     | Natural forests  | (Abere et al., 2017)    |

|                |                                      |               |      |    |  |                        |
|----------------|--------------------------------------|---------------|------|----|--|------------------------|
| Wondo Genet    | 7°06'–7°07' N and<br>38°37'–38°42' E | 1600–<br>2580 | 1210 | 20 | Natural forests and <i>Pinus patula</i> and <i>Eucalyptus grandis</i> plantation forests | (Alem et al., 2020a)   |
| Menagesha Suba | 8°56'–9°03' N and<br>38°28'–38°36' E | 2200–<br>3385 | 1100 | 16 | <i>Pinus radiata</i> plantation forests  | (Jemal and Getu, 2018) |

Note: MAP, mean annual precipitation; MAT, mean annual temperature.

### 3.2. Data sources

In this thesis, data for the four studies (papers) were gathered from a variety of sources to ensure a comprehensive understanding of fungal diversity, productivity, and ecological roles in Ethiopian forests. For **studies I and II**, primary data were collected through extensive fieldwork across five forest areas, including Taragedam, Alemsaga, Banja, Wondo Genet, and Menagesha Suba. These data included sporocarps sampling for edible macrofungi and soil sampling for both soil fungi and soil properties analysis across different forest stands and their influence on fungal yield and biomass. In **study III**, data were similarly obtained from field studies in four of the five study areas (excluding Menagesha Suba), focusing on the impact of natural forest conversion to plantation forest on arbuscular mycorrhizal fungi (AMF) composition.

Additionally, climate variables were gathered for each study area from nearby meteorological stations (**studies I-III**). These variables included daily, mean, minimum, and maximum temperatures (°C), as well as total annual precipitation (mm), and the average temperature (°C) and precipitation (mm) values for sporocarps and soil sampling season, i.e., the most representative weeks of the rainy season, were recorded. These details are presented in Table 1 in **study I**, Table 2 in **study II**, and Table 1 in **study III**.

**Study IV** relied on secondary data sources, synthesizing a wide range of existing literature on fungal biodiversity, ecology, and conservation, while incorporating relevant findings from the current research to provide a comprehensive overview of fungal threats and conservation strategies. Synthesizing information (**study IV**) incorporates both newly gathered field data and a review of previous

studies, linking the results to themes, such as threats, conservation, and prospects of appreciated mycological resources in Ethiopia.

### **3.3. Field plots establishments (Studies I, II & III)**

In this thesis, the field plots were established to comprehensively study fungal diversity, productivity, and ecological roles across different forest types in Ethiopia. For **studies I and II**, a total of 63 sample plots were set up in seven different forest sites, including both natural and plantation forests. The selected study areas included natural forests in Wondo Genet, Taragedam, Banja, and Alemsaga, and two plantation forests, comprising *Eucalyptus grandis*, *Pinus patula* in Wondo Genet and one plantation *Pinus radiata* stands in Menagesha Suba. In **study III**, 45 sample plots were established in three natural forests (Banja, Alemsaga, and Taragedam), and two plantation forests (*E. grandis* and *P. patula*) in Wondo Genet, to study the impact of natural forest conversion to plantation forest on arbuscular mycorrhizal fungi (AMF) composition. For all **studies (I, II, and III)**, a total of nine sample plots, with three in each area, were established as described in Gassibe et al. (2011) and Hernández-Rodríguez et al. (2013). Each plot was rectangular, measuring 2 m × 50 m (100 m<sup>2</sup>), and was organized into three blocks with three plots per block to ensure adequate spatial distribution and to minimize environmental heterogeneity (O’Hanlon and Harrington, 2012).

The plots were established at least 500 meters apart and were placed randomly within each forest stand to prevent spatial confounding and obtain independent estimates (Hiiesalu et al., 2017; Rudolph et al., 2018). The natural forest plots were characterized by dry Afromontane species such as *Juniperus procera*, *Podocarpus falcatus*, *Hagenia abyssinica*, and *Olea africana* in Wondo Genet, and species like *Maytenus obscura*, *Carissa edulis*, *Olea* sp., *Acacia abyssinica*, *Prunus africana*, and *Albizia gummifera* in the other forests. For plantation plots, exotic species were selected based on ecological similarities in terms of climate, altitude, and soil conditions.

Field data were collected weekly during the rainy season, and fungal fruit bodies were harvested, weighed, and identified for taxonomic purposes. This

comprehensive sampling design allowed for independent analysis of the sporocarps and soil samples, providing robust insights into fungal yield and biomass across different forest systems.

The plots were established systematically (Luoma et al., 1991) in areas with similar ecological conditions such as climate, altitude, and soil characteristics to ensure comparability between natural and plantation forest stands. However, the works in this study should be considered as case studies since the plots were established in a similar stand for each forest type, and conclusions regarding other studies need to be taken with caution.

### 3.4. Sampling

#### 3.4.1. Sporocarps sampling and species identification (Studies I & II)

For sporocarps sampling (**studies I and II**), 63 plots (100 m<sup>2</sup> each) were established across seven forest sites, including natural and plantation forests using a design based on Dejene et al. (2017b), Gassibe et al. (2011) and Hernández-Rodríguez et al. (2013). Plots were distributed randomly and placed at least 500 m apart to avoid confounding spatial effects, *i.e.*, to avoid spatial autocorrelation, inherent to such a plot-based design (Hiiesalu et al., 2017; Rudolph et al., 2018) and to reduce environmental heterogeneity (O’Hanlon and Harrington, 2012). The plots were analyzed as independent samples, as suggested by Ruiz-Almenara et al. (2019).

*Sporocarps collection:* all mature and young edible wild mushrooms were harvested weekly during the main rainy season (July and August). Fresh weight was measured on-site using a digital balance (SF-400) to quantify sporocarps production (yield) in kilograms per hectare per year. The number of mushrooms per species in each plot was also recorded.

*Morphological documentation:* collected specimens were photographed and their morphological and ecological characteristics were recorded for taxonomic identification (Adeniyi et al., 2018). Specimens were then dried and preserved as herbaria preservations and further identifications following morphological descriptions by Dejene et al. (2017b) and using additional identification keys by

Antonin (2007), Hama et al. (2010), Heinemann (1956), Morris (1990), Pegler (1969), Pegler (1968), Pegler (1977), Rammeloo and Walley (1993), Ryvarde et al. (1994), Singer (1965) and others. Fungal taxa names were updated using the Mycobank database (<http://mycobank.org>). The edibility of the species was determined following Bonet et al. (2004) and Moreno and Manjón (2010), and their ecological function was assigned using Pölme et al. (2020). If the taxon is described in the literature as both non-edible and edible, we classified it as non-edible. If the taxon is described in the literature as having doubtful edibility, we classified it as non-edible. As edible (E) are classified all species that are listed as such in the large majority of the literature consulted.

Molecular identification involves sequencing of the ITS region of the nuclear ribosomal genes (rDNA). For this, fungal DNA was extracted from dry sporocarps using an EZNA® Fungi 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).

In **study II** (Sporocarps yield prediction): The sporocarps data from **study I** were used to develop a predictive model for yield classification based on environmental variables such as soil characteristics and climate data. This model aimed to estimate edible mushroom productivity to optimize the value of valuable mushroom species in Ethiopian forests.

#### **3.4.2. Environmental variables sampling and analysis (Studies I, II, and III)**

In all **studies (I, II, and III)**, environmental data, including soil and climate variables, were collected across the established sample plots to assess their influence on fungal dynamics, yield, and community composition.

*Soil sampling and analysis:* in each study, soil samples were collected from each of the established sample plots using a soil corer (2 cm radius, 20 cm depth, and 250 cm<sup>3</sup>). Five soil cores were extracted from each plot: one from the center and four from the corners. The cores were pooled into a composite sample (~500 g) per

plot for further analysis. Before analysis, the soil samples were dried, sieved (1 mm mesh), and ground into a fine powder. The litter layer (comprising intact and partially decomposed leaves) was discarded because the composition of fungal communities in litter tends to diverge from that in soil (Voříšková et al., 2014).

*Soil physicochemical analysis:* soil pH was determined using a 1:2.5 soil-to-water suspension, measured with a pH meter (van Reeuwijk, 2002). Organic carbon (C) was assessed using the wet digestion method (Walkley and Black, 1934). Total nitrogen (N) was measured via the Kjeldahl method (Kim et al., 2005). Available phosphorus (P) was extracted using sodium bicarbonate (0.5 M NaHCO<sub>3</sub>), following the method described by Tan (2005). Soil analysis for all studies was conducted at Water Works Design and Supervision Enterprises, Addis Ababa, and Amhara Water Works Design and Supervision Works Enterprise, Bahir Dar, Ethiopia.

In addition to the soil samples, climate variables, including daily mean, minimum, and maximum temperatures (°C), total annual precipitation (mm), and average temperature and precipitation during the sporocarps sampling season (July and August 2019), were obtained from nearby meteorological stations for each study area. These variables were critical for assessing fungal productivity and composition during the rainy season, the most active period for sporocarps formation.

