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Fungal communities of West African ectomycorrhizal woodlands

BRENDAN R. FURNEAUX

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Abstract
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Ectomycorrhizal symbiosis is a widespread mutualist relationship between fungi and plants, often trees. It is most well-known in temperate and boreal forests, but also occurs in a variety of tropical ecosystems, including Sudanian savanna woodlands and gallery forests in West Africa. In addition to their important role in nutrient cycling, many ectomycorrhizal fungi also produce edible mushrooms as their fruit-bodies. In this thesis, I explore spatial patterns of above-ground and below-ground diversity in West African ectomycorrhizal communities, as well as the use of wild edible fungi by the local human population. In **Papers I** and **II**, I used soil DNA metabarcoding to investigate fungal communities in their vegetative state. **Paper I** used measurements of the scale of spatial autocorrelation within the fungal community in Sudanian woodlands in Benin as a test to compare different high-throughput DNA sequencing strategies, including short (≈350 bp) amplicon barcoding using the Illumina, Ion Torrent, and PacBio sequencing platforms, as well as long (≈1550 bp) amplicon barcoding using PacBio. There were some differences in species richness and community composition recovered by the two amplicon lengths, attributable to known primer biases for the short amplicons, but these did not lead to different ecological results. Additionally, **Paper I** introduced new software packages for analysis of long-amplicon metabarcoding data and integrating phylogenetic information into sequence-based taxonomic identification. In **Paper II** we sampled both Sudanian woodland and gallery forest sites in five countries across West Africa using long-amplicon metabarcoding with PacBio. We found significant differences in fungal community composition between Sudanian woodland and gallery forest sites, but not between different tree species within each vegetation type. **Papers III** and **IV** focused above-ground to study the natural production and human use of the mushrooms themselves. In **Paper III** we exhaustively collected mushrooms from nine Sudanian woodland plots in Benin during three consecutive rainy seasons. We measured the total biomass produced of each morphospecies, as well as environmental variables related to microclimate, host tree availability, and soil chemistry. Mushroom production and diversity were negatively correlated with soil nitrogen levels, and positively correlated with soil phosphorus levels. Although there were no clear differences in the fungal communities associated with the four host trees present in our plots, greater host tree diversity was associated with greater fungal diversity and productivity. Finally, **Paper IV** combined interviews with local people from four ethnic groups in five villages near the study sites from **Paper III** about their knowledge and preferences for edible mushrooms with DNA barcoding of specimens. Knowledge and preferences for different mushrooms varied between ethnic groups, but people living in a village where their ethnic group is a minority tended to absorb knowledge about mushrooms from the majority group in the village. Women over age 35 were the most knowledgeable about mushrooms, but the degree of gender difference varied between groups. We compiled a list of the most choice edible mushrooms in the area, which can inform the possibility for commercial trade in wild mushrooms to supplement the income of rural people and encourage sustainable forest management.

Keywords: ectomycorrhizal fungi, West Africa, metabarcoding, Sudanian woodlands, community ecology, ethnomycology, edible mushrooms, fungi

Brendan R. Furneaux, Department of Organismal Biology, Systematic Biology, Norbyv. 18 D, Uppsala University, SE-75236 Uppsala, Sweden.

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List of papers

This thesis is based on the following papers, which are referred to in the text by their roman numerals.

I **Furneaux, B.**, Bahram, M., Rosling, A., Yorou, N.S., Ryberg, M. Long- and short-read metabarcoding technologies reveal similar spatio-temporal structures in fungal communities. (In review at Molecular Ecology Resources)

II Meidl, P.*, **Furneaux, B.***, Tchan, K.**, Kluting, K.**, Ryberg, M., Guissou, M.-L., Bakary, S., Traoré, A., Konoumou, G., Yorou, N. S., Rosling, A. (2020) Soil fungal communities of ectomycorrhizal dominated woodlands across West Africa. (In review at MycoKeys)

III **Furneaux, B.**, Houdanon, R., Aïgnon, H., Boni, S., Codjia, J. E., Laourou, G., Bahram, M., Svanholm, A., Rosling, A., Yorou, N.S., Ryberg, M. (2020) Spatial drivers of ECM community composition and fruitbody production in West African woodlands. (Manuscript)

IV **Furneaux, B.***, Veldman, S.*, Riggi, L., Boni, S., Svanholm, A., Ryberg, M., Yorou, N. S. (2020) Comparison of wild mushroom use by ethnic groups surrounding the Upper Ouémé Forest Reserve in Benin, West Africa. (Under revision after initial review at PLOS ONE)

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* shared first authorship

** shared second authorship

Contents

Abbreviations

AM arbuscular mycorrhiza/mycorrhizal

ASV amplicon sequence variant

bp base pairs

DNA deoxyribonucleic acid

ECM ectomycorrhiza/ectomycorrhizal

HTS high-throughput sequencing

INSDC International Nucleotide Sequence Database Consortium

ITS internal transcribed spacer (of ribosomal DNA)

LSU large subunit (of ribosomal RNA/DNA)

NMDS non-metric multidimensional scaling

OTU operational taxonomic unit

PacBio Pacific Biosciences

PCR polymerase chain reaction

PERMANOVA permutational multivariate analysis of variance

qPCR quantitative polymerase chain reaction

rDNA ribosomal DNA

RDP Ribosomal Data Project

RDPC RDP (Naïve Bayesian) Classifier

RFLP restriction fragment length polymorphism

RNA ribonucleic acid

rRNA ribosomal RNA

SSU small subunit (of ribosomal RNA/DNA)

tr. tribe (taxonomic rank below subfamily)

Introduction

In this thesis I describe my research on fungi in ectomycorrhizal West African savanna woodlands, including the community ecology of these fungi from below-ground and above-ground perspectives, as well as the use of the many edible species by the local population. In the following sections I give a brief introduction to West African savanna woodlands, the fungi that are found there, and ectomycorrhizal symbiosis.

West African savanna woodlands

The West Sudanian savanna ecoregion (Figure 1) forms a belt across West Africa from Senegal and Gambia in the West to Nigeria in the east, bounded to the north by the drier Sahelian *Acacia* savanna, and to the south by the wetter Guinean forest-savanna mosaic (Olson et al. 2001). The southern part of this ecoregion is also known as the Guineo-Sudanian transition zone (Aubreville 1970; White 1983) or the Sudanian center of endemism (Yorou et al. 2014). The dominant vegetation is a mix of grasslands and open woodlands characterized by trees in the genus *Isoberlinia* (Fabaceae: Detaroideae tr. Amherstieae), particularly *Isoberlinia doka* (Adomou 2005; Yorou et al. 2014). Sudanian woodland canopy trees are typically 8–15 m tall, with overall canopy cover between 40 and 80% (Adomou 2005).

The region experiences contrasting wet and dry seasons, with the wet season lasting from May to October, and most trees deciduous during the dry season (Adomou 2005). Fire is also frequent during the dry season, with 25–50% of the region burning each year, and almost all sites experiencing fire every 2–3 years (Savadogo 2007). Along with the prevalence of termites, this reduces the amount of leaf litter and woody debris in Sudanian woodlands relative to most temperate and boreal forests. Bare soil and a litter layer consisting of litter-fall from a single year are common soil cover types (**Paper III**; Figure 1b). Soils are highly weathered, iron-rich, and poor in organic matter, and undifferentiated near the surface due to the action of termites (Nicou et al. 1993).

In addition to savanna woodlands, **Paper II** also investigated gallery forests, a distinct vegetation type found in the riparian zone along rivers

