



Mangrove fungi: A glimpse into Africa, its diversity and biotechnological potential

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Abstract

African Mangroves are among the unique forest ecosystems dominating mostly the coastal waters of the Indian Ocean that provide habitat for diversified biodiversity, including fungi. Mangrove fungal diversity represents the largest untapped reservoir of biodiversity for the potential discovery of new pharmaceuticals, enzymes, and unique bio compounds used for various biotechnological applications. However, they have been highly underappreciated. For ages, fungi from the marine environment have been considered aliens with low species diversity and richness, partly due to poor techniques deployed in exploring them. Advancement of culture-independent approaches, especially next-generation sequencing (NGS), has unveiled a tremendous fungal diversity, once hidden in plain sight in the surrounding environment. A spark of interest ignited in mycological and biotechnological research, and scientists focus on mangrove fungi to unearth novel metabolites with anticancer, antimicrobial, and biotechnological potentials. Many studies of marine endophytic fungi revealed a significant gap in the documentation of African mangrove fungi, their study methods, and their metabolites of biotechnological potential. This review highlights the information gap on African mangrove fungal diversity and the biotechnological potential of their metabolites for pharmaceutical and industrial applications. In addition, the study will discuss techniques used for their isolation and characterization.

Keywords – Ascomycete – Bioactive compounds – Endophytic fungi – Mangrove forest, Marine ecosystem.

Introduction

Marine fungi can belong to two distinct categories, obligate and facultative (Kohlmeyer & Kohlmeyer 1979). Obligate marine fungi are those that exclusively grow and sporulate in marine or estuarine habitats; in contrast, facultative marine fungi can originate from freshwater or terrestrial environments but can grow and potentially sporulate in the marine environment. They are usually found associated with different sea-dwelling marine organisms like seaweeds, mangroves, seagrass, and numerous other vertebrates and invertebrates (Richards et al. 2012, Pang et al. 2016, Raghukumar 2017). The fungi surviving in extreme ecosystems may be gems for biotechnological applications as their enzymes and secondary metabolites represent unique properties (Strobel & Daisy 2003, Capule et al. 2022). Mangrove forest ecosystems represent one of the rare taxonomic blind spots, hosting diverse microorganisms. Mangroves are recognized as biodiversity hotspots for marine fungi, which have a crucial role in the nutrient cycle and contribute to the overall health and

stability of the mangrove ecosystem (Shearer et al. 2007). These microorganisms, known as halophytes, exhibit specific adaptations to thrive in saline environments. Other microorganisms within these ecosystems have a wider distribution and can tolerate various conditions. They are mostly found as saprophytes on decaying organic matter, as parasites of plants in mangrove ecosystems, and as symbionts of plants and animals.

Mangrove fungi are reported as the most bountiful "life forms" in the marine environment, although they are still minimally explored (Gonçalves et al. 2022). This is due to the nature of the study, which is time-demanding, requiring a focus on bioprocess approaches, including aspects of molecular, physiological, and biochemical studies. Additionally, the low number of species in varying oxygen levels, salt concentrations, and organic matter quantity plays a significant role when examining mangrove ecosystems and their impact on species diversity.

Emphasis on the valuable facet of fungi has recently increased, paying attention to their implications in the ecosystems and their ability to produce beneficial bio compounds for biotechnology. Exploring the unique characteristics of these microorganisms in mangrove forests is considered an essential avenue for discovering new metabolites (Raghukumar 2017, Bibi et al. 2019). Many reports about fungi from freshwater and terrestrial environments are available, but relatively fewer for their marine counterparts (Schmit & Shearer 2003, Raghukumar 2017). However, the significant influence of mangrove fungi on biotechnology and global biogeochemical cycles demands their exploration for better insight (Gonçalves et al. 2022).

Earlier studies on fungi from mangrove environments have focused on taxonomy and descriptions of new species, new genera, and lists of marine fungi and surveys. Most of these studies concentrated in the Northern region of the world, while the Southern region, particularly Africa, has received less attention. As a result, a significant amount of information about mangrove fungi in this region of the world likely remains undiscovered. Research imbalance and the underrepresentation of mangrove fungi from Africa in academic literature have been identified as significant obstacles to discovering and utilizing these fungi from Africa. When searching for reports on mangrove fungi in African countries, a significant gap can be noticed in the documented records of these fungi, their study methods, and their known metabolites of biotechnological potentials. The objective of this review is to provide a synthesis of knowledge and knowledge gap on (i) the diversity of marine fungi from African mangroves, (ii) the techniques used for their isolation, (iii) the bioprospecting potential of their secondary metabolites for pharmaceutical and industrial applications and (iv) anthropogenic threats and opportunities for their sustainable conservation exploitations.

Habitat of marine fungi

In the marine environment, driftwood and mangrove wood are well-known, most extensively studied substrates (Jones et al. 1988, Sridhar et al. 2012, Raghukumar 2017, Tamayo & Álvarez 2022) that provide a habitat with a variety of niches in supporting a significant number of marine fungi (Hyde et al. 2000, Sridhar et al. 2012, Chatterjee & Abraham 2020). Mangrove trees host abundant microbial diversity, including fungi well-suited to thrive in challenging environments. These trees have evolved to withstand extreme, fluctuating brackish conditions, temperatures, and low oxygen levels.

Mangrove ecosystems serve as biodiversity hotspots for marine fungi (Thatoi et al. 2013). In the mangrove, fungal growth occurs on various substrates, including wood, leaf, sea grasses, soil, sand, corals, and calcareous material within mangroves (Kohlmeyer & Kohlmeyer 1979). Marine fungi on mangroves form the second-largest ecological group, many being new or inadequately described with the potential production of unique compounds (Sridhar et al. 2012, Walker & Robicheau 2021, Cadamuro et al. 2021). They constitute terrestrial, phylloplane, parasites, saprobes, and endophytes, and the latter form the most prominent group second to woody litter-associated fungi (Sridhar et al. 2012).