In **study I**, soil samples were collected from each plot to relate the composition of edible fungal taxa to edaphic variables. Climate data were specifically linked to the sporocarps sampling period (July and August 2019). In **study II**, the same soil sampling and analysis procedures were applied to relate fungal community composition to soil properties across forest types. Climate variables were similarly obtained to represent conditions during the main fungal growth period. In **study III**, environmental variables (including soil properties, temperature, rainfall, elevation, latitude, and longitude) were used to study their influence on arbuscular mycorrhizal fungi (AMF) communities. DNA extraction was performed alongside soil physicochemical analysis to study AMF diversity and composition. Detailed descriptions of the physicochemical properties of the soil and climate variables for

each study site are presented in relevant tables (Table 1 in **study I**, Table 2 in **study II**, and Table 1 in **study III**).

### 3.4.3. Sporocarps yield prediction and model development (Study II)

Similar to **study I**, soil samples were collected from each plot following the same procedure to relate sporocarps production to edaphic variables. These variables were incorporated into a predictive model to estimate sporocarps yield. The soil characteristics analyzed included pH, organic carbon, total nitrogen, and available phosphorus. These analyses provided crucial input for developing the classification model to predict sporocarps yields.

### 3.5. Molecular and bioinformatics analysis (Study III)

For the molecular analysis, soil samples were transported to the laboratory in sterile plastic bags and stored at 4 °C. Upon arrival, the samples were frozen at -20 °C until DNA extraction. Each sample was processed using approximately 100 g of soil for genomic DNA analysis. To avoid cross-contamination during field and laboratory work, sampling tools were cleaned with 96% alcohol after each plot. DNA was extracted from 0.25 g of soil per sample using the PowerSoil™ DNA Isolation Kit (MoBio Laboratories Inc., Carlsbad, CA, USA). Polymerase chain reactions (PCRs) were conducted in triplicate for each sample to minimize bias, and the triplicates were pooled before sequencing.

PCRs were performed in 20 µL reaction volumes containing MQ water, DNA template, buffer, MgCl<sub>2</sub>, dNTPs, bovine serum albumin (BSA), forward and reverse primers, and Platinum Taq polymerase. The ITS2 rDNA region (ca. 260 bp) was amplified using the forward primer fITS794 and reverse primer ITS495, both with Illumina adaptors. The PCR conditions included an initial denaturation at 94 °C for 3 minutes, followed by 35 cycles of 94 °C for 45 seconds, 50 °C for 1 minute, and 72 °C for 1.5 minutes, with a final elongation at 72 °C for 10 minutes. A second PCR was performed to append sample-specific tags to the Illumina adaptors using the Phusion HF PCR master mix. This reaction included six cycles with denaturation at 98 °C, annealing at 55 °C, and elongation at 72 °C. Negative controls were used to

confirm the absence of contamination, and sequencing was conducted using a paired-end (2×250 bp) Illumina MiSeq platform at BaseClear B.V. (Leiden, The Netherlands).

For bioinformatics analysis, sequencing primers and low-quality reads were removed using Cutadapt v.2.8, and the sequences were truncated to 200 bp to avoid clustering biases. Sequences with an expected error rate greater than 1 were discarded using USEARCH v.8.0. Unique sequences were collapsed on a per-sample basis while preserving read counts, and singleton sequences were excluded. Operational Taxonomic Units (OTUs) were clustered at a 97% sequence similarity threshold, resulting in 193 OTUs. Any sequences with less than 70% similarity or shorter than 150 bp when aligned to a fungal reference sequence were excluded.

Taxonomic assignment of OTUs was performed by comparing the sequences against the UNITE+INSD fungal ITS sequence database (version v.8.0, 2018), which contains species hypothesis (SH) groups (Kõljalg et al., 2013). Ecological functions were assigned for OTUs with more than 90% similarity to a fungal SH with known ecological roles (Põlme et al., 2020). OTUs were assigned to functional groups such as plant pathogens, animal parasites, ectomycorrhizal (ECM) fungi, arbuscular mycorrhizal fungi (AMF), and saprotrophs, based on the classification by Põlme et al. (2020). Only arbuscular mycorrhizal fungi OTUs were selected for further analysis. A complete list of AMF OTUs is provided in the supplementary data (Table S1 in **study III**).

### 3.6. Statistical analysis

**Study I** involved analyzing macrofungal data after necessary transformations to meet normality and homoscedasticity criteria. Sporocarps biomass was estimated, and differences in production across forest types were analyzed using linear mixed-effects models (LME), with blocks as random effects and forest type as a fixed factor. Tukey's test was employed to identify significant differences between forests. Non-metric multidimensional scaling (NMDS) was used to visualize relationships between sporocarps composition and environmental factors, while a permutation-based nonparametric MANOVA (PerMANOVA) (Anderson, 2001) was used to assess

differences in sporocarps communities across forest types and sites. Correlations between NMDS axis scores and environmental variables were tested using the *envfit* function, and the influence of environmental factors on fungal communities was examined via Mantel tests.

In **study II**, the focus was on predicting sporocarps yields and developing a classificatory model to categorize mushroom production in both natural forests and plantations. The dependent variable was sporocarps yield (fresh biomass weight per hectare), which was divided into four categories: <3 kg, 3–10 kg, 10–35 kg, and >36 kg. These categories allowed for assessing the potential of different forest conditions for mushroom production. To ensure the data met normality requirements, the mushroom yield data were log-transformed. Differences in yield across forest types were analyzed using Linear Mixed Effects (LME) models, with blocks (sets of plots) as random effects and forest types as fixed effects. Tukey's test was applied to check for significant differences between forest types. Pearson correlation tests were used to examine relationships between environmental variables and sporocarps yields, while scatter plot matrices were employed to help identify the most important predictor variables. The independent variables were divided into three groups: site (e.g., altitude, latitude, aspect), edaphic (e.g., organic matter, nitrogen, carbon, magnesium), and climate (e.g., rainfall, temperature). A multinomial classificatory model was developed using these variables to predict the yield categories. Sixteen models (eight for natural forests and eight for plantations), were fitted to determine the best yield predictors for each dependent variable (Gassibe et al., 2014).

Model selection was based on the Akaike Information Criterion (AIC) and Pseudo R<sup>2</sup> values, with the best model being the one with the lowest AIC and highest Pseudo R<sup>2</sup> (Yanagihara et al., 2012), which was chosen to predict the likelihood of each yield category. Once we obtained the best variable combinations, we selected one model for each forest type (i.e., natural forests and plantations). These models allowed us to predict the probability of the sporocarps yield for a particular multinomial discrete categorical choice. The coefficients of each model were used to estimate the sporocarps yield categories of the plantation and natural forests in the studied areas. The structure of the general discriminant rules was:

$$\beta_1 + \sum \beta_i X_i$$

Where  $\beta_0, \beta_1, \dots, \beta_n$  are parameters and  $X_i$  are environmental variables.

The performance of the equations was evaluated based on the AIC. The expression of AIC statistics is:

$$AIC = 2p - 2\ln(L)$$

Where  $p$  is the number of model parameters and  $L$  is the maximum of the likelihood function. These models will enable forest managers to predict the likelihood of different sporocarps yield categories and optimize forest management practices for enhancing edible mushroom production.

In **study III**, we examined arbuscular mycorrhizal fungi (AMF) diversity across forest types using diversity indices (Hammer et al., 2001), such as species richness (Chao1), Shannon–Wiener, and Simpson’s dominance index. The Rényi diversity profile (Tothmeresz, 1995), was used to depict the diversity curves of the five stands (Figure S1 in **study III**). Differences in AMF diversity between forest stands were analyzed using one-way ANOVA, followed by Tukey’s HSD test. Pearson’s correlation analysis assessed the relationships between AMF communities and environmental variables. PERMANOVA was performed to evaluate the statistical differences in AMF communities between forest types and forest stands. NMDS was used to visualize community composition, and the envfit function assessed correlations between NMDS axes and environmental variables (Clarke, 1993). Additional analyses, such as ANOSIM and SIMPER, were conducted to identify key AMF species responsible for community similarities and dissimilarities (Parravicini et al., 2010). All statistical analyses were performed using R software (R Core Team, 2020) and PAST software (Version 4.03) (Hammer et al., 2001).





**Results**

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## 4. Results

### 4.1. Taxonomic identification of wild edible mushrooms (Studies I and II) and arbuscular mycorrhizal fungi (Study III)

The findings from our studies indicated that Ethiopian forests harbor diverse fungal species. In Studies I and II, a total of 64 edible fungal species from 31 genera and 21 families were identified (Table 2 in **study I**), with 40 species found in natural forests and 16 species in plantation forests. Eight edible species were common to both forest types. Saprotrophs dominated the species composition (92.19%), followed by ectomycorrhizal fungi (6.25%).

In **study III**, 193 operational taxonomic units (OTUs) of arbuscular mycorrhizal fungi (AMF) belonging to the phylum Glomeromycota were identified (Table S1 in **study III**). These OTUs comprised three classes, six orders, nine families, and 15 genera. Most of the OTUs belonged to the class Glomeromycetes ( $n = 158$ ), which was also the most abundant class (81.9%), followed by Paraglomeromycetes ( $n = 12$ , 6.2%), and Archaeosporomycetes ( $n = 5$ , 2.6%). We were unable to identify 18 OTUs. Most of the OTUs belonged to the order Glomerales ( $n = 131$ , 68%), followed by Diversisporales ( $n = 21$ , 11%) and Paraglomerales ( $n = 10$ , 5%) (Figure 2 in **study III**). At the family level, most of the OTUs belonged to the Glomeraceae ( $n = 119$ , 61.7%), followed by Diversisporaceae ( $n = 12$ , 6.2%), and Claroideoglomeraceae ( $n = 10$ , 5.2%) (Table S1 in **study III**). The most frequently detected AMF species in the sampled plots were *Septoglomus fuscum*, *Diversispora insculpta*, and *Funneliformis mosseae* (Table 2 in **study III**).