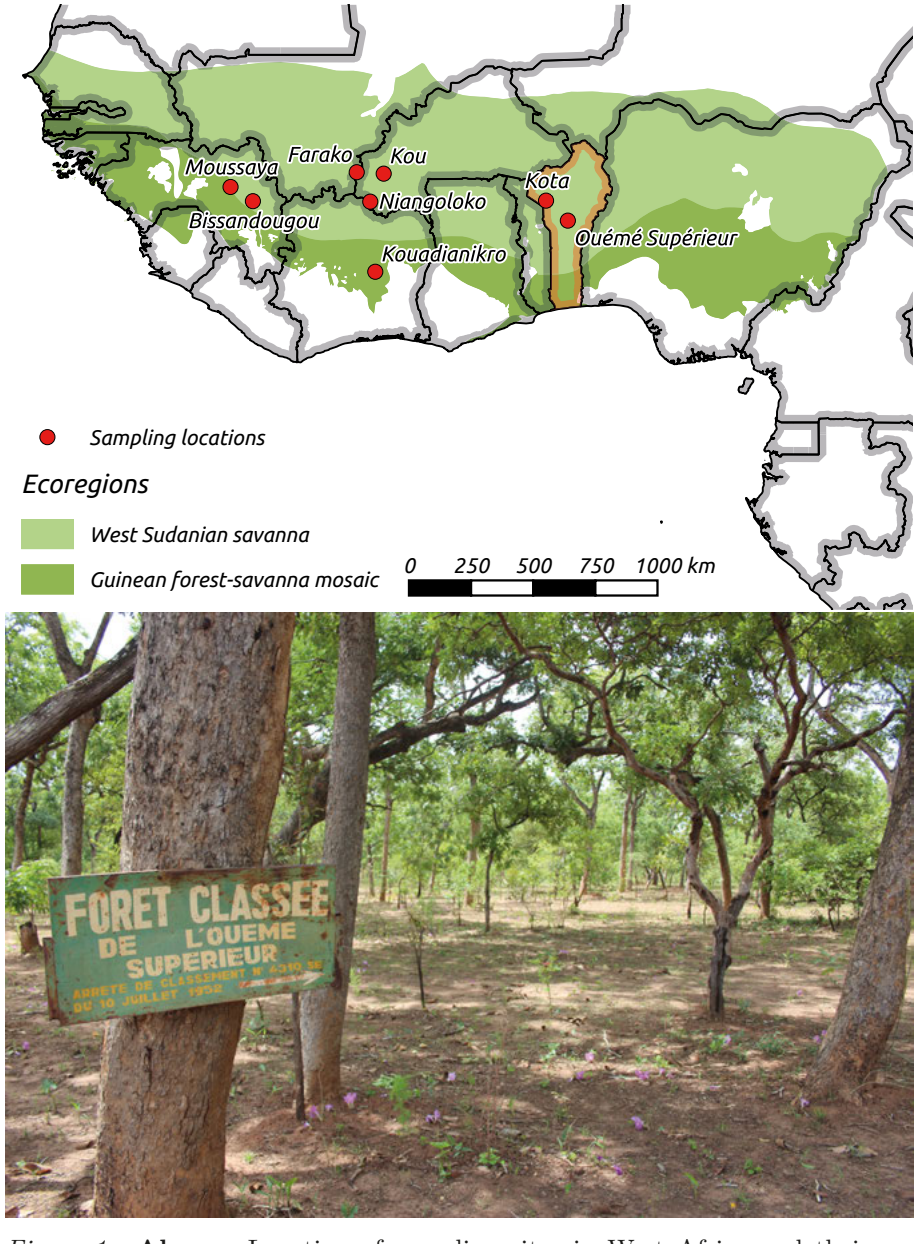

Figure 1. **Above:** Location of sampling sites in West Africa and their respective ecoregions, with Benin outlined in red. **Paper I**, **Paper III**, and **Paper IV** were conducted at *Ouémé Supérieur*; the other sites were sampled for **Paper II**. **Below:** Sudanian *Isoberlinia* woodland at *Ouémé Supérieur* near Angaradebou village.

in the Sudanian region. Increased water availability allows these narrow bands of closed-canopy forest to thrive in regions that are otherwise too dry (Natta et al. 2003). *Berlinia grandiflora* (Fabaceae: Detaroideae tr. Amherstiae) and *Cola laurifolia* (kola nut; Malvaceae), which also grow in wetter Guinean forests, are common tree species in gallery forests (Natta et al. 2003), and *Uapaca guineensis* and *Uapaca somon* (Phyllanthaceae) are also sometimes present (Bâ et al. 2016). Gallery forests represent a biodiversity hot-spot for West African fungi (Yorou and De Kesel 2011).

Both of these ecosystems are under threat both due to the harvest of individual trees for timber, charcoal, and firewood, and also due to conversion to plantations of non-native trees such as teak (*Tectona grandis*, Lamiaceae) and *Eucalyptus* spp. (Euphorbiaceae) or to cropland (Aweto 2001; Savadogo 2007; Ouedraogo et al. 2010; Yorou et al. 2014). *Isoberlinia* and *Berlinia* spp., like most other trees in tribe Amherstieae, disperse by explosive dehiscense of the seed pods (de la Estrella et al. 2018), which throws the large seeds up to 10 m from the mother tree. This relatively short-range (if impressive to witness!) disperal mechanism allows replacement of individually harvested trees in a mostly intact forest, but limits the rate at which these species can recolonize after large-scale depopulation (Glèlè Kakaï and Sinsin 2009). Many of the remaining woodlands are in legally protected areas, but disturbances from activities such as cattle grazing and illegal timber cutting remain frequent (Yorou et al. 2014, personal observation).

In addition to the native biodiversity they contain, West African woodlands also provide valuable ecosystem services, including the production of non-timber forest products. Non-timber forest products include herbs, fruits, edible insects, seeds, nuts, and wild mushrooms. The seeds of the trees *Vitellaria paradoxa* (shea; Sapotaceae) and *Parkia biglobosa* (African locust bean; Fabaceae: Caesalpinioideae), are of local economic importance in West Africa, with shea butter also being internationally traded (Teklehaimanot 2004; Lompo et al. 2017). However, edible mushrooms are the non-timber forest procuct which is considered in this thesis.

Edible mushrooms in West African woodlands

The use of wild mushrooms for food is widely documented across West Africa (Yorou and De Kesel 2001; De Kesel et al. 2002; Ducousso et al. 2003; Okhuoya et al. 2010; Koné et al. 2013; Codjia and Yorou 2014; Osemwegie et al. 2014; Yorou et al. 2014; Boni and Yorou 2015; Fadeyi et al. 2017; Kamou et al. 2017; Soro et al. 2019). Most edible mushrooms in the region are at peak abundance near the beginning of the rainy season (De

Kesel et al. 2002; Guissou et al. 2008), providing a valuable food resource at a time of the year when crops are just being planted and food stores from the previous season may be dwindling (Yorou and De Kesel 2001; Guissou et al. 2008; Degreef et al. 2016). Some species, especially larger *Termitomyces* (Lyophyllaceae) species, are traded at roadsides in some countries (Koné et al. 2013), but wild mushrooms are not widely commercialized in West Africa. The knowledge and use of edible mushrooms as a whole, as well as of particular species, is usually transmitted vertically within communities in West Africa, and consequenctly often varies considerably between ethnic groups (Guissou et al. 2008; Yorou and De Kesel 2001; Boni and Yorou 2015; Codjia and Yorou 2014; Ndolo Ebika et al. 2018, **Paper IV**), but it is generally observed that women, particularly over age 35, are the primary population group which harvests mushrooms, and the primary reservoirs of traditional knowledge about edible mushrooms (Yorou and De Kesel 2001; Codjia and Yorou 2014; Boni and Yorou 2015; Fadeyi et al. 2017, **Paper IV**).

Wild edible mushrooms in West African woodlands belong to four main ecological guilds: termite associated fungi, soil and litter saprotrophs, decomposers of wood and other primary plant material, and ectomycorrhizal fungi.

Many of the most prized edible mushrooms throughout the palaeotropics are termite-associated species of the genus *Termitomyces* (Koné et al. 2013; Koné et al. 2018). These fungi are cultivated by termites in the family Macrotermitinae within their nests, in a co-evolved, mutually obligate relationship (Rouland-Lefèvre and Bignell 2002). *Termitomyces* fruitbodies typically erupt from the sides of termite mounds after the winged termite alates leave the nest to mate (Vreeburg et al. 2020). Although vegetative *Termitomyces* mycelium can be grown in pure culture (Wiriya 2014), production of mushrooms only occurs in association with termites, so these must be harvested from the wild.

Edible West African soil and litter saprotrophs include species from genera such as *Agaricus*, *Chlorophyllum*, *Leucoagaricus*, and *Leucocoprinus* (all Agaricaceae; De Kesel et al. 2002). Many of these species, which grow on partially degraded organic matter, are most common in disturbed areas such as near roadsides, agricultural fields, and pastures. Although members of this group worldwide, which also includes the common European cultivated mushroom, *Agaricus bisporus*, can typically be cultivated using composted subtrates (Stamets and Chilton 1983), they are not among the species commonly cultivated in West Africa (De Kesel et al. 2008), and are instead gathered from the wild.

The third guild includes species which are primary decomposers of wood and other cellulosic materials. In West Africa, edible members

of this group include *Pleurotus* spp. (Pleurotaceae), *Lentinus* spp. (Polyporaceae), and *Psathyrella tuberculata* (Psathyrellaceae) on wood (De Kesel et al. 2002), *Marasmiellus inoderma* (Omphalotaceae) on oil palm (*Elaeis guineensis*, Arecaceae) waste (De Kesel et al. 2008), and *Volvariella volvacea* (Plutaceae) on various substrates (De Kesel et al. 2002). This group includes the most widely cultivated mushrooms in West Africa; *Pleurotus* species, often non-native cultivars, are most common, but *Marasmiellus inoderma* and *Volvariella volvacea* are also cultivated commercially (De Kesel et al. 2008).

The last guild, which represents about half of edible species in West Africa, are ectomycorrhizal (ECM) fungi. Edible members of this guild include many members of Russulaceae, *Amanita* (Amanitaceae), *Cantharellus* (Hydnaceae), and Boletaceae (De Kesel et al. 2002). In those habitats where they are found, which include both *Isoberlinia*-dominated woodlands and *Berlinia*/*Uapaca* gallery forests, they are the most common and abundant fleshy fungi, with yields of edible species up to 300 kg per hectare per year (Yorou et al. 2002, 2014, **Paper III**). This guild is the primary focus of three of the four papers included in this thesis (**Paper I**, **Paper II**, and **Paper III**), and its ecology is discussed in the following sections.