Mangrove ecosystems harbor diverse species, and their interactions are not seen in other ecosystems, including the marine fungal species whose interactions with mangroves extend from

beneficial to antagonist. Generally, the relationship between fungi and plants is reciprocally advantageous. Initially, fungi survive in dead plants reusing nutrients (saprophytic fungi) (Tan & Zou 2001, Ukoima et al. 2009). Nonetheless, other fungi, including mycorrhizas and endophytes, started interacting with live plants after some time. Most of these fungi continue to be mutually beneficial, while some develop novel metabolic pathways making them phytopathogenic (Osorio et al. 2017, Piatek & Yorou 2018). On the other hand, increasingly large numbers of fungi obtained from mangrove environments are identified as endophytic fungi (Strobel & Daisy 2003, Sridhar et al. 2012, Osorio et al. 2016, Kuzhalvaymani et al. 2020, Deshmukh et al. 2020).

Amidst the fungi from other marine environments, mangrove fungi have been essential in sourcing novel bioactive compounds that may have valuable novel functions and structures (Kuzhalvaymani et al. 2020, Deshmukh et al. 2020, Bibi et al. 2020, Cadamuro et al. 2021, Sopalun et al. 2021). These mangrove fungi with unique interactions with plants are a contemporary source of secondary metabolites. This potential calls for more scrutiny since in vivo chemical synthesis have shown to be economically not feasible (Tarman 2020).

Mangrove fungal diversity

The marine environment holds a large diversity of fungi known to science. One percent (about 1112) of documented fungi reportedly come from marine environments (Richards et al. 2012, Raghukumar 2017, Sarma 2019). As of 15th July 2022, the total documented marine fungi were 1857, grouped in 769 genera, 226 families, 88 orders, 22 classes, and seven phyla, namely: *Ascomycota*, *Aphelidiomycota*, *Basidiomycota*, *Blastocladiomycota*, *Chytridiomycota*, *Mortierellomycota* and *Mucoromycota* (Jones et al. 2019). This raises some concerns about the significance of fungal communities in the marine ecosystem.

Mangrove fungal diversity has heightened worldwide due to several works investigating the mycobiome of different mangrove species (Osorio et al. 2014). In various parts of the world, efforts have been projected to estimate fungal diversity; hence the importance of studies on fungal species is highlighted (Thatoi et al. 2013). Several kinds of research have been conducted to examine the mangrove's fungal diversity (Alias et al. 2010). Despite efforts towards unveiling the fungal diversity worldwide, such studies are lacking in most countries, revealing the gap in this knowledge with potentially immense biodiversity remaining uncovered (Osorio et al. 2021, Devadatha et al. 2021). For example, with the vast amount of microbial diversity estimated from the mangrove systems, only <5% has been estimated (Kathiresan 2019). Approximately 2200 fungal taxa have been globally reported from mangroves (Sridhar et al. 2012, Osorio et al. 2021), dominated by mangrove fungi from Asian countries, particularly India (45.8%), followed by Malaysia (5.1%), Bangladesh (5.1%), China (5.1%), Philippines (3.4%), Indonesia (3.4%), and 16.9% from elsewhere (Jones 2011, Bibi et al. 2019, Tamayo 2022). This shows that mangrove fungi are increasingly being surveyed, but many mangrove forests remain uninvestigated, especially those from Africa, Australia, New Zealand, and South America (Devadatha et al. 2021).

The literature shows over 85 species in 69 genera have been reported from Africa. Most species are Ascomycetes, with only a few *Basidiomycetes*, *Deuteromycetes*, and *Zygomycetes*. The figure only covers species identified so far reported in published peer-reviewed work. The list is incomplete because those surveys have only covered a limited number of communities or parts of each country, and the research and the discovery of new species is a continuous and ongoing work. The lack of regional inventories for African marine environments limits the results.

It can be agreed that fungi, particularly mangrove fungi, have been comparatively poorly exploited in most ecosystems. It is worth noting that fungal diversity differences occur across sites and geographical locations (Sridhar et al. 2012). Limited mangrove fungal explorations have been done on the coast of Africa (Shearer et al. 2007); these areas are, however, highly recognized among the world's hotspots for biodiversity. It is crucial to unveil these hidden potentials in relatively unexplored areas such as Africa (Kohlmeyer & Kohlmeyer 1971, Steinke & Jones 1993, Steinke 2000, Devadatha et al. 2021). This review summarizes important mangrove fungi reported from Africa and provides a list of the biotechnological potential of their metabolites. This work on

fungi in African mangroves is anticipated to be exciting and give a radar to promote and guide future exploration of mangrove fungi in Africa and the world.

Marine fungi in African mangroves

The high diversity of mangrove plants occupies about 75% of the world's tropical coastlines, mostly between 25° N and 25° S (Devadatha et al. 2021). Even though there are reported studies on mangrove fungi, the majority of these studies are from Asian countries, and few studies have been done in Africa (Aleem 1980, Steinke & Jones 1993, El-Sharouny et al. 1998, El-Sharouny et al. 1999, Steinke 2000, Abdel-Wahab 2000, Abdel-Wahab 2005, Ukoima et al. 2009, Sultan et al. 2013, Osorio et al. 2015, Osorio et al. 2016, Osorio et al. 2017, Piatek & Yorou 2018, Jenoh et al. 2019, Akinduyite & Ariole 2019, Muwawa et al. 2020, Bankole et al. 2020, Wacira et al. 2020, Kiti et al. 2021, Osorio et al. 2021, Aina et al. 2021). African mangroves are estimated to cover about 21% of the world's mangrove ecosystem, second to Asia, which covers 42% of the total world mangrove (Diop et al. 2002, Chatterjee & Abraham 2020).