When analyzing AMF species abundance and richness, the abundance of AMF was significantly higher in natural forests than in plantations ( $F = 39.93$ ;  $p = 0.000$ ; Figure 3A in **study III**). Furthermore, the abundance of AMF differed significantly between stands ( $F = 15.73$ ;  $p = 0.000$ ; Figure 3B in **study III**), with the highest level of AMF abundance detected in Taragedam natural forest soil and the lowest level detected in *Pinus* stand soil (Figure 3B in **study III**). AMF species richness was significantly higher in the Taragedam forest (106 AMF species,  $p < 0.05$ ; Table 3 in **study III**) and significantly lower in the *Pinus* plantation (13 species) and Alemsaga

forest (23 species) than in other forest stands. The total AMF species richness for each forest type and forest stand is shown in Table 3 in **study III**.

Considering the diversity of AMF species by forest types and forest stands, AMF taxa richness (Chao 1) was estimated to be significantly higher in natural forests than in plantations ( $F = 8.808$ ;  $p = 0.05$ ). The Shannon–Wiener diversity index indicated that AMF taxa richness differed significantly between forest types ( $F = 9.389$ ;  $p = 0.004$ , Table 3 in **study III**). A comparison of AMF species evenness in natural and plantation forests revealed no significant differences ( $F = 1.393$ ;  $p = 0.245$ ). However, AMF species dominance ( $F = 5.367$ ;  $p = 0.026$ ) and Simpson ( $F = 5.287$ ;  $p = 0.027$ ) indices varied significantly between the two forest types.

#### 4.2. Sporocarps production (Studies I and II)

Concerning sporocarps production, we found significant differences in edible sporocarps production between natural and plantation forests ( $F = 4.293$   $p = 0.04$ , Figure 4A in **study I**), with plantation forests producing a higher total fresh weight of 2097.57 kg ha<sup>-1</sup> compared to 731.18 kg ha<sup>-1</sup> in natural forests. Moreover, sporocarps production levels varied significantly across the five study sites ( $F = 9.24$ ;  $p = 0.0001$ , Figure 4B in **study I**), with the Menagesha Suba forest showing the highest production (7.49 kg ha<sup>-1</sup>), which was notably greater than other sites like Wondo Genet, Banja, Alemsaga, and Taragedam forests. This indicates clear differences in fungal diversity and productivity between forest types and among specific forest locations. Ecologically and economically important edible fungal species such as *Agaricus campestris*, *Agaricus subdulis*, *Tylophilus niger*, *Suillus luteus*, *Tricholoma portentosum*, *Tricholoma saponaceum*, *Morchella americana*, and *Morchella anatolica* were collected (Table 2 in **study I**, Table 3 in **study II**). The wild mushroom species collected during the study, the proportion of the total biomass that each species represented, and their life strategy are listed in Table 3 in **study II**.

#### 4.3. Taxa composition and environmental variables (Studies I, II, and III)

In the evaluation of the effect of forest types and stands on sporocarps composition, the perMANOVA analyses indicated that the two forest types differed significantly in their sporocarps composition ( $F = 5.343$ ,  $R^2 = 0.14$ ,  $p = 0.001$ ; Figure

5A in **study I**). When correlating environmental variables with total sporocarps production, we found strong correlations with edaphic variables, such as sodium (Na), OC, N, and P ( $p = 0.001$ ) ( $p < 0.05$ ; Table 3 in **study I** and Figure 4A in **study II**). Among the climate variables, the cumulative rainfall 20 days before the start of the collection period and the average daily minimum temperature during the collection year were significantly correlated with total sporocarps production ( $p = 0.001$ ). Latitude and longitude as spatial factors were also significantly correlated ( $p = 0.001$ ) with total sporocarps production. Spatial factors (i.e., latitude and longitude) aggregately had a stronger significant impact on sporocarps production ( $r = 0.64$ ,  $p = 0.0001$ ) than climate ( $r = 0.43$ ,  $p = 0.0001$ ) or edaphic variables ( $r = 0.32$ ,  $p = 0.0001$ ). Details of correlations between environmental variables (soil and climate variables) and sporocarps production are shown in Table 3 and Figure 5B in **study I**; and in Figure 4A&B in **study II**.

The Pearson correlation analysis (Table 4 in **study II**) of the six most abundant edible fungal species revealed some significant positive correlations with edaphic and climate variables. For example, *S. luteus* yield showed a strong positive correlation with the OM content ( $cor = 72.4\%$ ) of plantation forest soils, and *A. subedulis* yield was correlated with the N content ( $cor = 51.70\%$ ) of natural forest soils. *A. subedulis* yield was also positively correlated with the average daily minimum temperature ( $cor = 31.10\%$ ) in natural forests, whereas *S. luteus* yield was positively correlated ( $cor = 65.8\%$ ) with the annual rainfall in plantation forests.

The NMDS analyses indicated that the total AMF community composition differed significantly according to forest type ( $F = 7.969$ ,  $R^2 = 0.156$ ,  $p = 0.001$ ) (Figure 4A in **study III**) and forest stand ( $F = 2.999$ ,  $R^2 = 0.231$ ,  $p = 0.001$ ) (Figure 4B in **study III**). To elucidate the drivers of the gradient in AMF dissimilarities between forest type and forest stands, we fitted 31 environmental variables (Figure S2 in **study III**). Of these, soil pH, EC, soil OC, N, P, annual rainfall, CRF3d, and aspects such as longitude were significantly correlated with the AMF communities detected in the five different stands (Table 4 in **study III**).

Additionally, ANOSIM analyses also confirmed that AMF community composition differed significantly between forest types ( $F = 8.439$ ,  $R = 0.690$ ,  $p = 0.000$ ) and between forest stands ( $F = 3.250$ ,  $R = 0.327$ ,  $p = 0.000$ ). The SIMPER

analysis identified the cumulative contribution of the most influential OTUs to the dissimilarity between forest types and among forest stands is also shown in Table S2 in **study III**. At the family level, most OTUs contributing to the dissimilarity belonged to the Glomeraceae (almost 60% of the dissimilarity contribution) (Table 5 in **study III**). Other secondary contributors were OTUs belonging to the Ambisporaceae and Claroideoglomeraceae. Only two OTUs identified at the species level, *Funneliformis mosseae* and *Ambispora fennica*, contributed significantly to the dissimilarity, with an individual contribution to the dissimilarity of 2.6 and 1.7, respectively.

#### 4.4. Predictive modeling of sporocarps yields (Study II)

Sixteen simple classificatory models (Table 5 in **study II**) were obtained for the accurate prediction of sporocarps production levels, with eight models for each forest type. Among the grouped variables were the site factor latitude, edaphic factors OC, Na, N, and P, the average daily minimum temperature during the collection month, and cumulative rainfall 20 days before the start of the collection period (Table 5 in **study II**).

Two yield classification models (Table 6 in **study II**), one for the natural forest and one for the plantation forest type, were obtained to predict the fresh biomass production of macrofungi based on their AIC values (Table 5 in **study II**). Latitude, OC, and average daily minimum temperature during the collection month were used in both sporocarps production models. In the natural forest model, the sign of the coefficients was positive for the high sporocarps yield categories, which indicates that as the number of parameters increases, total edible mushroom production also increases. For the plantation model, the sign of the coefficients was only positive for the low-yield category, indicating that average sporocarps production would increase for every one-unit increase in the number of parameters used in the model.

#### 4.5. Synthesis of Ethiopian fungal biodiversity (Study IV)

Synthesizing the literature and findings from the current studies, we noted that Ethiopian forests harbor much-appreciated fungal diversity, which is ecologically and economically important. Noting fungal diversity in Ethiopia, the most important scholarly references in indigenous forests come from the comprehensive works of

Hjortstam and Ryvarde (1996) who reported fifteen *Corticaceae* species. Decock et al. (2005) also reported a total of four taxa from the highland forest regions. Some other taxa have also been reported by Tuno (2001); Abate (2008), (2014); Alemu (2013); Muleta et al. (2013); and Sitotaw et al. (2015a) from different parts of the country. Most recently, Alemu et al., (2012) and Megersa et al. (2017) reported some fungal taxa from Western dryland forests and Degaga natural forests respectively (Figure 1 in **study IV**). The taxa reported by Alemu et al. (2012) were provided only in their local names. On the other hand, Abate (1999), (2014); Alemu (2013), and Sitotaw et al. (2015a) also listed some taxa from highland grazing areas.

Despite the poor ethnomycological notes, Tuno (2001) described the traditional use of wild mushrooms by the Majangir ethnic groups as a subsidiary food gathered from forests in the Southern region of Ethiopia. Muleta et al. (2013) and Abate (2014) also documented such traditional culture in the Kaffa ethnic group from the southern region of the country. Furthermore, noticeable interest in edible wild mushrooms was also reported from the Bonga area (Muleta et al., 2013) and Benishangul Gumuz Region (Alemu et al., 2012). Additionally, the traditional medicinal uses of mushrooms are also reported by Abate (2014) from the Kaffa ethnic groups in the Southern region. Among other species, *Laetiporus sulphureus* was reported commonly used for lessening childbirth by the Kaffa people in the Southern part of Ethiopia (Abate, 2014).