Ectomycorrhizal symbiosis

ECM symbiosis occurs between certain combinations of fungi and plants, forming a characteristic structure called an ectomycorrhiza or ectomycorrhizal root tip, which involves fungal hyphae growing between the cortical cells of fine plant roots to form a *Hartig net*, and often also the formation of a distinctive mantle of fungal hyphae which surrounds the fine root (Smith and Read 2008). ECM symbiosis is generally considered to be mutualistic, with the plant partner providing carbon to the fungal partner in exchange for mineral nutrients. ECM may also aid in water absorption, as well as protecting the plant from pathogens and toxic metals (Duddridge et al. 1980; Marx 1972; Colpaert et al. 2011).

The capacity to form ECM has probably evolved independently at least 30 times in plants (Tedersoo and Brundrett 2017) and more than 80 times in fungi (Tedersoo et al. 2010; Tedersoo and Smith 2017). Altogether, only about 2% of plant species are ECM. However, this 2% includes regionally dominant tree species in boreal forests, many temperate forests in both the northern and southern hemispheres, and some tropical and subtropical areas, including Sudanian woodlands and gallery forests (Brundrett

2017), which together have been estimated to account for 60% of tree stems globally (Steidinger et al. 2019).

ECM fungi represent about 8% of described fungal species (Ainsworth 2008; Rinaldi et al. 2008). This fraction is higher in Agaricomycetes, which include the majority of fungi which form large fleshy fruitbodies, i.e., mushrooms. In particular, many well-regarded edible species are ECM, including for example 42 of 57 edible wild mushroom species in Sweden (Livsmedelsverket 2017) and 25 of 51 edible wild mushroom species in Benin (De Kesel et al. 2002, but this number was increased in **Paper IV**).

ECM symbiosis is obligate for many ECM plant species, although some ECM plants can also form symbiotic relationships with arbuscular mycorrhizal fungi (AM) and/or nitrogen-fixing rhizobia bacteria (Tedersoo and Brundrett 2017). Some ECM fungi can be cultured axenically in a laboratory setting, with varying growth rates, but none is known to complete its full life cycle without a plant partner, either in the laboratory or in nature (Douhan et al. 2011).

ECM in West African woodlands

The majority of studies on ECM fungi have been conducted in northern temperate and boreal forests, especially in Europe and North America, and comparitively little is known about the diversity of ECM fungi, or fungi in general, in West Africa (Gryzenhout et al. 2012; Piepenbring et al. 2020). Although many individual species remain to be described, all known ECM fungi in subsaharan Africa belong to lineages which are also known in northern temerate and boreal forests (Tedersoo et al. 2010), with *Amanita*, *Cantharellus*, *Scleroderma* (Sclerodermataceae), Boletaceae, and Russulaceae predominating among species with large, conspicuous fruitbodies (Verbeken and Buyck 2002). Inocybaceae (Matheny et al. 2009), *Tomentella* [Thelephoraceae;@ba2012], and *Sebacina* (Sebacinaceae; Corrales et al. 2018) are also common in African ECM communities, but are less frequently reported due to their more inconspicuous (and inedible) fruitbodies. Kennedy et al. (2012) hypothesized that all of these groups except Thelephoraceae and *Sebacina* originated in the palaeotropics and subsequently dispersed to temperate regions, and existing evidence seems to confirm this for at least *Amanita* sect. *Caesareae* (Sánchez-Ramírez et al. 2015), *Cantharellus* (Buyck et al. 2014), Inocybaceae (Matheny et al. 2009), and Russulaceae (but not *Russula* itself; Looney et al. 2016). However, some ECM fungal groups that are important in northern temperate ecosystems are apparently absent in subsaharan Africa, including *Laccaria* (Hydnangiaceae; Wilson et al.

2017), Suillaceae (except in introduced *Pinus* plantations; Tedersoo et al. 2010), and *Cenococcum* (Gloniaceae; Tedersoo et al. 2010), or are much more rare than in temperate regions, such as *Cortinarius* (Cortinariaceae; Tedersoo et al. 2010; Corrales et al. 2018).

ECM trees in Sudanian woodlands include members of Fabaceae subf. Detaroideae tribes Amherstieae (e.g., *Isoberlinia*, *Anthonotha*) and Afzelieae (*Afzelia*), which probably represent seperate ECM plant lineages, as well as *Monotes* from the entirely ECM Dipterocarpaceae, and the genus *Uapaca* (Phyllanthaceae), which forms a monogeneric ECM lineage (Tedersoo and Brundrett 2017). The ECM tree species found in gallery forests are distinct from those in Sudanian woodlands, but are derived from some of the same lineages, and include *Berlinia* (Amherstieae) and *Uapaca*.

ECM ecology

The study of fungal community ecology combines techniques and perspectives from plant ecology and microbial ecology. Some fungi form large, genetically uniform and physically connected individuals which may be tens or hundreds of meters (Vincenot and Selosse 2017, and references therein) or even kilometers (Ferguson et al. 2003) in extent, and which persist for decades or centuries. These spatial and temporal scales are comparable to or even greater than those of many forest trees.

On the other hand, the vegetative hyphae which comprise these individuals are microscopic, and inhabit a complex soil environment which may vary on a microscopic scale. This greatly complicates the observation of basic life history information, including the size and lifespan of individuals, as well as ecological community characteristics such as the presence and abundance of different species. Spores and newly germinated mycelial networks are also microscopic, making dispersal and establishment much more difficult to study for fungi than for plants. Studies of soil fungi in general, and ECM fungi in particular, have therefore utilized several different types of samples, including fruitbodies, ECM root tips, and bulk soil.

The relationship between the ECM fungal community, the ECM tree community, and soil chemistry is complicated by bidirectional effects, wherein fungi, plants, and soil all potentially drive changes in each other (Figure 2). Studies have demonstrated effects on the fungal community by various aspects of the tree community, including the percentage of ECM trees, species composition of ECM trees, and total ECM basal area (Villeneuve et al. 1989; Natel and Neumann 1992; Richard et al. 2004; Ishida et al. 2007; Bonet et al. 2010; Tedersoo et al. 2013; Solly et al.

2017). Some ECM fungi are known to be specific to certain host species or lineages, only forming ECM with those partners (e.g., *Suillaceae* with *Pinaceae*; Molina et al. 1992), while others display a preference for certain partners, while still retaining the capacity to form ECM with other species (Tedersoo et al. 2008). Existing research suggests that ECM plants and fungi in tropical ecosystems generally tend to show low partner-specificity (Corrales et al. 2018), which may in part explain the observed trend for lower species richness of ECM fungi in tropical than temperate forests (Tedersoo and Nara 2010). Studies in West African rainforest ecosystems and Central African miombo woodlands find widespread sharing of fungi between various members of the Amherstieae and *Uapaca* (Diédhiou et al. 2010; Tedersoo et al. 2011), but this had not been confirmed in Sudanian ecosystems until **Paper II** and **Paper III**. Milenge Kamalebo et al. (2019) found substantial differences in ECM fungal fruitbody community compositions between forest stands populated by different ECM trees in Amherstieae, Afzelieae, and *Uapaca* in rainforests in the Democratic Republic of Congo. However, these stands also differed in soil structure and chemistry, as well as containing mixtures of different tree species, so it is unclear whether variation in the fungal community was more directly attributable to the tree community or abiotic factors.

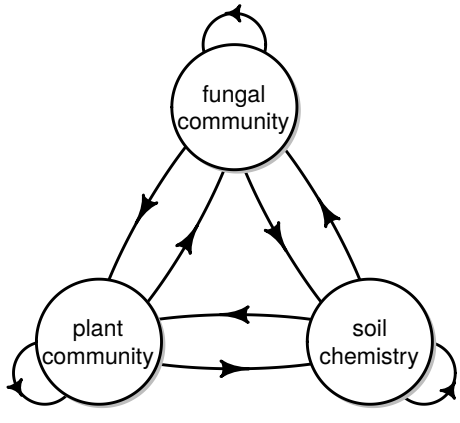

Figure 2. Conceptual diagram showing feedback between plant community, fungal community, and soil chemistry.

The relationship between ECM fungi and soil nitrogen is particularly complex. Nitrogen fertilization has been observed to reduce ECM fruitbody diversity and abundance and lead to shifts in the below-ground community composition (Peter et al. 2001; Avis et al. 2003; Högberg et al. 2010; Gillet et al. 2010). However, due to their high affinity for soil nitrogen, ECM fungi may also reduce soil nitrogen stocks over time, increasing the dependence of their partner trees (Franklin et al. 2014), while also pro-

viding a contributing factor to local dominance or co-dominance of ECM trees (Torti et al. 2001).

Fungi, partner trees, and soil characteristics also display autocorrelation in both space and time, due to the potential large size and long life spans of individuals, dispersal limitation, and underlying geology. These further complicate the analysis of the underlying processes in observational studies. The scale of autocorrelation within local communities determines the distances at which samples are statistically independent, which has implications for study design as well as management. Studies of ECM communities in temperate ecosystems have reported a scale for significant autocorrelation on the order of 2–3 m in western North American (Lilleskov et al. 2004) and Scotland (Pickles et al. 2012). A study in miombo woodlands showed autocorrelation at 10 m (Tedersoo et al. 2011), but because this was the smallest distance class, it is difficult to draw comparisons with the results from temperate systems. In a multicontinent meta-analysis, Bahram et al. (2013) showed that the scale of community autocorrelation is larger in tropical ECM communities than in temperate ECM communities, with a mean on 5.2 m in non-tropical communities, compared to 65 m in tropical communities; however there was considerable variation in tropical communities, with reported ranges varying from 8 to 150 m.