Studies from Africa are limited to a few countries, including Egypt, Kenya, Nigeria, Niger, Ghana, and South Africa, and the information from other countries remains very limited. From studied countries, only a few sampling spots have been included. Poor diversity is represented as most of these studies relied only on traditional morphological identification (Steinke 2000, Ukoima et al. 2009, Kiti 2021, Wacira 2020), while few performed molecular identification only based on the culturable fungi, neglecting the non-culturable fungi (Osorio et al. 2016, Jenoh et al. 2019, Osorio et al. 2021).

Some studies from Africa have reported interesting fungal species from mangroves. Ukoima et al. (2009) surveyed fungi from red and white mangrove forest trees in Rivers State, Nigeria. The author isolated 13 fungal species belonging to the *Alternaria*, *Aspergillus sp.*, *Botryodiplodia*, *Colletotrichum*, *Fusarium*, *Lindreina sp.*, *Penicillium sp.*, *Phomopsis sp.*, *Rhizopus* and suggested that most of them are saprobes. However, the study only relied on a microscope to identify fungi and recommended that more studies be conducted on these fungi to ascertain their identity. Likewise, Akinduyite & Ariole (2019) obtained seven endophytic fungi from the leaves of the black mangrove (*Avicennia africana*) in Rivers State, Nigeria. The fungal genera isolated included: *Aspergillus*, *Collectotrichum*, *Epicoccum*, *Fusarium*, *Penicillium*, *Phomopsis*, and *Rhizopus*, only one isolate from this study (*Fusarium phylophillum*) was confirmed by sequencing data.

There are several studies documenting mangrove fungi from the Kenyan coastline. Seventy-six fungal isolates were obtained, identified using morphological features, and affiliated with eight genera: *Alternaria*, *Aspergillus*, *Chaetomium*, *Cladosporium*, *Fusarium*, *Lasiodiplodia*, *Nigrospora*, and *Penicillium*. (Wacira et al. 2020). Kiti et al. (2021, 2022) dealt with mangrove fungal endophytes of *Avicennia marina*, *Ceriops tagal*, *Rhizophora mucronata*, and *Sonneratia alba* based on cultural, morphological, and sequence data. They were able to document a total of 18 fungal isolates and explore their potential antimicrobial activities. On the other hand, from the same locality using only *Sonneratia alba*, a total of fifteen fungi from the genus *Aspergillus*, *Cladosporium*, *Gibberella*, *Penicillium*, *Talaromyces*, and *Trichoderma* were reported by Jenoh et al. (2019) with their potential implication in *Sonneratia alba* wood borer infestation. Muwawa et al. (2020) obtained 33 fungal isolates from the rhizospheric sediments *R. mucronata*, *A. marina*, *S. alba*, and *C. tagal* along the Kenyan Coastline. Phylogenetic analysis grouped these isolates into eleven genera; *Aspergillus*, *Diatrypella*, *Fulvifomes*, *Geosmithia*, *Hypocreales*, *Massarina*, *Paracremonium*, *Peniophora*, *Penicillium*, *Talaromyces*, *Thielavia*. Most of these studies from Kenya incorporated sequence data, which is advantageous as it provides more information on fungal diversity. However, from these studies, it can be seen that they mainly concentrated on two main sampling sites, Mida Creek and Gazi Bay, and a little from Tudor Creek; hence more studies are required to reach excellent coverage.

Similarly, fifteen fungal species were identified by Sultan et al. (2013) from the mangrove soil of Nabq and Ras Mohammed in Egypt, with most of them belonging to *Ascomycotina* and a few belonging to *Deuteromycotina* and *Zygomycotina*. The *Aspergillus* spp. had the highest number

of species, followed by *Cladosporium*, and *Trichoderma* spp. had the lowest number of species. The finding substantiated that *Aspergillus* spp. has been reported as the dominant fungi in the mangrove ecosystems in other parts of the world. Abdel-Wahab (2005) explored the diversity of marine fungi in Egyptian Red Sea mangroves and suggested that it is comparable to that recorded from subtropical mangroves but lower than that recorded from tropical mangroves. The work documented 39 more species bringing the total number of mangrove fungi from the Egyptian Red Sea to 84. This number is a collective contribution of jobs made by El-Sharouny et al. (1998, 1999) and Abdel-Wahab (2000, 2005). However, all of these studies are based on the microscopic identification of the mangrove fungi in question, and no information was reported using molecular techniques, which might have contributed to the low representation of diversity.

Mangrove fungi with potential pathogenicity and those found in polluted mangroves with bioremediation potentials have been scantily documented. Most of these reports are the first reports from Africa, indicating the massive gap in information from this part of the world.

Piatek & Yorou (2018) analyzed samples of *Avicennia germinans* from Quidah and Togbin Forest, Benin, and provided the first record of *P. avicenniicola* in West Africa, hence recommended more work in other parts of Africa. Osorio et al. (2016) studied the endophytic *Botryosphaeriaceae* from ten locations and six mangrove species in South African mangroves. These authors identified 14 taxa from four genera based on the DNA sequence of four gene regions, and they identified five new taxa. The novel species reported include *Diplodia estuarina* sp. nov., *Lasiodiplodia avicenniae* sp. nov., *Lasiodiplodia bruguierae* nov., *Neofusicoccum lumnitzerae* sp. nov. and *Neofusicoccum mangroviorum* sp. nov. Nothing was known about the diversity of endophytic *Botryosphaeriaceae* from South African mangroves, but the genus was recorded for the first time from mangroves in this country.