Some of the edible wild mushrooms (Table 1 in **study I**) are also reported in previous studies by Abate (1999), (2008), (2014); Tuno (2001); Alemu (2013); Muleta et al. (2013) and Sitotaw et al. (2015a). Edible wild mushrooms are also available in some local markets (Abate, 2014), where they are sold by the local people to earn some income to supplement their household economy. For example, in Bonga and Assosa, mushrooms are available in association with other vegetal products. *Agaricus* spp., *Laetiporus* spp., and *Termitomyces* spp are among the most available species in the local market (Abate, 2014).

Many threats affecting fungal resources are similar to those that globally affect the biodiversity in Ethiopia (IBC, 2014). The most important of all, deforestation, comes as a consequence of anthropogenic change, like forest encroachment to expand agricultural land, to which global environmental and climate

change also add (Lulekal et al., 2011). According to Teketay (2001), deforestation is immense and estimated between 150000 – 200000 ha of land per year. This adversely influences the macrofungi and diminishes their diversity and production (Miller and Lodge, 1997). Such impact also limits the benefits that can be obtained from fungal resources from the forests. Thus, conservation strategies and actions are needed, giving special consideration to those species currently used by the local communities.



## Discussion



## 5. Discussion

### 5.1. Taxonomic identification of edible wild mushrooms (Studies I and II) and arbuscular mycorrhizal fungi (Study III)

In the most rural parts of Ethiopia, the local people are dependent on forest resources, either in the form of subsistence or as a cash income derived from NTFPs (Lulekal et al., 2011). The collection of edible wild mushrooms by local people is a common practice, particularly in the southwestern parts of the country (Dejene et al., 2017c). However, wild mushrooms are less or not considered important sources of food and medicine by rural communities in the northern part of the country (Zelege et al., 2020). This might be due to the continuing exodus of people from the countryside, which has meant that local communities are gradually losing their traditional knowledge, particularly about wild mushroom species. Furthermore, although a limited number of studies have reported the availability of wild mushrooms in Ethiopia and their importance as sources of food, medicine, and to some extent, income for local communities (Dejene et al., 2017c; Sitotaw et al., 2020), information about the type of edible wild fungal species that are available, their potential production, and their status in different forest systems is scant (Sitotaw et al., 2015). This study is the first systematic survey focused on edible wild mushrooms, which was carried out in forests located in central, northern, and southern Ethiopia, where remnants of natural forests and plantations of exotic trees exist (Faye et al., 2011). We collected a total of 64 edible fungal species from the study sites. The majority of the edible species ( $n = 40$ ) were collected only from study sites in natural forests.

Additionally, in **study III**, 193 operational taxonomic units (OTUs) of arbuscular mycorrhizal fungi (AMF) belonging to the phylum Glomeromycota were identified (Table S1 in **study III**). These OTUs comprised three classes, six orders, nine families, and 15 genera. Most of the OTUs belonged to the class Glomeromycetes ( $n = 158$ ), which was also the most abundant class (81.9%), followed by Paraglomeromycetes ( $n = 12$ , 6.2%), and Archaeosporomycetes ( $n = 5$ , 2.6%).

We collected wild edible species that have both economic and ecological significance belonging to the genera *Morchella*, *Suillus*, and *Tylopilus* in plantation forests and *Tricholoma* in natural forests (Sundriyal and Sundriyal, 2001). In addition, we found some *Agaricus* species and *Termitomyces*, which are known to be used by rural people in the southwest part of the country (Abate, 2014; Muleta et al., 2013), and a *Schizophyllum* species, which is eaten by local people in southern Ethiopia (Sitotaw et al., 2020; Tuno, 2001). Of these species, *Suillus luteus* is consumed by local people and is also sold in markets at a good commercial price in different developing countries, along with other NTFPs (Pérez-Moreno et al., 2008). Furthermore, these kinds of mushrooms could help sustain communities during periods of food scarcity, serving as an important source of nutrients for local people (Sundriyal and Sundriyal, 2001). The use of wild mushrooms by rural people as a food source during lean periods has been documented in Ethiopian ethnomycological literature. In most cases, these species are collected for subsistence use (Yehuala, 2010). However, in some places, mushrooms can provide households with additional income when sold in the markets. For example, in local markets in the southern and southwestern parts of the country, *Agaricus* sp. and *Termitomyces* sp. are available occasionally in association with other vegetal products, which the local people sell to earn some extra money to supplement their household income (Abate, 2014). Therefore, the conservation and development of these kinds of valuable species deserve special attention given their possible role in increasing food security and income generation to subsidize rural household economies. In addition, as mushroom collection from wild habitats is seasonal, maintaining some of these edible species through local small-scale cultivation practices or in private forest areas would be very remunerative. Therefore, a strategy is needed for the adoption and cultivation of important species from the wild, which will not only increase their utilization but also create new sources of income for rural people and contribute to food security.

## 5.2. Sporocarps production (Studies I and II)

The overall sporocarps yield from plantation forests (2097.57 kg ha<sup>-1</sup>) was higher than that from natural forests (731.18 kg ha<sup>-1</sup>) owing to the abundance and

high biomass of some edible species of *Suillus luteus*, *Tylopilus niger*, *Schizophyllum commune*, *Morchella anatolica*, *Omphalotus illudens*, *Lycoperdon umbrinum* and *Agaricus campestroides*. Although we collected more edible species from plots in natural forests than in plantation forests, sporocarps production levels were higher in plots in plantation forests than in natural forests. The greater number of species but lower sporocarps production levels in natural forests is unsurprising given that almost all the species found were saprotrophic and they were mainly composed of singleton taxa, with a small number of frequent species, which is in agreement with the findings of previous studies (Alem et al., 2021). The saprophytic fungal species collected were also characterized by low levels of biomass production, following Gassibe et al. (2011) and Mediavilla et al. (2014). Nonetheless, they are relevant for decomposition processes and ecosystem functioning (Deacon, 2006), particularly in tropical forest systems such as the natural forests in this study, where decomposition is rapid (Powers et al., 2009). This may reflect the accumulation of favorable substrates, which is likely to enhance the richness (Wardle et al., 2004) of these systems. The conspicuous sporocarps produced by these saprophytic fungi may also have favored the collection of this particular fungal class, although basidiomycete mycelia are reported to be everywhere in forests (Cairney and Bastias, 2007). Overall, the sporocarps yield obtained from plantation forests (2097.57 kg ha<sup>-1</sup>) was significantly higher than that from natural forests (731.18 kg ha<sup>-1</sup>). Interestingly, nearly 25% of the species collected from plantation forests were marketable species and hold economic significance, including *Morchella* sp., *Suillus* sp., and *Tylopilus* sp (Pérez-Moreno et al., 2008; Sundriyal and Sundriyal, 2001) (Table 2 in **study I**; Table 3 in **study II**). These species were characterized by their high levels of biomass production. For example, in Peru and Mexico, *Suillus* and *Morchella* species are commercial NTFPs produced in plantation forests. They guarantee the economic performance of those forests (Pérez-Moreno et al., 2008; Toivanen et al., 2012) and the livelihoods of local communities (Elizabeth et al., 2018), thus providing incentives for farmers to plant and manage more plantations in their surroundings. Furthermore, in Mexico, *Morchella* species are also exported to generate income (Pérez-Moreno et al., 2008). Although the overall biomass produced by sites in this study was low, the most productive site (Menagesha Suba) had mean production levels per stand of

7.49 kg ha<sup>-1</sup>, which suggests the potential production levels of edible sporocarps in forests with similar conditions in this area. This also provides a starting point in terms of broadening the management of forests for the production of NTFPs, such as edible mushrooms in Ethiopia, depending on the location and type of forests.

Although natural forests produced lower sporocarps yields than plantation forests and had fewer marketable species, the overall yields and species were still valuably enhanced by plantations of exotic conifer species. A recent study (Alem et al., 2021) in the northern part of Ethiopia indicated that the overall land connectivity of natural forests with that of plantations provided important ectomycorrhizal species such as *Tricholoma* and *Suillus* in natural forest systems, indicating that such forest management activities could create important microniches with suitable resources and abiotic conditions to support more valuable mushroom species (Gómez-Hernández and Williams-Linera, 2011). Thus, enrichment of natural forest systems through planting diverse tree species could potentially offer suitable habitats to enhance the richness and productivity of valuable edible species in natural forests in the study areas.