The studies presented here investigate patterns of aboveground (**Paper III**, **Paper IV**) and below-ground (**Paper I**, **Paper II**) community composition, using fruitbody surveys and soil DNA metabarcoding, respectively. The following is a general discussion of the benefits and challenges of these techniques, as well as ECM root tip sampling, which was considered but not conducted.

Fruitbody surveys

Many ECM fungi produce macroscopic fruitbodies, and study of fruitbodies is the oldest and simplest technique for investigating mushrooms. Fruitbodies can be collected without any special equipment, and can often be identified by their macromorphology, although species-level identification sometimes requires observation of microscopic characters, and may be difficult even then. Many fruitbodies, including those formed by ECM fungi, are ephemeral, so a complete sample of the diversity of a site requires multiple visits. However, with sufficiently frequent surveys, it is possible to exhaustively sample fruitbodies, and thus measure the total fruitbody production of a site. Harvesting fruitbodies in itself probably does not reduce fruitbody production later in the season or in future years, although repeatedly walking on the soil during frequent site

visits may damage mycelium and fruitbody primordia (Egli et al. 2006; Ruiz-Almenara et al. 2019).

In the case of economically valuable (in a general sense which includes household use as well as commercial exchange) edible species, the total fruitbody yield is a quantity of interest in itself. For other species, it is an indicator of investment in reproduction, while also representing a lower bound on photosynthetic carbon received from the host tree. As such an indicator, fruitbody biomass has a strong species bias, since large, stipitate fruitbodies are more likely to be collected than small, hypogeous, or resupinate forms, and at least one common ECM species, *Cenococcum geophilum*, has no known sexual stage (Peter et al. 2016). Even exhaustive sampling may undercount or completely fail to detect species which fruit outside of the study period or which do not fruit every year. Different species rely on different cues to trigger fruiting, and may be influenced differently by rainfall and temperatures at different times of the year (Sato et al. 2012; Büntgen et al. 2013; Ágreda et al. 2016).

Fruitbodies also represent a relatively large tissue normally composed of a single individual, which is useful as a starting point for sterile culture, and also for molecular work. DNA extracted from fresh or preserved fruitbodies is amenable to PCR amplification and direct Sanger sequencing for DNA barcoding (Kõljalg et al. 2013, see below) or to produce multigene phylogenies. Full *de novo* genome sequences have also been produced from fruitbodies (Bahram et al. 2018).

Fruitbody surveys using morphology and DNA barcoding for identification are used in **Paper III** and **Paper IV**. As **Paper IV** demonstrates, many of the common species are useful to the human communities near *Ouémé Supérieur*, so this perspective on the ECM community was valuable in itself. Additionally, it was feasible, with the help of dedicated Beninese master's students, to survey fruitbodies nearly exhaustively over several complete rainy seasons (**Paper III**), which would have been impractical for molecular sampling requiring preservation and analytical methods not available in rural Benin.

ECM root tip sampling

Sampling ECM root tips is an attractive method for investigating the ECM community, because root tips are the actual site of symbiosis. Early studies of ECM root tips identified species by painstakingly tracing hyphae from a fruitbody to associated root tips, and identifying root tips by morphological characters (Agerer 1991). Cultures of ECM fungi can sometimes be obtained from root tips, although the success rate can be

very low. Subsequently, amplicon-based identification using restriction fragment length polymorphism (RFLP) or sequencing have been used to identify the fungus, drastically increasing the number of root tips that could be identified in a study, as well as the precision and accuracy of identification (Horton and Bruns 2001). This method also alows identification of the plant host as well, using plant-specific primers, thus directly proving the compatibility of particular plant and fungal species (e.g., Wilson et al. 2007). Root tip sequencing has also been instrumental in the discovery of ECM fungal lineages which do not produce conspicuous fruitbodies (Tedersoo et al. 2010; Tedersoo and Smith 2013, 2017, and references therein).

Root tips are the site of carbon transfer from the plant partner to the fungal partner, so counting root tips of different species is a natural quantification of relative abundance in the ECM community. However, it has been suggested that plants may have the capacity to differentially direct photosynthetic carbon to roots or even root tips which more effectively provide nutrients (Franklin et al. 2014), as has been demonstrated for AM symbiosis (Kiers et al. 2011; Fellbaum et al. 2012). If this is true, the number of root tips may not be an accurate measure of the relative quantity of carbon/nutrient exchange. Indeed, some ECM species have been found to form a large fraction of the fruiting body community, and thus must have access to a relatively large pool of carbon, while being poorly represented in the root tip community (Gardes and Bruns 1996). It is possible that these taxa which fruit abundantly but seem underrepresented in root tip samples are undetected due to their preference for deep soil horizons, which may be neglected during sampling (Rosling et al. 2003).

Because below-ground ECM communities are often very species-rich and there can be substantial spatial variation in the community composition of root tip samples even under a single host, a large number of samples is required to accurately characterize the relative abundance of species at a given site (Horton and Bruns 2001). Additionally, sampling of fine roots is inherently destructive, and exhaustive sampling in a field study is impractical. Counting root tips and sorting them into morphotypes is also a time-intensive process which requires significant expertise.

Despite the relatively direct observation of host-fungus association provided by root tip sampling, it was not conducted in any of the papers presented in this thesis. This is primarily due to the greater time efficiency of bulk soil DNA metabarcoding (see below).

Bulk soil metabarcoding

Ectomycorrhizal communities can also be characterized using chemical analysis of bulk soil. Unlike fruitbody or root tip sampling, this approach leads to individual samples which contain a mixture of many fungal and non-fungal species. Like root tip sampling, soil sampling is destructive, and exhaustive sampling is not possible. However, bulk soil sampling is more time-efficient than root tip sampling, because the time-consuming step of separating and individually processing root tips is bypassed.

DNA metabarcoding uses universal or taxon-specific PCR primers, for fungi usually designed to amplify one of the ribosomal internal transcribed spacer (ITS) regions (Hibbett et al. 2016, Figure 3), to build amplicon libraries which are then sequenced using high-throughput sequencing (Buée et al. 2009; Lindahl et al. 2013; Schmidt et al. 2013), although early studies instead used cloning and Sanger sequencing (O'Brien et al. 2005). A single biological species is typically represented by many different unique sequences in a metabarcoding dataset, due to sequencing errors as well as biological within-species variation. Because the level of within-species variation is different for different species, metabarcoding studies generally avoid designating species, instead clustering reads by sequence similarity into molecular operational taxonomic units (OTUs), which are treated analogously to species in subsequent ecological analyses. Clustering at 97% similarity, a threshold which is also commonly used for taxonomic assignment (see below), is a common strategy for generating OTUs from metabarcoding reads, but in this case it is not possible to distinguish true, biological variation from amplification and sequencing errors. Newer methods such as MED (Eren et al. 2015), DADA2 (Callahan et al. 2016), UNOISE2 (Edgar 2016b), and Deblur (Amir et al. 2017) incorporate relative read abundances and, in the case of DADA2, read quality scores from the sequencing reads in order to "denoise" the reads and determine the set of true amplicon sequences, known as amplicon sequence variants (ASVs). Once generated, ASVs may treated as the units of ecological analysis (so-called "100% OTUs") or further clustered, depending on the requirements of the analysis (Callahan et al. 2017).

The fraction of sequences belonging to each OTU (whether derived from clustering, denoising, or both) is frequently treated as a measurement of the fractional abundance in the soil in community analysis, but there are several sources of bias which may complicate this relationship. At a strictly biological level, the ratio of nuclei to biomass may vary between species and life stages, e.g., between actively growing hyphae and spores, sclerotia, and dormant mycelium which are not actively growing or participating in nutrient cycles. DNA may also persist in necromass (Carini et al. 2017). One of the reasons ITS, as well as the large and

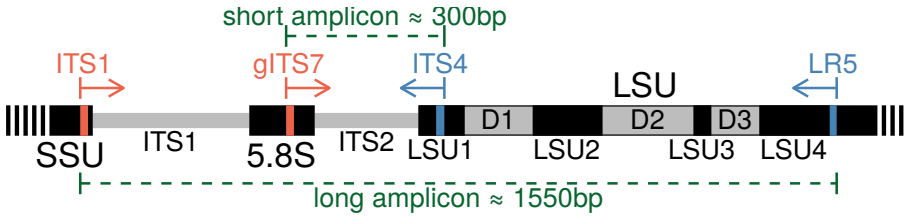

Figure 3. Partial map of rDNA showing the 5.8S rDNA, partial SSU and LSU rDNA, and internally transcribed spacer (ITS) regions. D1–3 represent the first three variable regions in LSU, while LSU1–4 represent the conserved regions. Primer sites used in the included studies are indicated in red (forward primers) and blue (reverse primers), and the resulting amplicons are shown with green braces. Results based on long and short amplicons were compared in **Paper I**; only long amplicons were sequenced in **Paper II**. Figure reproduced from **Paper I**.

small subunits (LSU, SSU) of the ribosomal operon (Figure 3), is used for barcoding is that the ribosomal operon is repeated many times in eukaryotic genomes (Schoch et al. 2012). This means that it makes up a larger fraction of the DNA than any individual protein coding gene. The existence of multiple copies also leads to concerted evolution through gene conversion, which operates to homogenize ITS within sexually reproducing populations, despite its generally high rate of mutation (Brown et al. 1972). However, variation in copy number between species and even individuals introduces another source of error to the relationship between active biomass and sequence abundance. Baldrian et al. (2013) found that variation in ITS sequence abundance per biomass, assessed using quantitative PCR (qPCR) on samples from fruitbodies, was greater than the variation in ergosterol, a component of the fungal cell wall which is used as a non-species-specific marker for fungal biomass (Seitz 1979).