From Niger Delta in oil-polluted mangroves, Aina et al. (2021) isolated fungi belonging to *Aspergillus* spp. and *Candida* spp. from the roots of *R. racemosa* and found that they could degrade hydrocarbon. The results are more or less similar to what was reported by Ghizelini et al. (2019), a similar study on oil-polluted mangrove and found fungi belonging to *Penicillium* and *Aspergillus*. These works established that oil spills drive fungal community composition in the most polluted sites. However, unlike Ghizelini et al. (2019), Aina et al. (2021) did not perform molecular characterization, potentially limiting the proper diversity assignment.

Aleem (1980) reported 14 species encountered in Sierra Leone, which showed similarity with what was found elsewhere in the world; for example, 13 were found in the Western Atlantic, 12 in the Pacific, and ten in the Indian Ocean. This suggested a common origin for the mangrove fungi based on their similarity in the three oceans. It is interesting to note that the finding of these researchers portrays the resemblance of the biodiversity of marine fungi from Africa to that of other regions, such as South America, India, and Malaysia. A list of mangrove fungi reported from African studies and the method used to study them is summarized in Table 1.

Uncovering the hidden diversity of mangrove fungi is crucial for its application and developing protection programs to protect biodiversity and their biotechnological potential, as most of the mangrove areas are under advanced anthropic destruction. Modern techniques and tools, such as molecular techniques, are of great help to identify fungal diversity and its ecosystem functioning. However, only relatively few studies in Africa have exploited molecular means to apprehend the ecology of mangrove fungi.

Table 1 Mangrove fungi species obtained from various studies on mangroves from African countries.

Fungal species	Host mangrove	Technique	Origin	Reference
<i>Acrocordiopsis patilii</i> , <i>Anastasiou Phoma</i> spp., <i>Alternaria</i> sp., <i>Asteromyces crucialis</i> , <i>Basidiomycotina</i> , <i>Camarosporium roumeguerii</i> , <i>Caryospora rhizophorae</i> , <i>Chaetomastia typhicola</i> , <i>Cirrenalia</i> sp., <i>Dactylospora haliotrepha</i> , <i>Deuteromycotina</i> , <i>Epicoccum</i> sp., <i>Fusarium</i> sp., <i>Halosarpheia</i> sp., <i>Halocyphina villosa</i> , <i>Humicola</i> <i>alopallonella</i> , <i>Hydronectria glabra</i> , <i>Hypoxylon</i> <i>oceanicum</i> , <i>Leptosphaeria</i> spp., <i>Lignicola laevis</i> , <i>Linocarpon</i> sp., <i>Lophiostoma mangrovei</i> , <i>Lulworthia</i> sp., <i>Marinosphaera mangrovei</i> , <i>Mycosphaerella</i> <i>pneumatophorae</i> , <i>Periconia prolifica</i> , <i>Phaeosphaeria</i> spp., <i>Pleospora</i> spp., <i>Rhabdospora avicenniae</i> , <i>Rhizophila</i> spp., <i>Sphaeropsidales</i> spp., <i>Stagonospora</i> sp., <i>Thalassogena sphaerica</i> , <i>Trematosphaeria</i> sp., <i>TrichacIadium</i> spp., <i>Verruculina enalia</i> .	<i>Avicennia marina</i> , <i>Hibiscus tiliaceus</i> , and <i>Rhizophora mucronata</i> , unidentified mangrove driftwood	Direct microscopic observation	South Africa	Steinke (1993)
<i>Dactylospora haltotrepha</i> , <i>Kallichroma</i> spp., <i>Leptosphaeria</i> spp., <i>Mtata</i> spp., <i>Phoma</i> spp., <i>Swampomyces</i> spp.	<i>Rhizophora mucroflata</i>		South Africa	Steinke (2000)
<i>Alternaria</i> , <i>Aspergillus</i> , <i>Chaetomium</i> , <i>Cladosporium</i> , <i>Fusarium</i> , <i>Lasiodiplodia</i> , <i>Nigrospora</i> , and <i>Penicillium</i> .	<i>Bruguiera gymnorrhiza</i> , <i>Heritiera littoralis</i> , <i>Xylocarpus granatum</i> , <i>Rhizophora mucronata</i> , and <i>Avicennia marina</i>	Fungi were grown in culture media (PDA)	Kenya	Wacira et al (2020)
<i>Aspergillus</i> , <i>Blastomyces</i> , <i>Cephalosporium</i> , <i>Fusarium</i> , <i>Penicillium</i>	<i>Rhizophora mucronata</i> (red mangrove), <i>Sonneratia alba</i> (mangrove apple), <i>Avicennia marina</i> (grey or white mangrove), and <i>Ceriops tagal</i> (spurred mangrove)	Fungi were grown in culture media (PDA)	Kenya	Kiti (2021)
<i>Absidia</i> spp, <i>Acremonium</i> spp, <i>Alternaria</i> spp, <i>Aspergillus</i> spp, <i>Cladosporium</i> spp, <i>Penicillium</i> spp, <i>Rhizopus</i> spp, and <i>Trichoderma</i> spp.	<i>Unspecified</i>	Suspension plating method; direct plating method Three types of media were used Czapek s agar media, MEA, PDA,		Sultan (2013)

Table 1 Mangrove fungi species obtained from various studies on mangroves from African countries.