### 5.3. Taxa composition and environmental variables (Studies I, II, and III)

Considering macrofungal community composition, we observed distinct fungal communities in the natural and plantation forests in Ethiopia (**studies I and II**). Fungal communities in natural forests were characterized by a large number of species, which may have been due to the greater spatial heterogeneity of the soil in natural forests compared with plantation forests. A heterogeneous soil environment and high rainfall levels create microhabitats in which saprotrophic species should be able to find the resources they require to survive in natural forests. The vegetation composition also impacts the composition of edible fungal species via the quantity and quality of the organic inputs, which mainly affects the saprotrophic community structure (Read and Perez-Moreno, 2003). Most of the species found in the natural forests were associated with litter decomposition, which is typically characteristic of tropical forests (Tedersoo et al., 2014). However, some specific species such as *Termitomyces* and *Tricholoma* species were exclusively found in natural forests. The

genus *Termitomyces* comprises a group of gilled mushrooms that have formed a termitophilic association with a particular family of termites, the Macrotermitinae (Isoptera), which are commonly found in Africa in places with a dry and humid climate (Kirk et al., 2008). This might be because our sampling sites in the natural forest areas were generally classified as dry Afromontane forest areas, characterized by high humidity and prolonged dry seasons (Friis et al., 2010). These conditions might favor the occurrence and formation of distinct fungal community compositions in natural forest systems. Distinct fungal community compositions were also observed for plantation forests. Ectomycorrhizal fungi characterized the fungal composition of plantation forests along with some saprotrophic species. *Tylopilus* and *Suillus* species were site-exclusive species that were significantly more abundant in plantation forests comprised mainly of *Pinus* than in other plantation forests. Some mushroom species, such as *Agaricus campestris*, *Coprinellus domesticus*, *Leucoagaricus holosericeus*, *Hygrophoropsis aurantiaca*, and *Leucocoprinus cepistipes* were common in both forest systems, indicating that these genera might be characterized as generalists.

Previous studies have shown that different environmental variables govern the composition of fungal species and that different fungal taxa are likely to respond to edaphic variables in different ways, depending on their characteristics (Crowther et al., 2013; Koide et al., 2014) and, in turn, the composition of fungal communities is directly correlated with soil parameters (Cozzolino et al., 2016). In this study (**study I**), organic matter, P, and N were significantly correlated with the whole edible fungal species community dataset. This is likely to be because organic matter influences the fungal community through its impact on the water-holding capacity of the soil and nutrient availability (Harrington, 2003). Thus, organic matter may favor more fungal assembly in an area, particularly saprotrophic fungi. Furthermore, the finding that N was an important factor correlated with fungal taxa compositions follows previous studies (Gassibe et al., 2015; Kranabetter et al., 2009; Reverchon et al., 2010) that noted the influence of N on fungal distribution patterns. These studies reported that fungi showed community specialization toward more soil N-rich sites. This might be because nitrogen can influence the formation of extraradical mycelium in the soil and play a vital role in sporocarps formation (Trudell and Edmonds, 2004). Other studies

have also noted that fungal communities adapt to more nitrogen-rich sites (Kranabetter et al., 2009; Toljander et al., 2006). Furthermore, the microclimate directly influences ecological processes and reflects subtle changes in ecosystem function, particularly in forests where the majority of the identified edible species are saprotrophic and depend on a suitable microclimate for their growth and production. In that context, a mosaic forest management scheme is needed that considers both timber production and edible wild mushroom production. Such a scheme must uphold the environmental variables needed to create habitats, with variable microclimates to promote diverse sporocarps. This could increase the value of Ethiopia's remnant natural forests and provide incentives for forest owners to sustainably manage and conserve the forests' resources in different forms.

Furthermore, other studies have also demonstrated that fungal fruiting can be governed by various climate variables in addition to landscape heterogeneity (Bahram et al., 2015; Ferrari et al., 2016; Peay et al., 2010; Tedersoo et al., 2014b). The combined effects of edaphic characteristics and climate variables influence fungal fruiting spatial variation (Chen et al., 2015; Li et al., 2020). Thus, evaluating climate variables is also essential to identify their relative contributions to fungal sporocarps production. Although climate variables cannot be modified by forest managers, they can in some cases explain between 60 and 80% of the variation in fungal sporocarps production (Dahlberg and Stenlid, 1994). In our model, the average daily minimum temperature during the collection month was also used as a predictive variable to estimate sporocarps production in the two forest types. This might be because temperature can play a role in nutrient cycling (Geng et al., 2017). An increase in temperature generally facilitates the decomposition of OM in the soil, which accelerates the availability of nutrients. This is likely to favor some fungal species, particularly saprotrophic fungi, the dominant trophic group recorded in this study (Nicolás et al., 2019), which was reflected by their higher sporocarps production levels. In addition, latitude as a spatial factor was correlated with sporocarps production. Although this needs further investigation to determine an ecologically meaningful explanation for the influence of latitude on sporocarps production in our study areas, Golan and Pringle (Golan and Anne, 2017) indicated that distance as a spatial factor could affect the dispersal of fungal propagules, which would have an

impact on the large-scale connectivity of different fungal species, leading to the formation of similar community structures or phenology (Calhim et al., 2018).

Our analysis of AMF diversity revealed that AMF communities detected in plantation and natural forests were distinctly different from each other in terms of diversity and structure (Figure 4A in **study III**). The presence of distinctly different communities in plantation and natural forests can be attributed to several interrelated factors specific to each forest type. For example, natural forests in Ethiopia are characterized by their relatively undisturbed ecological processes, which provide a diverse range of habitats and niches that support a rich variety of plant species (Chen et al., 2022; Gong et al., 2012; He et al., 2017; Melo et al., 2017; Vieira et al., 2019). The wide diversity of plant species provides a wide range of resources and ecological niches for AMF colonization and proliferation, leading to a complex and diverse AMF community structure (Alemu, 2013; Dejene et al., 2017d). By contrast, plantation forests, which are typically managed for commercial purposes and are often composed of monocultures or limited species compositions, have a simpler ecological environment than natural forests, with reduced plant diversity and altered soil conditions (He et al., 2017; Melo et al., 2017). Such ecosystems may favor specific AMF species that are better adapted to conditions prevailing in plantation forests, resulting in distinct AMF communities. In addition, management practices such as soil disturbance, fertilization, and pesticide use in plantation forests can further influence AMF communities by altering soil properties and disrupting natural ecological processes (Gong et al., 2012; Kazenel et al., 2019; Kivlin et al., 2011; Tian et al., 2018; Torrecillas et al., 2013). These considerations highlight the importance of considering ecological context when studying fungal biodiversity and ecosystem dynamics (Chen et al., 2022; Gong et al., 2012; He et al., 2017; Melo et al., 2017; Vieira et al., 2019).

The Shannon–Wiener diversity index of AMF species varied across different forest types and stands (Table 3 in **study III**). Specifically, higher AMF diversity was detected in natural forests than in plantation forests. The abundance, richness, and number of AMF species were also significantly higher in natural forest environments than in plantations. However, a significant number of AMF species were identified in

*Eucalyptus* stands, indicating a potential influence of forest management practices on the taxonomic composition of AMF communities within plantation forests. Plant diversity plays a crucial role in shaping the resources available to fungi for survival and growth, as highlighted in previous studies (Tedersoo et al., 2016; David A Wardle et al., 2004). Analyses of AMF richness in the five different stands revealed that AMF richness and diversity values were greatest in the Taragedam and Banja forests. This finding might be associated with the greater availability of a broader host range (Alem et al., 2020a; Roy et al., 2008) in these forests than in the Alemsaga forest or the plantations. This suggests that stands with several plant species have a positive effect on AMF diversity (Oehl et al., 2010). A previous study (Ayana, 2021) reported that the richness of ectomycorrhizal fungal species was highest in Taragedam forests. Among the three natural forests, the lowest abundance, diversity indices, and species richness levels were detected in soil samples from Alemsaga forest, which could be attributed to the land-use history of the forest. Alemsaga forest was converted to agricultural land in 1990, which could have had a negative impact on fungal resources in this area (Ayana, 2021; Tervonen et al., 2019). A decline in vegetation and the constant removal of dead wood from forests results in the loss of associated fungi (Berg et al., 2002; Jiang et al., 2018). The lower levels of AMF diversity and species richness in the Alemsaga forest could also be due to the lower soil fertility level of Alemsaga forest compared with that of Taragedam or Banja forests (Garo et al., 2022; Oehl et al., 2010; Soudzilovskaia et al., 2015), and perhaps due to an absence of other forests in the vicinity that could serve as a source of fungal propagules (Redondo et al., 2020). In addition, the host could influence AMF diversity (Melo et al., 2017; Tedersoo et al., 2016) through its impact on the quantity and quality of carbon resources (Genevieve et al., 2019).

Many other environmental factors can also influence AMF communities, such as soil nutrients, temperature, light availability, rainfall, and possible interactions with these factors (Chaudhary et al., 2014; Gong et al., 2012; Vieira et al., 2019). In our study (Figure 4B in **study III**), AMF community composition was significantly affected by soil pH, EC, N, OC, P, annual rainfall, CRF3d, and longitude. Soil pH, EC, and N had a positive influence on AMF communities, whereas OC and P had a negative influence on AMF communities. Similar observations have also been reported in previous

studies (Lakshmipathy et al., 2012). The available P in soil plays an important role in the composition of the AMF community by influencing mycorrhizal colonization and spore production. Several studies (Gong et al., 2012; Tervonen et al., 2019) have indicated that high available P content could reduce mycorrhizal colonization and spore production. The high level of available P in the plantation soil samples seems to have had a significant negative influence on AMF communities. Previous studies have also reported that high P availability modifies the composition and diversity of AMF communities as well as spore and mycelium densities in temperate and tropical systems (Lakshmipathy et al., 2012; Melo et al., 2017; Wang et al., 2015). Our analyses indicate that forest type and forest stand significantly influence the composition of AMF communities, which suggests that the conversion of native forests to exotic plantations impacts the diversity of AMF communities. This conclusion aligns with the conclusions drawn by other studies (Kivlin et al., 2011; Melo et al., 2017; Öpik et al., 2010).