In addition to these biological sources of bias, additional technological biases are introduced during PCR and sequencing. Organisms with large mismatches to the PCR primers utilized may be completely absent from sequencing results, but organisms with small mismatches may be inefficiently amplified due to competition for primers, leading to underrepresentation (Kanagawa 2003; Kalle et al. 2014). When multiple primers are used in combination, to avoid such mismatches, primers which fit most species in the sample may become depleted early in the PCR, leading species which match less common primers to instead be overrepresented (Lindahl et al. 2013). Both PCR and sequencing steps can also be biased in favor of shorter sequences. This can be ameliorated in PCR by using long extension times, and was found to be a minor effect between different sequencing technologies in **Paper I**. For so-called "short-read" HTS sequencing technologies, amplicons longer than about 400 bp are strongly

supressed (Castaño et al. 2020). Although this could lead to substantial bias, asorganisms with insertions in the region of interest being completely absent from sequencing results, this may be of minor importance in practice. No such organisms were detected in a natural system in **Paper I**, despite parallel sequencing with a "long-read" technology.

Newer sequencing technologies from Pacific Biosciences (PacBio) and Oxford Nanopore can produce much longer sequences, with less length bias than earlier high throughput sequencing technologies. These have been applied in metabarcoding to sequence longer regions, including portions of SSU and/or LSU in addition to the full ITS (Tedersoo et al. 2018) or even full repeats of the ribosomal operon (Wurzbacher et al. 2019), allowing the use of primers with more complete phylogenetic coverage, as well as improved placement of novel taxa without close relatives in sequence databases. However, these methods are currently much more expensive per sequenced base than Ion Torrent and especially Illumina, so their benefits must be balanced against reduced sequencing depth and fewer samples per study (Kennedy et al. 2018). Amplification of these long regions which include alternating conserved and variable regions also increases the risk of chimera formation during PCR, although this can be controlled to some extent by using long extension times and low cycle numbers (Kalle et al. 2014).

Soil DNA metabarcoding with PacBio is used in **Paper I** and **Paper II** to measure the diversity and spatial variation in the belowgound fungal community. Additionally, **Paper I** tests different sequencing strategies for barcoding, including alternative HTS technologies and different choices of amplicon length (Figure 3), and finds that they produce equivalent ecological results. **Paper I** also presents new algorithms in the packages `LSUx` and `tzara` which address the denoising of long amplicons, as described in the supplementary methods of that paper.

Taxonomic identification

Another thread which runs through my work in this thesis is taxonomic identification. Accurate taxonomic identification is clearly of primary importance in studies focusing on diversity, but it also gives important clues to address ecological function. Many functional traits are shared between closely related species, and databases such as FUNGuild (Nguyen et al. 2016) and Fun^{Fun} (Zanne et al. 2020) compile known functional trait data for taxonomic groups, generally from the species to the family level. Of particular relevance to my research, the more than 80 fungal lineages which have developed the capacity to form ECM typically correspond

to taxonomic groups at the (sub)genus or family level (Tedersoo et al. 2010; Tedersoo and Smith 2013, 2017). Taxonomic assignment to at least the family level, and ideally to genus, is thus an important step for determining the ECM status of fungi which are not directly sampled from ECM root tips. Identification to approximately the species level, either using vernacular common names or scientific binomials, is also important from the perspective of harvesting mushrooms for consumption or sale. Identification poses additional challenges in understudied regions such as West Africa, due to the large fraction of undescribed species and the consequent lack of comprehensive reference texts (Piepenbring et al. 2020) as well as under-representation in DNA sequence databases (Khomich et al. 2018).

For fruitbodies, taxonomic identification has traditionally been based on macroscopic and microscopic morphology, as well as characteristics such as taste, smell, and chemical reactions. Morphological description, along with the preservation of voucher specimens or cultures, is still the standard for describing new fungal species (Turland et al. 2018). However, confidently identifying specimens to species, or alternatively determining that they do not conform to any existing species description, often requires access to a microscope and either taxon-specific expertise or a great deal of time and access to reference materials. This combination of expertise and equipment is often not available in field studies such as those presented in this thesis, which are not devoted to the taxonomy of a narrowly defined group.

DNA barcoding represents an alternative method for taxonomic identification, but one which is not without its own complications (Hibbett et al. 2016; Hofstetter et al. 2019). Ideally, it would be possible to identify any species by sequencing one DNA locus using universal primers for PCR amplification, and consult a comprehensive and reliable database, wherein there is a clear delineation between sequence similarities which indicate conspecifity and those which do not. Sadly, no part of this ideal is yet reality. Although the ITS region, which is the official barcode for fungi (Schoch et al. 2012) has broad primer support, certain fungal groups, including several lineages of ECM fungi in Cantharellales, posess partial or complete mismatches at the most common primer binding sites (Tedersoo et al. 2015). ITS also posesses no clear "barcoding gap" between within-species and between-species variation; although a threshold of 3% sequence dissimilarity is often used for both taxonomic identification and OTU clustering, intra-species variation as high as 15–25% has been reported for species from several fungal phyla (Nilsson et al. 2008), while (Vu et al. 2019) reported that 10% of species could not be distinguished at all based on ITS, even in a highly curated set of ex-type cultures. Finally, the commonly used INSDC databases (Karsch-Mizrachi et al. 2018) unfor-

tunately contain many sequences which are taxonomically misannotated (Nilsson et al. 2006; Steinegger and Salzberg 2020) or of poor technical quality (Nilsson et al. 2012). Even specialized databases, such as the Unite database (Nilsson et al. 2019) contain many sequences which are not annotated to species level, (44 000 of 84 000 fungal species hypotheses in the most recent version; Abarenkov et al. 2020). Aside from the fact that these sequences are not useful for species-level identification, automatically updating their annotations to conform to changes in taxonomy is much more difficult than for species-level annotations. Furthermore, the majority of described fungal species do not currently have any publicly available ITS sequence. Hawksworth and Lücking (2017) estimated 120 000 valid named species of Fungi, and a few thousand more have been described since that estimate, but the latest release of the Unite database contains only 23 500 unique species names (Abarenkov et al. 2020). Additionally, many species of fungi, encluding entire clades at the class or phylum level which are known only from environmental sequences (Tedersoo et al. 2017), remain undescribed, with estimates of the total number of fungal species ranging into the millions (Blackwell 2011; Hawksworth and Lücking 2017).

Obtaining positive species-level identification through DNA barcoding is a time-consuming task which involves examination of results on a case-by case basis (Hofstetter et al. 2019), so it is not practical for HTS metabarcoding studies, where at least preliminary taxonomic identification must be performed automatically. The most straightforward method is assigning each OTU to the identity of its best BLAST hit (Altschul et al. 1990), possibly truncating the assignment at a taxonomic rank determined by sequence identity thresholds (as given in, e.g., Vu et al. 2019). Alternatively, a variety of taxonomic assignment algorithms have been published which automatically determine the lowest rank at which the sequence can be confidently identified using the distribution of dissimilarities within each taxon in the database. These algorithms are generally based on BLAST alignment scores or kmer distances, and include the RDP naïve Bayesian classifier (RDPC; Wang et al. 2007), mothur's k-nearest-neighbor method (Schloss et al. 2009), USEARCH's original UTAX (Edgar 2010) and updated SINTAX (Edgar 2016a), LCAClassifier (Lanzén et al. 2012), and IDTAXA (Murali et al. 2018). Several of these, including RDPC, UTAX, SINTAX, and IDTAXA, provide a measure of confidence for each rank that is assigned to a query sequence, with user-configurable cutoffs, although the calibration of these confidence scores varies (Murali et al. 2018). While all of these primary algorithms perform a database search and assign taxonomy themselves, there also exist consensus algorithms which combine the outputs of other searches, including CONSTAX (Gdanetz et al. 2017), the taxonomy module of the

AMPtk pipeline (Palmer et al. 2018), and PROTAX (Abarenkov et al. 2018). These approaches can increase both the success rate and accuracy of predictions.

DNA barcoding to species level, when possible, was used as a complement to morphological identification in **Paper IV**. The large number of specimens collected in **Paper III** made this detailed approach impractical, so identification in that study was restricted to the family level. Taxonomic identification of metabarcoding sequences in **Paper II** was made by SINTAX using the UNITE database, followed by manual refinement using a phylogenetic tree generated from the sequences. This process was expanded and automated in **Paper I** with the development of the PHYLOTAX algorithm, which is a phylogenetic consensus algorithm that combines information from one or more primary assignment algorithms, potentially run using different databases and for different rDNA regions, with a phylogenetic tree.