Fungal species	Host mangrove	Technique	Origin	Reference
<i>Zasmidium mangrovei</i> sp. nov.	<i>Avicennia marina</i>	Phylogenetic analyses using multigene sequence data LSU and ITS.	South Africa	Osorio et al. (2020)
<i>Botryosphaeria</i> , <i>Botryosphaeriaceae</i> , <i>Diplodia</i> , <i>Lasiodiplodia</i> , and <i>Neofusicoccum</i> .	<i>A. marina</i> , <i>B. gymnorrhiza</i> , <i>C. tagal</i> , <i>L. racemosa</i> and <i>R. mucronata</i>	Multigene sequence ITS, beta-tubulin (tub2), partial translation elongation factor 1-alpha 30 (tef1- α), rpb2) regions.	South Africa	Osorio et al. (2016)
<i>A. niger</i> , <i>A. solani</i> , <i>Aspergillus</i> sp., <i>B. theobromae</i> , <i>C. gloeosporioides</i> , <i>F. moniliforme</i> , <i>Fusarium</i> sp., <i>Lindraea</i> sp., <i>P. dictyeta</i> , <i>Penicillium</i> sp., <i>Phomopsis</i> sp., <i>R. stolonifer</i> .	<i>R. mangle</i> , <i>R. racemosa</i> , <i>R. harrisonii</i> (Red mangrove), and <i>A. africana</i> (White mangrove)	Culturing and microscopic observation	Niger	Ukoima et al. (2009)
<i>Aspergillus niger</i> , <i>Aspergillus flavus</i> and <i>Candida albicans</i> .	<i>Rhizophora racemosa</i>	Culturing and microscopic observation	Niger delta, Nigeria	Aina et al. (2021)
<i>Aspergillus awamori</i> , <i>Penicillium sclerotiorum</i> , <i>Trichoderma inhamatum</i>	Unidentified	Fungal isolation by culturing in PDA; species identification using ITS gene amplification.	Kenya	Jenoh et al. (2019)
<i>Pseudocercospora avicenniicola</i>	<i>Avicennia germinans</i>	Culturing and microscopic observation	Benin	Piatek & Yorou (2018)
<i>Corollospora maritima</i> , <i>C. portsaidica</i> , <i>Cumulospora marina</i> , <i>Leptosphaeria oraemaris</i> , and <i>Periconia prolifica</i> .	<i>Pongamia pinnata</i>	Unidentified	Egypt	Abdel-Aziz (2010)
<i>Aspergillus</i> , <i>Collectotrichum</i> , <i>Epicoccum</i> , <i>Fusarium</i> , <i>Penicillium</i> , <i>Phomopsis</i> , and <i>Rhizopus</i> .	<i>Avicennia africana</i>	Culturing and molecular identification	Nigeria	Akinduyite & Ariole (2019)
<i>Aspergillus sydowii</i>	Unidentified	Fungal isolation by culturing in PDA; species identification using ITS gene amplification.	Nigeria	Bankole et al. (2020)
<i>Penicillium herquei</i>	<i>Laguncularia racemosa</i>	Fungal isolation by culturing in MEA; species identification using DNA barcodes.	Ghana	Hayibor et al. (2019)

Methods used in characterizing mangrove microbiomes.

In most available studies, mangrove fungal diversity has been explored by combining techniques ranging from culture-dependent to advanced molecular methods. Both conventional and molecular techniques are deployed in characterizing mangrove fungi, including directly examining sporulating structures, culturing, and metagenomics. Molecular techniques have so far been deemed superior in fungal identification and identification of its diversity compared to culture-dependent studies. However, these techniques for identification function perfectly when used in combination. Here is a list of methods used in mangrove fungi studies highlighted.

Traditional techniques

Direct examination method

When dealing with marine substrates, sporulating forms of fungi are detected by examination under the microscope, coupled with isolation in culture. This is the most routine method of observing fungi occupying plant tissue under light or electron microscope (Cazabonne et al. 2022). This technique studies fungi occurring on biological samples such as mangrove wood by examining them under microscopes to pinpoint and identify fungal fruiting structures (Raja et al. 2017). Steinke & Jones (1993) collected samples from mangroves and moist-incubated them in sterile plastic boxes while examining their fructifications periodically. Finally, they identified them regarding the marine fungal culture collection. Limited in the taxonomic information it provides, this method can hardly be used for the biodiversity and phylogenetic investigation of fungi (Subudhi et al. 2019). It secludes information about fungi within a substrate but doesn't bear sporulating structures.

Culture-dependent techniques.

Microscopy and cultural studies are crucial for fungal diversity studies, and their significance cannot be overlooked. Identifying marine fungi from substrates may be made by culturing them and obtaining a pure culture associated with known or unreported marine fungi. This method involves culturing mangrove samples into suitable isolation media at some stages for isolation (Hyde et al. 2000, Subudhi et al. 2019). Finally, identification is made by morphological and microscopic observations (Bonugli-Santos et al. 2015). Given that the procedure necessitates the isolation and cultivation of fungi to obtain uncontaminated fungal cultures, it is thereby referred to as a culture-dependent technique. Cultural-dependent studies and microscopic analysis are helpful when a quick, less expensive diversity estimate is desired. Nevertheless, conventional isolation by cultivation and characterization of fungi isolates is crucial in understanding the species diversity and population structure (Subudhi et al. 2019) and disclosing its implication in plant survival (Damare et al. 2011, Bonugli-Santos et al. 2015, Kathiresan 2019).

Shortcomings of traditional methods used in mangrove fungal studies

Culture-dependent approaches have technical biases and are unreliable and unrealistic in reporting diversity (Subudhi et al. 2019). Reportedly, the total microbial diversity from the environmental samples that culture-based methods unveil is about 1–5% (Kennedy et al. 2010). Most of the taxa recovered through culture-dependent methods (more than 90% of the total described marine species) belong mainly to *Ascomycota* and *Basidiomycota* (Jones et al. 2019, Gonçalves et al. 2022). Species that share similar morphological characters through cultural techniques might, with high probability, belong to different species; thus, relying on cultural conditions could be misleading (Halder & Nazareth 2019). Other shortcomings include the inefficiency of the growth medium, the high risk of contamination, laborious, tedious laboratory procedures (Subudhi et al. 2019), and inexperience of personnel obscure suitable identification. The shortcoming of culture-dependent techniques can be overcome by molecular tools, which have recently shifted the trajectory of fungi ecological studies. With molecular advancements, the data obtained from culturable fungi are also enriched with molecular data, and unidentified fungi

cultures get identified with a high degree of certainty. Several novel species have been increasingly reported by incorporating molecular data (Abdel-Wahab et al. 2010, Devadatha et al. 2021).