From a management perspective, although latitude cannot be modified by management, understanding its relationship with other variables is useful for landscape-level planning to identify forest stands in which mushrooms production could be integrated as one of the NTFPs (Bonet et al., 2010). Latitude affects the climate of an area. As the latitude increases, solar energy decreases, and humidity increases (Andrew et al., 2016). In this case, temperature would have a stronger impact than other climate variables on the occurrence of most fungal groups and, therefore, higher levels of sporocarps production at higher latitudes (Andrew et al., 2018). In line with this, another study has also concluded that our chosen environmental parameter together with other environmental parameters best predicted the mushroom yield in *Pinus pinaster* forests using classification models (Gassibe et al., 2014). This is because temperature comprehensively affects fungal phenology and is positively correlated with sporocarps production, although this correlation could be improved by precipitation just before and during the sporocarps season (Collado et al., 2019; Sánchez-González et al., 2019). Gassibe et al. (2015) suggested that classificatory models can be valuable for optimizing the management and harvesting of wild mushrooms; however, the variables identified should be further investigated, as mushrooms yield are typically influenced by environmental

and geographical factors, including rainfall, temperature, latitude, longitude, and soil conditions (Castaño et al., 2018b). These factors directly impact the accuracy of models when applied to estimate mushrooms production in areas beyond the original study site. Furthermore, forest characteristics, such as stand structure, stand age, and stand management, must be included in the model because they have a critical influence on wild mushroom biomass production. Thus, the applicability of any conclusions to other similar forest stands should be considered with caution. Moreover, our yield estimations were based on one year of data, which we consider to be a limited dataset. Thus, to obtain more accurate and reliable yield estimations of edible wild mushrooms, we recommend several years of sampling to observe inter-annual variations in sporocarps production. These measures include emphasizing the inclusion of a substantial variety of edible mushroom species, underscoring the significance of selecting diverse sampling locations, taking note of distinct forest attributes, and highlighting the relevance of spatial variation.

#### 5.4. Predictive modeling of sporocarps yields (Study II)

The classificatory model (**study II**) is the first study to attempt to model edible wild mushroom production in natural and plantation forest systems in Ethiopia. In this study, the relationship between sporocarps production and environmental parameters was expressed using a multinomial yield classification model. The identified model enabled accurate estimations of the mushroom biomass yields that could be obtained from natural and plantation forests in the study areas. In our model, among the edaphic variables, OC, Na, N, and P were used as predictive variables to estimate sporocarps production in the two forest types. Other studies have indicated that fungal taxa are likely to respond differently to different edaphic variables, depending on their characteristics (Crowther et al., 2013; Koide et al., 2014). Thus, in turn, fungal fructification is directly correlated with edaphic parameters (Cozzolino et al., 2016). This is likely to be because organic carbon (OC) in relation to OM could influence the fungal community through its impact on the water-holding capacity of the soil and nutrient availability (Harrington, 2003). Thus, OC may favor the fructification of more fungal species in an area, particularly of saprotrophic fungi. Specifically, our analyses also revealed that certain edible

fungal species, particularly ECM species, were most correlated with OC and OM. For example, *Tylophilus niger* and *Suillus luteus* were positively correlated with OC. In addition to the fact that organic matter holds up to 90 percent of its weight in water, the reason is that ECM mycelia are mostly found in the organic horizon of the soil (Lindahl et al., 2007), as they directly or indirectly (Phillips et al., 2014) access soil carbon pools for their survival and growth, although photosynthesis is the primary source of carbon used by ECM species (Holden et al., 2016). Furthermore, ECM fungi are thought to have a key role in mobilizing organic nitrogen that is trapped in soil organic matter (Shah et al., 2016). Also, some fungi are thought to have a unique ability to degrade lignin and other phenolic compounds of forest SOM (Baldrian, 2008).

The edaphic cation element of sodium was also correlated with the overall level of sporocarps production, which indicates that soil cation concentrations could influence fungal biomass. Cations in general play an important part in several 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 soil fungi (Shi et al., 2014). Furthermore, the correlation of nitrogen with fungal taxa supports previous findings by Kranabetter et al. (2009), Reverchon et al. (2010), and Gassibe et al. (2015), who stated the influence of nitrogen on fungal distribution patterns. In these reports, fungi showed community specialization towards soil with higher nitrogen values. This might be because nitrogen can influence the formation of extra-radical mycelium in the soil, and play a vital role in sporocarps formation (Trudell and Edmonds, 2004). Furthermore, Kranabetter et al. (2009) and Toljander et al. (2006) noted that fungal communities can be adapted to nitrogen-rich sites.

### 5.5. Synthesis of Ethiopian fungal biodiversity (Study IV)

Ethiopian forests are considered to be major reservoirs of fungal biodiversity (Aerts et al., 2016; Aynekulu et al., 2016; Nyssen et al., 2014). Despite the abundant biodiversity and ecological significance of Ethiopian forests, only a limited number of studies have characterized the diversity of edible wild mushrooms and AMF communities within these ecosystems. Hence, in our studies (I-IV), we intend to fill an

information gap in this regard. Our findings from these studies have shown that a huge number of wild edible mushrooms and sporocarps production (**studies I and II**) and AMF species (**study III**) in the studied forest locations, including Taragedam, Banja, Alemsega, Wondo Genet, and Menagesha Suba forests in Ethiopia. It was noted that clear differences in fungal community composition between these forests across the forest stand among the five study areas. The diverse fungal species in such forest systems may largely be attributed to the higher diversity of tree species (Chen et al., 2017) and the enhanced soil fertility from nutrient inputs during the decomposition of wood materials, which supply the necessary nutrients for various fungal groups (Siciliano et al., 2014)

In the natural forests (**studies I and II**), various marketable fungi, such as species of *Agaricus*, *Termitomyces*, and *Schizophyllum* (Sitotaw et al., 2015; Sitotaw et al., 2020; Tuno, 2001), were also collected. The presence of these locally used species highlights the need for adequate management and conservation of these forests if wild mushrooms are meant to be used as NTFPs. Currently, the management of forests based on valuable NTFPs is attracting more attention due to their market value, consumer demand, and interest in developing countries (Rijsoort and Pater, 2000). Hence, the potential commercialization of indigenous edible mushrooms within the studied regions holds the promise of significant socioeconomic advantages for collectors, serving to enhance household income (Bonet et al., 2014). This, in turn, could have a meaningful influence on the livelihoods of local communities dependent on the forest resources in these areas. Indeed, in certain regions such as the Mediterranean, the value of wild edible mushrooms surpasses the value of timber (Bonet et al., 2010). In addition, edible wild mushrooms from forests form the basis of multiple manufactured products, including medicine, and are the focus of a new wave of tourism resulting from recreational programs linked to nature (Martínez-Peña et al., 2012).

In **study III**, we found a high level of AMF diversity (193 OTUs, Figure S1 in **study III**) in the four studied forests (Table S3 in **study III**) areas we examined. This high level of diversity could be attributed to factors such as plant diversity (Janos, 1996; Laurindo et al., 2021) and favorable environmental conditions (Hanson et al.,

2012; Hazard et al., 2013; Melo et al., 2017), which promote diversity across the country (Wardle et al., 2004). Thus, the observed AMF richness in this study suggests the necessity of obtaining comparable descriptive data on soil fungal communities through more comprehensive sampling designs across diverse ecosystems (Tchabi et al., 2008) in Ethiopia.

Pegler and Rayner (1969) and Pegler (1977) noted that the East Africa region that includes Ethiopia is rich in macrofungal species. Many of these species are presumed to be either cosmopolitan or to be widespread across Africa (Munyanziza, 1994; Pegler, 1977). However, most regions and habitats of fungi in Ethiopia have been seldom studied. Furthermore, reports regarding fungal diversity and a list of important species rarely exist (Megersa et al., 2017; Sitotaw et al., 2015). This is due to a lack of research infrastructures as well as to a lack of fungal taxonomists and specialists in fungal ecology. Finally, and likely as a result, fungi are not included in the biodiversity database of the country (IBC, 2014). The poor knowledge of fungal flora in Ethiopia is also worrying as fungi are highly sensitive towards habitat disturbances (Figure 4 in **study IV**), namely anthropogenic threats that are rife across the country (IBC, 2014). The information on fungal resources (Table 2 in **study I**, Table 3 in **study II**, Table S1 in **study III**, and Figure 1 in **study IV**) provides basic information about fungal flora in the country that will help create awareness for conservation, wider use of mycological resources and also serve as baseline information for further mycological studies in the country. The diversity and availability of fungal species reported (Table 2 in **study I**, Table 3 in **study II**, Table S1 in **study III**, and Figure 1 in **study IV**) from different forests might be a lot richer than what has been so far reported.

Despite poor information on fungal resources, ethnomycology has been a traditional common practice among the local tribes in Ethiopia (Tuno 2001; Semwal et al. 2014). Mushrooms have been used for their nutritional, traditional, and medicinal properties (Abate, 2014; Tuno, 2001). However, the ethnomycological and socioeconomic experiences were not assessed for the majority of the ethnic groups, indicating the information contained is inadequate and lack to convey the full picture of the country, as Ethiopia is characterized by many communities that might have a

long history of wild mushroom usage with wider traditional knowledge on the use. Thus, more studies and documentation are important to reveal the human mushroom relationship, and the traditional experiences in depth in the country.