Study questions

The central questions of microbial community ecology have been stated as "Who is out there?" (community composition) and "What are they doing?" (community function) (Urich et al. 2008). In the case of ECM fungi, especially those producing large fruitbodies, these may be followed (or more often, preceded) by the additional questions, "Where are they?" and "Can I eat this?". This last question is important both in the interest and appreciation it can bring to the public, and also in terms of the incentives it can provide for conservation and responsible forest management.

The studies in this thesis mostly address the questions, "Who is out there?" and "Where are they?". Where functional information is obtained, such as division into functional guilds, it is done *via* databases which link functional information to taxonomy. However, the last question, "Can I eat this?" is also addressed. All of the studies described in this work focus on specific aspects of these questions as they apply to West African ECM woodlands:

(a) What is the spatial scale of soil fungal community turnover? (**Paper I**)
(b) What is the regional diversity of soil fungi, and how is this related to different vegetation types and ECM tree partners? (**Paper II**)
(c) What biotic and abiotic factors control the productivity and distribution of ECM fruitbodies at a local scale? (**Paper III**)
(d) What species of mushrooms do local people know and value, and how does this vary between genders, ages, villages and ethnic groups? (**Paper IV**)

Paper I, **Paper III**, and **Paper IV** were conducted in and around the *Forêt Classée de l'Ouémé Supérieur* (Upper Ouémé Forest Reserve; hereafter *Ouémé Supérieur*) in Bourgou province, Benin (Figure 1). **Paper II** investigates West African ECM communities more broadly, with samples taken from seven different sites in Benin, Burkina Faso, Mali, Guinea, and Côte d'Ivoire.

In addition to these ecological questions, **Paper I** compares a variety of methods for DNA metabarcoding and taxonomic identification, and presents new software for the analysis of long amplicon metabarcoding data, and for incorporating information from a phylogenetic tree into taxonomic identification of DNA sequences.

Study summaries

Summary of Study I

Long- and short-read metabarcoding technologies reveal similar spatio-temporal structures in fungal communities

Furneaux, B., Bahram, M., Rosling, A., Yorou, N.S., Ryberg, M.

This study investigates the scale of spatial and temporal turnover in the soil fungal community in two transects through *Isoberlinia doka*-dominated woodland in *Ouémé Supérieur*. It also tests alternative soil metabarcoding schemes, to assess whether the use of different sequencing technologies or amplicon lengths affect conclusions in a real ecological study, as well as alternative methods for assigning taxonomy to metabarcoding results. In the process of performing the analysis, I developed several new algorithms for analysis of long-amplicon metabarcoding data, which became the R packages `LSUx`, `tzara`, and `phylotax`, described fully in the supplementary methods for the paper.

Each of the two 24 m linear transects consisted of 25 soil cores taken at a spacing of 1 m. Soil cores were collected in the same locations in two consecutive years. After DNA extraction, two different PCR amplicons were generated (Figure 3): a short amplicon of around 300 bp including the ITS2 region, generated using the primers gITS7 (Ihrmark et al. 2012) and ITS4 (White et al. 1990); and a long amplicon of around 1550 bp, including the ITS1, 5.8S, ITS2, and part of the LSU regions, generated using the primers ITS1 (Hopple and Vilgalys 1994) and LR5 (Hopple and Vilgalys 1994). The resulting short amplicon library was aliquoted and sequenced using Ion Torrent Ion S5, Illumina MiSeq and PacBio RSII sequencing platforms. The long amplicon library was sequenced only using the RSII.

The use of long amplicon sequences including the conserved 5.8S and LSU regions allowed a pan-Eukaryote phylogenetic tree to be built directly from metabarcoding reads, although the fungal portion of the tree was the focus of the paper. In order to incorporate information from the tree to improve taxonomic identification of sequences, I developed the PHYLOTAX algorithm, which improved the fraction of reads in the

long amplicon dataset identified at genus level to 73%, versus 46% for alternative methods.

Estimates of ASV richness in each sample (after rarefaction) were highly correlated between all three technologies in the short-amplicon dataset, although Ion Torrent over-estimated richness by approximately 20% relative to Illumina and PacBio. Total read abundances per ASV in the short-amplicon dataset were also correlated, but this correlation increased when ASVs were clustered at 97% similarity. Both the differing richness estimates in the Ion Torrent dataset and the improved correlation in abundances after clustering are probably indicative of variable performance of `DADA2` denoising between the different sequencing technologies. Richness estimates and ASV/OTU abundances were somewhat less strongly correlated between the long- and short-amplicon datasets. In the case of richness estimates, this is probably due to different primer mismatches for the two amplicons selecting somewhat different species from the soil community; in particular the long amplicon dataset consisted about 20% of non-fungal groups, predominantly Alveolata, which are not amplified by the primers used for the short amplicon.

Spatial analyses based on Bray-Curtis dissimilarities detected significant autocorrelation at ranges up to 2–3 m, and 95% confidence intervals for the range of the distance-dissimilarity relationship which overlapped in the range of 15–25 m, for all sequencing strategies. The autocorrelation distance is consistent with that found for both temperate (Lilleskov et al. 2004; Pickles et al. 2012) and tropical (Tedersoo et al. 2011) ECM ecosytems. The distance-dissimilarity relationship is somewhat smaller than the 65 m reported in previous data from Benin (Bahram et al. 2013), which was based on ECM root tip barcoding rather than bulk soil metabarcoding. Weak interannual autocorrelation was also detected, with a highly uncertain temporal distance-dissimilarity range of 2–20 years. Given that the study only covered a span of one full year, a more accurate estimate of this value would require additional sampling.

The overall conclusion of the study is that ecological results from metabarcoding are repeatable across HTS sequencing technologies. Although different amplicons do bias the recovery of certain taxa, this did not effect our ecological conclusions. The use of long amplicons for metabarcoding, facilitated by new software packages developed for this paper, can improve taxonomic identification of sequences, especially those which lack close matches in reference databases, through integration of phylogenetic information.

Summary of Study II

Soil fungal communities of ectomycorrhizal dominated woodlands across West Africa

Meidl, P.*, **Furneaux, B.***, Tchan, K.**, Kluting, K.**, Ryberg, M., Guissou, M.-L., Bakary, S., Traoré, A., Konoumou, G., Yorou, N. S., Rosling, A.

*shared first authorship

**shared second authorship

This study examined the diversity of soil fungi in West African ECM woodlands at a regional scale, with nine plots sampled at seven different sites (Figure 1). Although fruitbodies were opportunistically collected on the same expedition, the geographic scope precluded the intensive fruitbody sampling used in **Paper III**, so only soil metabarcoding is used to characterize the soil community.

The nine plots at seven sites were initially categorized into two vegetation types: two gallery forests and the remaining seven woodlands. At each woodland plot, we established a temporary plot of approximately 0.25 ha. Within each plot we identified and surveyed the girth of all ECM trees, as well counting and measuring girth of non-ECM trees. We then collected soil samples at 10 of the ECM trees, selected in approximate proportion to their relative abundance in the plot. DNA extracted from the samples was amplified using ITS1 and LR5, the same primer pair used for the long amplicon in **Paper I** (Figure 3) and amplified using the PacBio Sequel system.

The `LSUx/tzara` pipeline from **Paper I** was not yet fully developed at the time these sequences were being analyzed, and the greater read depth and improved read quality of Sequel over RSII led to an acceptible 65% of reads being successfully denoised. The 1014 fungal ASVs were grouped into 520 species hypotheses using a Bayesian implementation of the model-based poisson tree process method, an alternative to *a priori* selection of a clustering threshold, which is based on the theory that phylogenetic branching patterns within species are generated via a different process than branching patterns between species (Zhang et al. 2013). Species accumulation curves based on sequencing depth, number of samples per site, and number of sites showed that additional samples per site, and especially additional sites, would be required to more completely recover the diversity of soil fungi in West African ECM communities.

Non-metric multidimensional scaling (NMDS) ordination and permutation-based analysis of variance (PERMANOVA; Anderson 2001) based on Bray-Curtis dissimilarities in fungal community composition revealed a

clear division between woodland and gallery forest sites. However, after accounting for plot-level correlation, there was no statistically significant effect of the particular tree species that samples were collected from, supporting earlier reports that African ECM fungi tend to be host generalists (Diédhiou et al. 2010; Tedersoo et al. 2011).

Analysis of the tree communities at different sites using NMDS revealed that the plot at Kouadianikro (Figure 1), although originally categorized as a woodland site due to its location on a sloping hillside several hundred meters from the nearest waterway, had a tree community which was much more similar to the gallery forest sites. This is probably due to its location in the wetter Guinean forest-savanna mosaic ecoregion, where *Berlinia grandiflora*, the dominant tree species at the site, is not restricted to riparian areas. NMDS ordination of the soil fungal communities also grouped the Kouadianikro samples with the gallery forest sites rather than the woodland sites, suggesting that the differences between the fungal communities in the two ecosystem types are not directly related to the proximity to a river *per se*. Instead, these may reflect weak host preferences operating at a larger spatial scale than individual tree, or abiotic factors such as water availability or soil chemistry.