Modern techniques

Recently there have been promising advancements to explore microbial diversity through technologies such as molecular biology (Thatoi et al. 2013, Kathiresan 2019). The scientific thirst for understanding marine fungal diversity and functions has increasingly been quenched through culture-independent approaches, among other techniques (Richard et al. 2015, Hamza et al. 2018).

Nucleic acid analysis of the cultured isolates

Isolates obtained from culture-dependent procedures with morphological and growth characteristics similarities cannot be easily distinguished and hence reported as morphotypes (Raja et al. 2017). However, diversity cannot be established using morphotypes as they are dismissed as taxon units and thus fail to develop phylogenetic lineage (Subudhi et al. 2019). The application of molecular techniques has remarkably overcome this limitation.

Fungal DNA barcodes like nuclear ribosomal internal transcribed spacer (ITS) have been very useful in detecting diversity in the community and identifying sporulating and non-sporulating fungi (Cazabonne et al. 2022). Comprehending species diversity within the community and assigning taxonomic places for it has been much easier with molecular analyses based on DNA markers (Cazabonne et al. 2022). Analysis of molecular markers coupled with morphological information became the preferred practice for inferring biodiversity among the fungal isolates in their ecology (Hamzah et al. 2018, Subudhi et al. 2019). In a study by Norphanphoun (2018), three new species, *Cytospora lumnitzericola*, *C. thailandica*, and *C. xylocarpi*, were introduced with the support of phylogeny. A combined multigene DNA sequence dataset (ITS, ACT, LSU, and RPB2) were studied to critically investigate the phylogenetic relationships of isolates and provide reliable species identification. The 37 fungi isolates obtained in a study by Sopalun et al. (2021) were further identified using their morphological characteristics and internal transcribed spacer (ITS) sequences.

However, exclusive identification and understanding of the diversity of isolates that could be cultured in artificial media limit nucleic acid analysis techniques using DNA markers (Subudhi et al. 2019). This method does not encourage the growth of all fungi in the environment in artificial media in vitro; it fails to explain the relationship between them and their surrounding environment. On the other hand, culture-independent techniques, such as metagenomics, offers a greater understanding of microbial diversity (Guo et al. 2015, Chauhan 2019, Abdel-Wahab et al. 2020, Fadji & Babalola 2020, Zhuang et al. 2020).

Metagenomic techniques in community analysis of fungi

Metagenomics (environmental genomics, ecogenomics) stands for the genomic analysis of microorganisms through direct nucleic acids extraction from environmental samples, such as soil, water, sediments, or plant tissues (Thatoi et al. 2013, Cazabonne et al. 2022). Recent advances bring to light the use of next-generation sequencing (NGS) techniques in carrying out Metagenomics analysis; this enables to uncover the information on the microorganisms present in any environment much beyond in vitro cultivation (Bengtsson-Palme 2018, Verma 2019, Chauhan 2019). With such advancement, the obstacle once put through by the necessity to isolate microorganisms at the individual level is overcome, and the entire community DNA of the environmental samples can be analyzed at a molecular level.

Metagenomics DNA usage provides a quick and effective high-throughput method to deal with and analyze large-sized genome and to translate it into understandable information via suitable software (Verma 2019). Metagenomics is the best tool for dealing with the total DNA of all the assemblage from environmental samples, bypassing in vitro culturing of individual organisms in a given microbiome. Reportedly non-culturable microbial population is much higher (90–99%) in any environmental sample than the culturable ones (Kennedy et al. 2010, Thatoi et al. 2013). As a

result, fungi-environment interactions, contributed by culturable and non-culturable microbes, can be better realized. These are valuable approaches in resolving species relationships across different taxonomic levels and potentially uncover new fungal taxa from marine environments that the culture-dependent method cannot (Kennedy et al. 2010, Ladoukakis et al. 2014, Chauhan 2019, Verma 2019, Fadiji & Babalola 2020).

Metagenomic-based exploration of marine microbiomes raise interest in marine biotechnologist, and it exposes a large diversity of uncultured fungi being newer fungal taxa (Kennedy et al. 2010, Singh et al. 2011, Damare et al. 2011). Amidst the fungal sequences detected by the metagenomics studies in Baeza et al. (2017), thirty-seven (37) fungi corresponded to genera that were never cultivated before from Antarctica. Abdel-Wahab et al. (2021) also obtained seven deep branching lineages that did not cluster with any known microbial taxa, thus clearly indicating that an extensive diversity of microbes are yet to be uncovered.

Shi et al. (2021) used metagenomics to study the rhizospheres of two mangroves. They identified seven fungi belonging to *Ascomycota*, including *Arthrinium* spp., *Aspergillus* spp., *Neorousoella* spp., *Penicillium* spp., *Talaromyces* spp., *Trichoderma* spp., and *Westerdykella* spp. Subsequently, this study ended up assembling the whole genome of these fungi, generating six novel fungi genomes. In a study by Imchen et al. (2018), mangrove sediments from India, Brazil, and Saudi Arabia were analyzed regarding taxonomic and functional community structures using next-generation sequencing (NGS). The study identified *Proteobacteria*, followed by *Firmicutes* and *Bacteroidetes*, as the most abundant groups associated with mangroves.

Recent technological developments involving NGS technologies enabled the revealing of uncovered microbial potentials of environmental fungal communities and the understanding of their functional diversity. Zhuang et al. (2020) applied amplicon and metagenomics sequence data to analyze the fungal communities of mangrove roots and found different functional patterns associated with carbohydrate metabolism, lipid transport, and methane production within the compartments. This analysis facilitated the deduction of essential insights, including the selective influence of roots on the assembly of fungal communities and the impact of soil-root interfaces on the structure of these communities.