Mushroom cultivation practice in Ethiopia is still very low and limited numbers of species have been cultivated commercially. Owing to their flavor and nutritional value, the consumption of cultivated mushrooms is now constantly increasing in the urban area (Figure 3 in **study IV**). However, a lack of mushroom cultivation skills still leaves plenty of room for improvement and growth (Muleta et al., 2013; Yehuala, 2008). Conservative eating habits, on the other hand, are also hindering the transfer of cultivation technology at a local level, particularly in areas where mushroom consumption is not a common practice. Thus, more efforts have to be made, i.e., systematic field research, as in the case of these studies (I-III) (Figure 5 in **study IV**) and awareness creation training for youths (Figure 6 in **study IV**) and women (Figure 7 in **study IV**) should be encouraged to promote the cultivation and wider utilization of mushroom in the country. Furthermore, the integration of appreciated valuable fungal species into forest management plans like mycosilviculture approach could increase the value of Ethiopian forests and provide incentives for forest owners to sustainably manage and conserve their forest resources in alternative forms.



**Conclusion**

## 6. Conclusions

- 1) The findings of the studies conclude that natural forests in Ethiopia exhibit higher species richness of edible mushrooms, primarily saprophytic species producing small sporocarps. However, plantation forests, despite hosting fewer species, demonstrated significantly higher sporocarps production. The study findings reveal the presence of unique species in both forest types, including marketable species that could provide supplementary income to local communities. Environmental factors, particularly spatial and climatic variables, had a stronger influence on fungal composition and production than soil-related factors. The findings suggest that a mosaic landscape combining natural and plantation forests could enhance both timber and mushroom production, promoting biodiversity conservation in natural forests. A management approach that integrates timber and mushroom production would yield economic and ecological benefits, especially in areas affected by deforestation. The scheme should account for environmental conditions to foster diverse fungal species and boost sporocarps yields, particularly in natural forests with low sporocarps production.
- 2) This study, despite being limited to one year of data, highlighted the presence of several valuable edible fungal species such as *Morchella anatolica*, *Suillus luteus*, *Tylopilus niger*, and *Tricholoma portentosum* across two forest systems in Ethiopia. It found that plantation forests yielded higher sporocarps production compared to natural forests. These insights suggest the potential for managing forests to optimize wild mushroom production as a non-timber forest product (NTFP), which can offer significant economic value. The study also introduced a preliminary yield classification model for predicting mushroom production, identifying latitude, organic matter (OM), and minimum daily temperature as key variables influencing yields. However, to improve the accuracy of these models, extended monitoring over multiple years is needed, considering more comprehensive environmental variables and annual variations. This could help refine forest management strategies, particularly in areas affected by degradation and deforestation.

- 3) The findings from this study also highlight the significant impact forest type has on the diversity, abundance, and composition of arbuscular mycorrhizal fungi (AMF) communities. The conversion of Ethiopia's natural forests to crops or monospecific plantations presents a major threat to biodiversity, particularly for microorganisms like AMF, which play crucial roles in ecosystem functioning. This loss of diversity could lead to irreversible ecological consequences. The study underscores the importance of prioritizing the sustainable development of degraded natural forests rather than promoting plantation forests to preserve the habitats that support AMF communities. Future research should focus on disentangling the environmental factors driving these changes and include long-term monitoring or controlled experiments. Additionally, parallel studies on AMF and ectomycorrhizal (ECM) fungi across different forest systems are necessary to better understand their ecological roles and interactions. Furthermore, a considerable number of AMF taxa were not identified at the genus or species level, highlighting that much of Ethiopia's fungal diversity remains undocumented. This suggests that Ethiopian forest systems likely harbor numerous taxa that are new to science. Therefore, we recommend further long-term scientific research to fully explore and document the country's fungal biodiversity, contributing to a more comprehensive understanding of these ecosystems and supporting future conservation efforts.
- 4) Our findings from the synthesis of fungal distribution, diversity, and conservation challenges across various land uses in Ethiopia revealed significant fungal diversity, with a notable presence of edible species, highlighting Ethiopian forests as a rich source of edible wild mushrooms. Saprotrophic fungi dominate, playing a key role in nutrient cycling, while ectomycorrhizal fungi contribute to forest health through symbiotic relationships. The threats of land use change, deforestation, and climate change necessitate effective conservation strategies. Understanding the distribution and ecological roles of fungi is critical for these efforts, with a focus on protecting vulnerable species and promoting sustainable use. The study's findings have practical implications for policy, practice, and public awareness in conserving fungal diversity and supporting sustainable forest management in Ethiopia. Hence, the application of the mycosilviculture approach

is vital for preserving fungal biodiversity while enhancing SFM. Furthermore, the information obtained from all four studies in this thesis significantly enhances the understanding of macrofungal and soil fungal communities in Ethiopian forest ecosystems. This knowledge offers valuable guidance for forest management and conservation strategies, emphasizing the vital role fungi play in maintaining forest health and supporting ecosystem services, including their potential as a critical food resource for local populations during periods of food scarcity.

- 5) Overall, the implications of these studies are useful in the National Adaptation Plan, National Mitigation Plan, and National Determined Contributions of Ethiopia, including the Sustainable Development Goals Agenda 2030 and Agenda 2063. This will help develop strategies for the sustainable management of forests and biodiversity.

## 7. Conclusiones

- 1) Los resultados de los estudios concluyen que los bosques naturales de Etiopía presentan una mayor riqueza de especies de hongos comestibles, principalmente especies saprofitas que producen pequeños esporocarpos. Los bosques de plantación, a pesar de albergar menos especies, demostraron una producción de esporocarpos significativamente mayor. Los hallazgos del estudio revelan la presencia de especies únicas en ambos tipos de bosques, incluidas especies comercializables que podrían proporcionar ingresos complementarios a las comunidades locales. Los factores ambientales, en particular las variables espaciales y climáticas, tuvieron una mayor influencia en la composición y producción de hongos que los factores relacionados con el suelo. Los hallazgos sugieren que un paisaje en mosaico que combine bosques naturales y de plantación podría mejorar la producción de madera y hongos, promoviendo la conservación de la biodiversidad en los bosques naturales. Un enfoque de gestión que integre la producción de madera y hongos produciría beneficios económicos y ecológicos, especialmente en áreas afectadas por la deforestación. El plan debería tener en cuenta las condiciones ambientales para fomentar diversas especies de hongos e impulsar los rendimientos de esporocarpos, particularmente en bosques naturales con baja producción de esporocarpos.
- 2) Este estudio, a pesar de estar limitado a un año de datos, destacó la presencia de varias especies de hongos comestibles valiosas como *Morchella anatolica*, *Suillus luteus*, *Tylopilus niger* y *Tricholoma portentosum* en dos sistemas forestales de Etiopía. Encontró que los bosques de plantación produjeron una mayor producción de esporocarpos en comparación con los bosques naturales. Estos conocimientos sugieren el potencial de gestionar los bosques para optimizar la producción de hongos silvestres como un producto forestal no maderable (PFNM), que puede ofrecer un valor económico significativo. El estudio también presentó un modelo preliminar de clasificación de rendimiento para predecir la producción de hongos, identificando la latitud, la materia orgánica (MO) y la temperatura mínima diaria como variables clave que influyen

en los rendimientos. Sin embargo, para mejorar la precisión de estos modelos, se necesita un seguimiento extendido durante varios años, considerando variables ambientales más integrales y variaciones anuales. Esto podría ayudar a refinar las estrategias de gestión forestal, particularmente en áreas afectadas por la degradación y la deforestación.

- 3) Los hallazgos de este estudio también destacan el impacto significativo que tiene el tipo de bosque en la diversidad, abundancia y composición de las comunidades de hongos micorrícicos arbusculares (HMA). La conversión de los bosques naturales de Etiopía en cultivos o plantaciones monoespecíficas presenta una gran amenaza para la biodiversidad, en particular para microorganismos como los HMA, que desempeñan papeles cruciales en el funcionamiento del ecosistema. Esta pérdida de diversidad podría conducir a consecuencias ecológicas irreversibles. El estudio subraya la importancia de priorizar el desarrollo sostenible de los bosques naturales degradados en lugar de promover los bosques de plantación para preservar los hábitats que sustentan las comunidades de HMA. Las investigaciones futuras deberían centrarse en desentrañar los factores ambientales que impulsan estos cambios e incluir un seguimiento a largo plazo o experimentos controlados. Además, son necesarios estudios paralelos sobre los HMA y los hongos ectomicorrícicos (ECM) en diferentes sistemas forestales para comprender mejor sus funciones e interacciones ecológicas. Además, no se identificaron un número considerable de taxones de HMA a nivel de género o especie, lo que destaca que gran parte de la diversidad fúngica de Etiopía sigue sin documentarse. Esto sugiere que los sistemas forestales etíopes probablemente albergan numerosos taxones que son nuevos para la ciencia. Por lo tanto, recomendamos realizar más investigaciones científicas a largo plazo para explorar y documentar completamente la biodiversidad fúngica del país, contribuyendo a una comprensión más completa de estos ecosistemas y apoyando futuros esfuerzos de conservación.
- 4) Nuestros hallazgos a partir de la síntesis de la distribución, diversidad y desafíos de conservación de hongos en varios usos de la tierra en Etiopía revelaron una diversidad fúngica significativa, con una presencia notable de especies