Summary of Study III

Spatial drivers of ECM community composition and fruitbody production in West African woodlands

Furneaux, B., Houdanon, R., Aïgnon, H., Boni, S., Codjia, J. E., Laourou, G., Bahram, M., Svanholm, A., Rosling, A., Yorou, N.S., Ryberg, M.

This study investigates the ECM communities of *Ouémé Supérieur* from the perspective of fruitbody community composition and production over three years of intensive sampling, and relates this to a wide range of environmental variables.

Fruitbodies were exhaustively collected biweekly over three successive mushroom seasons (June-October) from nine 50 × 50 m plots divided in to 10 × 10 m subplots. Specimens were grouped into morphospecies and weighed by subplot and morphospecies, with one voucher per morphospecies preserved on each sampling day. Additionally a wide range of environmental data were collected from the nine plots, including microclimate (ground cover, canopy cover, soil moisture, soil temperature), soil chemistry (nitrogen, phosphorus, organic carbon, calcium, pH, granulometry) and host availability (presence and sizes of different ECM tree species).

Because of inconsistent species-level indentification of specimens, I analyzed fungal community composition at the family level, roughly corresponding to ECM lineages *sensu* Tedersoo et al. (2010). The highest producing groups were Sclerodermataceae, Russulaceae, and Amanitaceae, all with more than 2 kg dry mass per hectare per year, and Boletaceae, with 0.4 kg dry mass per hectare per year. Although all of these groups were also detected in soil from *Ouémé Supérieur* **Paper I** and other woodland sites **Paper II**, only Russulaceae was similarly dominant in read abundance. Amanitaceae and Sclerodermataceae together represented less than 15% of reads from woodland sites in **Paper II**, and Boletaceae less than 1%.

Microclimate was the strongest correlate of variation in community composition out of the measured environmental parameters, explaining 11% of spatial variation. Soil temperature, soil moisture, and leaf cover were the most important components of microclimate in explaining community composition. Canopy cover and soil moisture, as well as some leaf cover, were positively correlated with fungal diversity and richness. However, canopy cover was not associated with greater total fruitbody production, and was negatively correlated with production of edible species. Both total production and production of edible species were positively corre-

lated with bare soil, possibly reflecting a preference for fruiting away from ground cover which might interrupt the dispersal of spores.

Richness, diversity and productivity of fruitbodies were positively correlated with richness of ECM tree families, but only a small fraction (1.6%) of variation in fruitbody community composition was explained by the availability of a particular ECM tree species within 5 m of a particular subplot. These apparently contradictory results, along with the lack of a significant host tree effect within plots in **Paper II**, suggest that the tree partner community effects ECM fungi in these systems at a larger spatial scale than the interactions of a single mycelium with a single tree.

Soil nitrogen levels were negatively correlated with richness, diversity, and productivity of ECM fruitbodies, in accordance with fertilization experiments in temperate and boreal forests (Peter et al. 2001; Avis et al. 2003; Gillet et al. 2010; Högberg et al. 2010), but did not significantly effect community composition.

Summary of Study IV

Comparison of wild mushroom use by ethnic groups surrounding the Upper Ouémé Forest Reserve in Benin, West Africa

Furneaux, B.*, Veldman, S.*, Riggi, L., Boni, S., Svanholm, A., Ryberg, M., Yorou, N. S.

*shared first authorship

This study combined collection and identification of fungal specimens with interviews of the inhabitants of villages adjacent to *Ouémé Supérieur* about the mushrooms they know, the names they use for them, and which ones they consider to be desirable edibles. We used statistical methods from community ecology to investigate how people's knowledge of and preferences for different species of mushrooms varied by age, gender, ethnic group, and village.

The primary data for this study came from six focus groups and 70 individual interviews conducted with the inhabitants of five villages adjacent to *Ouémé Supérieur*. The interviewees ranged in age from 17 to over 70, and included men and women mostly belonging to four local ethnic groups: the Bariba, Gando, Lokpa, and Yom [1], each of which spoke their own language. At both focus groups and interviews, participants were shown photos of local mushroom species, as well as fresh specimens when available, and asked to say whether they recognized it. If they did, they were further asked the name of the mushroom in their language, whether they considered it edible, and if so to rate how well they liked it on a scale of 0–4.

In accordance with previous ethnomycological studies in West Africa (e.g., Yorou and De Kesel 2001; Fadeyi et al. 2017), we found that people over 35 and women recognized more different species than younger people and men. However, we found that the effect of gender varied between ethnic groups, with men and women nearly equal in their mycological know-how among the Yom. There was also significant variation in the total number of species recognized by members of the different ethnic groups, but contrary to our expectations this did not seem to be related to the length of time each group had been present in the area.

In addition to differences in the number of species recognized, we also found variation between ethnic groups in which species were known and

[1] Interviews were also conducted with a few people belonging to the Nagot and Peulh ethnic groups, but there were not enough of these interviews to include them in most of the analysis.

preferred. Among the Gando in particular, we also found differences in the set of mushrooms known by men and women.

We recorded a total of 70 edible species, an increase over the 51 species previously known from Benin (De Kesel et al. 2002). The most highly preferred mushrooms across ethnic groups were *Psathyrella tuberculata*, two species of *Termitomyces*, *Chlorophyllum palaeotropicum*, *Macrocybe lobayensis*, and *Lactifluus edulis*.

Concluding remarks and future perspectives

The papers presented in this thesis explore the diverity of fungi in West African woodlands at scales ranging from meters to thousands of kilometers. They examined these systems biologically from both belowground and aboveground perspectives, as well as from the viewpoint of the human inhabitants of the region. Additionally the data collected from these systems were used to advance methodology for DNA metabarcoding using long amplicons covering multiple regions of the rDNA.

Paper II and **Paper III** confirmed results from other subsaharan African ECM systems, which find little consistent variation in ECM fungal community composition associated with different co-ocurring partner tree species, while still finding significant changes between different vegetation types in **Paper II**. **Paper II** also found that diversity of tree partners was positively correlated with diversity of ECM fungi, implying at least weak partner preference.

Paper I found evidence for spatial correlations at scales at least close to the size of the 50 × 50 m plots used in **Paper II** and **Paper III**, and certainly larger than the 10 × 10 m subplots in **Paper III**. Similarly, both **Paper II** and **Paper III** found that plot-level effects were much stronger than any tested within-plot effects. This suggests that, although these plots are suitable for analysis as individual sampling units, as in **Paper II**, future studies of local-scale spatial processes in these ecosystems should ideally cover larger spatial distances, for instance by rearranging the 10 × 10 m subplots into a 250 × 10 m transect. Such designs would also be likely to uncover greater species richness for a similar amount of sampling effort.

There are multiple avenues available to expand upon this work, in regards to the study of the particular systems I investigated, to the study of West African fungi more broadly, and to the methodology of molecular fungal ecology in general.

Additional data from *Ouémé Supérieur*

Soil samples for metabarcoding for the nine plots at *Ouémé Supérieur* described in **Paper III** were collected from the same locations as the

soil chemistry samples. Sampling and sequencing of both long and short amplicons (as in **Paper I**) with PacBio Sequel and Illumina MiSeq, respectively, are already complete, but analysis was not ready in time for inclusion in this thesis. Analysis of this data, either parallel to or in combination with the fruitbody data, would provide a more comprehensive picture of the ECM community in *Ouémé Supérieur*.

Three years of data are analyzed in **Paper III**, but fruitbody surveys continued at the plots in *Ouémé Supérieur* for an additional two years. Additionally, the analysis in **Paper III** does not consider temporal dynamics, instead pooling observations across time to focus on spatial processes. Incorporation of these data to examine seasonal and interannual dynamics of fruitbody production would increase our understanding of the impacts of climate events, and ultimately climate change, on the potential for future mushroom harvests, as well as on West African ECM woodland ecosystems more generally.

Phylogenetics in metabarcoding

Both **Paper I** and **Paper II** utilized the long-read capabilities of PacBio to generate phylogenetic trees from metabarcoding data, and used these for phylogenetically informed taxonomic assignments (**Paper I** and **Paper II**), species hypotheses (**Paper II**), and ecological distance measures (**Paper I**). The use of guild- or trait-annotated reference sequences in a metabarcoding-based phylogeny could also allow assignment of function to sequences using a modification of PHYLOTAX without passing through a taxonomic annotation step. This would be especially useful in cases where the presence of a phylogenetically clustered trait such as ECM-formation does not correspond exactly to a group occupying one of the main Linnean ranks, resulting in errors using the taxonomic approach of annotation used by FUNGuild and Fun^{Fun} (Nguyen et al. 2016; Zanne et al. 2020). For example, the genus *Amanita*, which is ancestrally saprotrophic but contains a large ECM clade (Wolfe et al. 2012), is annotated as ECM with the highest confidence ranking in FUNGuild. There are also several ECM lineages which are known only from sequencing of ECM root tips and have no taxonomically described members, and so cannot be recognized taxonomically (Tedersoo et al. 2010; Tedersoo and Smith 2017). Although annotations in Unite make it possible to identify these lineages through sequence similarity (Tedersoo and Smith 2017), a phylogenetic approach would be more rigorous.

High throughput DNA barcoding of specimens (in Africa!)