Metagenomics enables DNA analysis, tackling a big challenge in grouping fungi based on morphology and other physical traits. Imchen et al. (2018) compared mangrove and terrestrial samples on genes of resistance to heavy metals and antibiotics; mangrove resistome consistently showed increased resistance to fluoroquinolone and acriflavine.

Shortcomings of modern methods used in mangrove fungal studies

However, several shortcomings accompany these methods, including the difficulty in molecular techniques to distinguish among dormant spores, actively growing mycelium, and senescing mycelium (Fadiji & Babalola 2020). The procedures require specialized labs and expertise as well as powerful computers to analyze molecular data, which makes it difficult and expensive to be performed in most laboratories from developing countries.

Statistical methods for handling metagenomics data are also faced with many problems. This is attributed to the high dimensionality posed by metagenomics data, meaning more genes are observed than biological replicates (Ladoukakis et al. 2014). On top of it, there is a considerable variation between samples of the same group; hence, more considerable numbers of replicates are required to detect statistically significant differences (Jonsson et al. 2017, Bengtsson-Palme 2018).

DNA sequencing for metagenomics studies is comparatively expensive (Fadiji & Babalola 2020), leading to many studies being performed without replicates, affecting the reproducibility of data. Conversely, aggregate sequences are presented with no similarities in available databases (Verma 2019, Fadiji & Babalola 2020). There is a need for harmonization between gathering adequate sequencing depth for quantifying genes in each separate sample and sequencing enough replicate samples to detect significant differences (Bengtsson-Palme 2018).

The use of traditional and modern techniques together is needed for a rigorous, solid, and critical description of fungi. Studies on mangrove fungi in Africa have applied most of these

methods; however, during this review, no analysis was found that used NGS techniques, such as metagenomics, which uses environmental DNA. This might be due to several factors, including limited technological advancement and the high cost of generating and analyzing NGS data. Nevertheless, this has implications for the mangrove fungal diversity documentation from these fascinating ecosystems, as the vast amount of diversity will remain hidden. On the other hand, researchers should increasingly use affordable molecular techniques such as fungal DNA barcodes. This will enable a smooth comparison of data generated from African coastlines to the data available from the rest of the world.

Bioprospecting the potential of mangrove fungi

In the quest for peculiar bioactive molecules from plants such as mangroves, extinction is becoming a threat to these essential medicinal plants as a result of their exploitation beyond their present capacity to meet the rising demand in pharmaceutical and agricultural markets (Strobel & Daisy 2003, Teka et al. 2019, Agrawal et al. 2019, Liao et al. 2020). As a solution, the focus is being shifted toward fungal metabolites due to their extraordinary production of secondary metabolites, fast growth on standard media, and many biological potentials (Wang et al. 2014, Deshmukh et al. 2020, Kuzhalvaymani et al. 2020, Anugraha et al. 2021, Paranetharan et al. 2022).

Initially, the focus was only on those microorganisms quickly within reach, like those that host corals; however, the attention has been swayed away recently by mangrove fungi since their importance by providing abundant sources for novel chemical entities. However, mangrove fungi remain insufficiently explored, with their full biotechnological potential still hidden in plain sight (Bugni & Ireland 2004, Imhoff 2016, Silber et al. 2016, Overy et al. 2019). A recent report by Cadamuro et al. (2021) showed the mangrove fungi to contain novel bioactive compounds and structure potential for biotechnological and pharmacological application. Several beneficial metabolites have been well explored and documented. Among them include antimicrobial activities, antioxidants, enzymes, and secondary metabolites.

Some studies shed light on the molecular mechanisms underlying the diversity of metabolites produced by mangrove fungi. Factors like the presence of unique gene clusters associated with secondary metabolism, the protein expression patterns involved in secondary metabolite biosynthesis, distinct genomic features that facilitate secondary metabolite synthesis and fungal adaptation in the challenging mangrove environment have been identified and reported (Hilário & Micael 2023). On the other hand, some studies focused on protein expression, uncovering specific proteins and pathways involved in secondary compound production (Wang et al. 2015, Blessie et al. 2020, Chen et al. 2022). This highlighted the biosynthetic pathways and genetic mechanisms behind secondary compound production. Together, these studies provide valuable insights into mangrove endophytic fungi's ecological and biological significance, expanding our knowledge of their metabolite diversity, genomic characteristics, and protein expressions in diverse environments.

Despite the exciting potential for the biotechnological application of mangrove fungi, the current body of knowledge regarding their biotechnological applications in Africa remains limited. Consequently, there is a pressing need to address this research gap and unravel the untapped potential of these unique fungal organisms. Here, we provide a comprehensive summary of the existing literature on exploring mangrove fungi in Africa. By analyzing this information, we hope to shed light on the current state of knowledge and emphasize the significance of further investigations in this field.

Crude extracts of mangrove fungi are effective against various bacteria and fungi of medical importance. Kiti et al. (2022) measured the minimum inhibitory concentration of ethyl acetate crude extracts of nine mangrove fungal isolates in Kenya. They found that the most active fungal isolate had a MIC of 0.82 ± 0.052 mg/ml and 0.91 ± 0.05 mg/ml against *E. coli* and *S. aureus*, respectively. Thirty-three fungal isolates were evaluated for antibacterial activity using the disk diffusion method, where 17 isolates produced inhibition zones against three pathogenic bacterial strains (Muwawa et al. 2020). The results show that mangrove fungi from the coasts of Africa are effective against important medical bacteria and fungi, hence a promising source of novel organic

natural metabolites. However, most of them end up at crude extract level with no isolation and testing of the pure compound, which will signify their probability for industrial application.