comestibles, destacando los bosques etíopes como una fuente rica de hongos silvestres comestibles. Los hongos saprotróficos dominan, desempeñando un papel clave en el ciclo de nutrientes, mientras que los hongos ectomicorrícicos contribuyen a la salud de los bosques a través de relaciones simbióticas. Las amenazas del cambio de uso de la tierra, la deforestación y el cambio climático requieren estrategias de conservación efectivas. Comprender la distribución y los roles ecológicos de los hongos es fundamental para estos esfuerzos, con un enfoque en la protección de las especies vulnerables y la promoción del uso sostenible. Los hallazgos del estudio tienen implicaciones prácticas para la política, la práctica y la conciencia pública en la conservación de la diversidad fúngica y el apoyo a la gestión forestal sostenible en Etiopía. Por lo tanto, la aplicación del enfoque de micosilvicultura es vital para preservar la biodiversidad fúngica y al mismo tiempo mejorar la GFS. Además, la información obtenida de los cuatro estudios de esta tesis mejora significativamente la comprensión de las comunidades de hongos macrofúngicos y fúngicos del suelo en los ecosistemas forestales etíopes. Este conocimiento ofrece una valiosa orientación para las estrategias de gestión y conservación forestal, destacando el papel vital que desempeñan los hongos en el mantenimiento de la salud de los bosques y el apoyo a los servicios ecosistémicos, incluido su potencial como recurso alimentario crítico para las poblaciones locales durante períodos de escasez de alimentos.

- 5) En general, las implicaciones de estos estudios son útiles en el Plan Nacional de Adaptación, el Plan Nacional de Mitigación y las Contribuciones Nacionales Determinadas de Etiopía, incluidos los Objetivos de Desarrollo Sostenible Agenda 2030 y la Agenda 2063. Esto ayudará a desarrollar estrategias para la gestión sostenible de los bosques y la biodiversidad. Se necesitan más estudios para investigar las respuestas de los hongos a los factores ambientales en diferentes sistemas forestales y para mejorar nuestra comprensión de la dinámica de los hongos en el espacio y el tiempo mediante el establecimiento de parcelas de estudio permanentes.

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## Original articles

## Original article I

## Forest Type and Site Conditions Influence the Diversity and Biomass of Edible Macrofungal Species in Ethiopia

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## Abstract

Ethiopian forests are rich in valuable types of non-wood forest products, including mushrooms. However, despite their nutritional, economic, and ecological importance, wild edible mushrooms have been given little attention and are rarely documented in Ethiopia. In this study, we assessed mushroom production levels in natural and plantation forests and the influence of climate and environmental variables on mushroom production. Sporocarps were sampled weekly from July to August 2019 at a set of permanent plots (100 m<sup>2</sup>) in both forest systems. We analyzed 63 plots to quantify sporocarp species' richness and fresh weight as well as to elucidate the degree of influence of forest types and site conditions, including soil and climate. Morphological analyses were used to identify fungi. In total, we recorded 64 wild edible fungal species belonging to 31 genera and 21 families from the plots established in the natural and plantation forests. A significantly greater total number of edible fungi were collected from natural forests (n = 40 species) than from plantations. Saprotrophs (92.19%) were the dominant guild whereas ectomycorrhizal fungi represented only 6.25% of species. Ecologically and economically important fungal species such as *Agaricus campestris*, *Tylophorus niger*, *Suillus luteus*, *Tricholoma portentosum*, and *Morchella americana* were collected. The sporocarp yield obtained from plantation forests (2097.57 kg ha<sup>-1</sup>) was significantly greater than that obtained from natural forests (731.18 kg ha<sup>-1</sup>). The fungal community composition based on sporocarp production was mainly correlated with the organic matter, available phosphorus, and total nitrogen content of the soil, and with the daily minimum temperature during collection. Accordingly, improving edible species' richness and sporocarp production by maintaining ecosystem integrity represents a way of adding economic value to forests and maintaining biological diversity, while providing wood and non-wood forest products; we propose that this approach is imperative for managing Ethiopian forests.

**Keywords:** edaphic variables; edible mushrooms; natural forests; plantation forests; sporocarp yield

## Original article II

## Assessing the potential of forest stands for edible mushrooms productivity as a subsistence ecosystem service in Ethiopia.

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### Abstract

Wild edible mushrooms are recognized as a fundamental component of forest management and rural development initiatives, offering farmers a substantial supplementary source of income. Thus, exploring the valuable wild mushrooms and modeling fungal fruiting in different forest systems in the tropics could provide additional insight into fungal responses to environmental factors and allow for better decision-making related to forest management in the face of climate change. In many parts of the world, edible wild mushrooms are considered economically valuable non-timber forest products (NTFPs). In Ethiopia, forest management policies based on NTFPs are needed to make better use of these resources. A thorough assessment of wild mushrooms as NTFPs that occur in Ethiopian forests and their uses is key to understanding what actions are needed to manage forests at the local level. We aimed (1) to record the fresh weight of edible wild mushrooms produced in natural and plantation forests in Ethiopia and (2) to develop models to predict sporocarp production in these two forest systems. We established 63 sample plots of 100 m<sup>2</sup>. All mature and young edible wild mushrooms were harvested weekly during the main rainy season to quantify their abundance and fresh weight. Composite soil samples collected from each plot and climate data recorded for each study area were used to develop models. In total, 64 edible fungal species were collected. The average annual total fresh weight production in plantations (2097.57 kg ha<sup>-1</sup>) was significantly greater than that produced in natural forests (731.18 kg ha<sup>-1</sup>). Six alternative models were fitted, and three yield categories were also defined as possible responses. Latitude, soil organic matter, and minimum daily temperature were identified as relevant explanatory factors. Our yield classification models were fitted to predict the annual yields of edible fungi based on climate, soil, and area-specific information in Ethiopia. The developed models should serve as a basis for further studies in Ethiopian forests to optimize forest management based on NTFPs, specifically edible wild mushrooms.

**Keywords:** *Climate, natural forests, NTFPs, plantation forests, site factors, soil, mushroom.*

## Original article III

## Untangling the effect that replacing Ethiopia's natural forests with exotic tree plantations has on arbuscular mycorrhizal fungi

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## Abstract

Arbuscular mycorrhizal fungi (AMF) have a broad distribution and establish symbiotic relationships with vascular plants in tropical regions. They play a crucial role in enhancing plant nutrient absorption, mitigating pathogenic infections, and boosting the resilience of host plants to abiotic stresses, including drought under specific conditions. Many natural forests in Ethiopia are being replaced by monospecific plantations. However, the impact of these actions on AMF is unknown and, despite their ecological functions, AMF communities in various forest systems have not been thoroughly investigated. In this study, we assessed soil AMF communities in natural and plantation forests by DNA metabarcoding of the ITS2 rDNA region and assessed the influence of climate and environmental variables on the AMF community. In total, 193 AMF operational taxonomic units (OTUs), comprising nine families and 15 genera, were recorded. Glomerales were the dominant order (67.9% of AMF OTUs) and *Septoglomus fuscum*, *Diversispora insculpta*, and *Funneliformis mosseae* were the dominant species. AMF were more abundant in natural forests than in plantation forests and the composition of AMF communities differed significantly from those of plantation forests. In plantation forests, soil pH, organic carbon, total nitrogen, and available phosphorus significantly influenced the composition of AMF communities, whereas in natural forests, electrical conductivity, annual rainfall, and cumulative rainfall before sample collection were significantly correlated with AMF. SIMPER analysis identified the AMF responsible for composition variances among different forest types, with the Glomeraceae family being the most significant contributor, accounting for nearly 60% of the dissimilarity. Our findings further our understanding of the ecological niche function and the role of AMF in Ethiopia's natural forest systems and highlight the importance of prioritizing the sustainable development of degraded natural forests rather than plantations to ensure the preservation of habitats conducive to maintaining various AMF communities when devising conservation and management strategies.

**Keywords:** Arbuscular mycorrhizal fungi, Natural forest conservation, Ethiopian forest, Fungal composition, Soil fungi, Non-wood forest products.

## Original article IV

### Fungal Biodiversity in Ethiopia: Distribution, Threats and Prospects

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#### Abstract

Fungi are an integral part of the natural world, playing important roles in ecological processes and having considerable potential for use in diverse industries. Despite the rich fungal diversity in Ethiopia, limited information exists regarding their distribution, threats, and conservation efforts. Even, fungi are not included in the biodiversity database of the country. This work provides a synthesis of information gathered from different sources to understand fungal biodiversity, focusing on the distributions, threats to, and conservation of fungal species across various land uses and sites in Ethiopia. The fungal biodiversity in the country is extensive, encompassing a wide range of fungal species. However, fungi in Ethiopia are threatened by multiple factors, including land use/land cover changes, deforestation, habitat degradation, the expansion of invasive plant species, and climate change. Efforts, thus enhancing the resilience and productivity of habitats, different ecosystems, and mycological resources will lead to effective conservation and management of biodiversity to ensure their sustainable use. To this end, this work will contribute to the existing body of knowledge and help in the formulation of strategies for sustainable management of fungal biodiversity.

**Keywords:** *Biodiversity conservation, Ethiopia, mycological resources, non-wood forest products rural livelihoods.*