Initial specimen barcoding using Sanger sequencing revealed that the species names assigned in the field to the 4000+ collections in **Paper III** were not consistent between individual collectors and sampling events. This is not surprising given the high degree of expertise required to accurately identify mushrooms to species, especially in a region where, despite ongoing efforts, there is still much work to be done cataloguing the existing diversity (Yorou et al. 2014; Piepenbring et al. 2020) and truly comprehensive reference works are lacking. However, this proved problematic for ecological analysis of the dataset. In the current manuscript, observations are clustered at the family level, which is relatively reliable but leaves much to be desired in terms of resolution.

DNA barcoding of all the remaining voucher specimens would allow them to be identified to species where applicable reference sequences exist, or at least divided into consistent, species-level OTUs. This would also facilitate identification of potential new species. Several groups have applied HTS to barcoding large specimen collections (Shokralla et al. 2014; Wurzbacher et al. 2019; Loit et al. 2019). This promises to be especially cost-effective using the "Flongle" adapter for Oxford Nanopore devices (e.g., Eaton et al. 2020), which reduces the price point for a single sequencing run to only €80 plus library prep.

The small size of the Oxford Nanopore devices and availability of refrigeration-free library prep kits also make them potentially suitable for use during field expeditions. We successfully tested protocols using the miniPCR system (miniPCR bio, Cambridge, Massachusetts) for DNA extraction and PCR from fresh fruitbodies on the National Geographic expedition where soil samples for **Paper II** were collected. However, on that expedition we sent our PCR products to an commercial lab in Europe for Sanger sequencing. Developing affordable and reliable protocols for barcoding with the miniPCR plus Flongle, and training our colleagues in Africa to use them, would improve the development of local sequencing capacity and research independence, as well as ensuring high quality data for future collaborations.

Svensk sammanfattning

Ektomykorrhiza är en symbios mellan växter, oftast träd, och svampar, där svampens hyfer, d.v.s. celltrådar, bildar ett nätverk mellan växtens rotceller och även täcker ytan på rotspetsarna. Både växten och svampen gynnas av att utbyta näringsämnen genom detta nätverk. De flesta skogsträd i Sverige, till exempel tall, gran, ek, björk, bok, asp, al, lind, och hassel, bildar ektomykorrhiza, och många välkända svampar, som till exempel kantareller, soppar, flugsvampar, riskor, och kremlor, är ektomykorrhizasvampar. Eftersom de bara växer i samexistens med sina trädpartner, kan ektomykorrhizasvampar inte odlas, utan bara plockas i naturen.

Det finns även ektomykorrhizasvampar i tropiska länder. Västsudansk savann är en ekologiskt region som ligger mellan Saharaöknen och Västafrikas regnskogar. Det finns två olika skogstyper i västsudansk savann där det växer ektomykorrhizaträd och ektomykorrhizasvampar, savannskog och galleriskog. Savannskog är en öppen skog där krontaket inte är heltäckande. Galleriskogar växer vid floder där det finns gott om vatten, och den är tätare än savannskogar. I båda dessa skogstyper finns det ektomykorrhizasvamparter som tillhör taxonomiska grupper som även finns i Norden. De vanligaste grupper är kantareller, soppar, flugsvampar, riskor, kremlor, trådingar, och rottryfflar. Många av dessa är ätbara, och människorna som bor i den västsudanska savann regionen plockar och äter dessa svampar.

I denna avhandling har jag studerat svamparnas mångfald i den västsudanska savann regionen, med fokus på ektomykorrhizasvampar. Den makroskopiska delen av svampen som växer ovanför marken och kan plockas kallas “fruktkropp”. Fruktkroppar är temporära men resten av svampen, som heter mycelet och består av mikroskopiskt hyfer, kan överleva i marken i många år. Hyfer i marken kan hittas och identifieras genom DNA sekvensering av jordprover. I de olika studierna i denna avhandling har jag har samlat både fruktkroppar och jordprover.

I artikel I jämförde vi olika metoder för DNA sekvensering av jordprover. Vi använde tre olika sekvenseringsteknnologier, Illumina, Ion Torrent, och Pacific Biosciences (eller kort och gott PacBio). Alla tre teknologier kan sekvensera korta DNA fragment på ungefär 350 baspar. Vi sekvenserade ITS2 regionen, som är en av de officiella DNA “streckkoderna” för svampar. Det vill säga en föredragen region för att identifiera svamparter.

ITS2 regionen är mycket variabel mellan olika arter, vilket gör att den är en bra streckkod. Men den är för variabel för att kunna härleda fylogenetisk släktskap mellan arter som inte är nära besläktade. För detta behövs längre DNA fragment och det kan man få med den sistnämnda teknologin, PacBio. Med PacBio sekvenserade vi även en längre DNA region på ungefär 1550 baspar, som innehöll ITS2 samt dess grannregioner, ITS1, 5,8S, och en del av LSU regionen. LSU och 5,8S är mindre variabla än både ITS1 och ITS2. Det är därför möjligt att använda dessa regioner för att skapa ett fylogenetiskt träd över all svampar i provet. Att kunna få fram ett fylogenetiskt träd är till hjälp när man ska identifiera svampar baserat på sekvenser för vilka det saknas referensmaterial, vilket är fallet för många av svamparna i våra prover. Jordproverna som vi sekvenserade kom från savannskog i det västafrikanska landet Benin, och vi använde sekvenseringsresultat från de olika metoder för att beräkna artmångfald och svampsamhällets rumsliga variation. Oberoende av sekvenseringsmetod fick vi likartade resultat. Det betyder att studier som använder olika sekvenseringsmetoder är jämförbara, vilket är bra för svampekologi som forskningsfält

I artikel II samlade vi jordprover från savannskogar och galleriskogar i fem västafrikanska länder för att studera svamparnas mångfald och skillnader i svampsamhällen som finns i de två skogstyperna. Vi använde PacBio för att sekvensera samma långa region som i artikel I, och byggde ett fylogenetiskt träd för att underlätta sekvensidentifieringen. Vi hittade skillnader i vilka svamparter som lever i savannskogar och galleriskogar, men kunde inte visa på någon skillnad i vilka svamparter som lever med olika trädarter i samma skogstyp. Detta överensstämmer med resultatet från tidigare forskning i andra afrikanska ektomykorrhizaskogstyper. Vidare uppskattar vi att fler arter skulle ha hittats om vi hade tagit fler prover på varje plats vi studerade, och särskilt om fler platser hade undersökts.

I artikel III studerade vi faktorer som kan påverka produktionen av ektomykorrhizasvamp fruktkroppar i savannskog i Benin. Vi samlade alla fruktkroppar två gånger per vecka från nio platser under tre svampsäsonger, och alla fruktkroppar från varje art vägdes. Vi mätte även flera miljöfaktorer som har visats vara viktiga för svampproduktion i andra ekosystem, inklusive fuktighet och temperatur i jord och luft, halten av organiskt kol, kväve, fosfor, och kalk i marken samt partikelstorlek och pH i jorden. Vidare mätte vi ektomykorrhizaträdarters förekomst och storlek samt marktäckets sammansättning och platsens krontäcke. Mångfalden av svampar var positivt korrelerade med mångfald av ektomykorrhizaträd, krontäcke, jordfuktighet, jordens fosforhalt och var högst med medeltjockt marktäcke av löv. Vidare var svamparnas mångfald negativt korrelerad med markens kvävehalt samt lägst när marktäcket bestod av

gräs eller ved. I detta ekosystem var den totala produktionen av svamp i mångt och mycket korrelerad med samma faktorer, men den var negativt korrelerad med krontäcke, och högst produktionen fann vi vid bar jord, alltså inget marktäcke. Genomgående var kvävehalten och ektomykorrhizaträdens mångfald de viktigaste faktorerna som påverkade svamparnas mångfald och den produceerade massan. Det är alltså viktigt att bevara olika ektomykorrhizaträd och förhindra kvävenedfall för att värna om mångfalden av svamparna i savannskogar.

I artikel IV fokuserade vi på lokalbefolkningens användning av och kunskap om svampar från en savannskog i Benin. Vi intervjuade människor framförallt från fyra etniska grupper, Bariba, Gando, Lokpa och Yom, som bor i fem byar intill skogen. Vi samlade svampar från skogen och visade bilder från tidigare insamlingar Intervjupersonerna berättade vilka svampar de kände till, vad dessa svampar hette på deras språk, och hur mycket de tyckte om att äta de olika svamparna, på skala från noll till fyra. I likhet med tidigare forskning i Västafrika var det kvinnor över 35 års ålder som kunde mest om svampar. Kunskap och preferens om olika svampar varierade mellan etniska grupper, men vi hittade stöd för att olika etniskgrupper som bor i samma by utbyter svampkunskap. Flera av de mest omtyckta svamparna var termitsvampar, som lever i symbios med termiter och utvecklar svampar på stora termitbon, och alltså samlas från naturen. Även många ektomykorrhizasvampar var välkända och omtyckta hos personer från olika etniska grupperna. För att bevara tillgängligheten av dessa svampar krävs att skogen, särskilt ektomykorrhizaträden, bevaras. Utbildning av befolkningen om förhållandet mellan svampar och träd är också ett möjligt sätt att skapa stöd för skogsbevarande.

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