Akinduyite & Ariole (2019) reported a bioactive ester, dibutyl phthalate, as the primary bioactive compound produced by the isolated *Fusarium phyllophilum*, which has many bioactive functions, including antimicrobial and anticancer activity. Hayibor et al. (2019) isolated oxylipin (9Z,11E)-13-oxooctadeca-9,11-dienoic acid from an endophytic fungus, *Penicillium herquei* strain BRS2A-AR obtained from the *Laguncularia racemosa* Leaves in Ghana. The compound showed antiparasitic activity and hence the potential to further engineer its structure into a potent anti-Trichomonas scaffold.

Bioremediation potential is another important property that mangrove fungi have displayed in Africa. Aina et al. (2021) isolated hydrocarbon-utilizing fungi from *Rhizophora racemosa*, demonstrating the ability to degrade hydrocarbon at up to 100% rate. Bankole et al. (2020) reported *Aspergillus sydowii* isolated from mangrove soil in Delta State, Nigeria. The fungi portrayed biodegradation activity on polycyclic aromatic hydrocarbons (PAHs), which are acute mutagenic, carcinogenic, and teratogenic toxicity to humans and living organisms and are usually deposited through oil spillage during loading and transfers and petrochemical industry wastes.

However, studies exploring potential bioactive compounds from mangrove fungi have been extensively conducted in other parts of the world and have yielded promising results. These investigations have unveiled a rich source of secondary metabolites with diverse biological activities, including anticancer, antimicrobial, antioxidant, and anti-inflammatory activity. Here we will delve into the literature surrounding these studies, discussing the various bioactive compounds discovered from mangrove fungi and their potential applications. Through examining these findings, we aim to provide a comprehensive overview of the bioactive potential of mangrove fungi and highlight the importance of further exploring this untapped resource in Africa.

While studying secondary metabolite biosynthesis gene clusters, Shi et al. (2021) were able to notice that mangrove fungi averagely contain 18 Type I Polyketide (t1pks) synthase, significantly higher than 13 in non-mangrove fungi. Deshmukh et al. (2020) characterized 183 compounds obtained from mangrove fungi, with 91 possessing antibacterial and 42 antifungals, while 33 were reported to have anti-viral activity and 17 portrayed action against mycobacteria. Ling et al. (2016) isolated metabolites from mangrove fungi, *Guignardia* sp. and *Neusartoya* sp., which contained trimeric catechin and helenalin, and displayed antibacterial properties against *Bacillus* spp., *Escherichia* spp., and *Staphylococcus* spp., and auspicious antifungal properties towards *Aspergillus* spp. and *Candida* spp. Leaf mangrove fungi showed potential antifungal activity toward indicator phytopathogens (Khruayay & Pilantanapak 2012). *Alternaria*, *Cladosporium*, *Colletotrichum*, *Guignardia*, *Pestalotiopsis*, and *Phomopsis* isolated from *Aegiceras corniculatum* displayed antimicrobial activities against several microbes, such as *Bacillus* spp. *Klebsiella pneumoniae* and *Pseudomonas* spp. (Bin et al. 2014).

In a research done by Wang et al. (2014), it was found that *Alternaria* sp. isolated from the root of a mangrove plant *Myoporum bontioides* revealed antioxidant activity against DPPH radical. Strong antioxidant potential in the form of extracellular polysaccharides was displayed by *Fusarium* spp., obtained from *Ipomoea pescaprae* (Linn.) (Chen et al. 2015). Hamzah et al. (2018) observed a significant radical scavenging capacity from methanol-extracts of *F. lateritium* and *Xylaria* sp. with that of *Xylaria* sp. reducing the absorbance of DPPH free radical to a great extent. Methanolic extract of an isolate of *Xylaria* sp. contains phenolic compounds that reportedly contribute enormously to antioxidant activities.

A plentiful source of microbial enzymes is hidden in plain sight within mangrove fungi (Kathiresan 2019). Reports are available on the potential of the mangrove fungi to produce enzymes, such as oxidases, amylase, cellulose, and protease with practical applications in food, pharmaceutical, textile, and paper industries (Damare et al. 2011, Yousef 2014, Kathiresan 2019, Bankole et al. 2020, Paranetharan et al. 2022).

Shi et al. (2021) compared mangrove and non-mangrove fungi and found that carbohydrate-binding modules (CBM32), a sub-family of carbohydrate-active enzymes detected in only two

mangrove fungi. The enzymes produced by mangrove fungi are more potent when compared to non-mangrove fungal enzymes during analysis. Additionally, the two subfamilies of hydrolases and polysaccharide lyases differ substantially in gene copy number. The effect of mangrove ecology on the potential of decomposition and, consequently, enzyme production of rhizosphere fungi is indicated in these results.

Sopalun et al. (2021) evaluated 37 isolates for extracellular enzyme production potential and observed high lipase production, followed by cellulose, protease, and pectinase. The enzyme production capacity of the isolates is not uniform; some produce one enzyme in significant amounts than another. This can be seen from Sopalun et al. (2021), where one isolate had important lipase enzyme activity based on extracellular enzyme production ratio values while another had the highest lipase activity. Differences in the type and the enzyme level necessitate screening a range of isolates, improving the chances of finding the best enzyme producer. *Aspergillus Niger*, isolated from mangroves, synthesizes alkaline xylanase, with high xylanase activity and the ability to bleach sugarcane bagasse in short periods in relatively low temperatures (Raghukumar et al. 2004)

The unique ecological conditions of mangrove ecosystems provide an ideal habitat for producing bioactive compounds by fungi. Based on this reported information, it can be seen that a lot is yet to be done in African mangrove fungi to explore their bioactive compounds to their full potential. Therefore, further exploration of the mangrove fungal diversity in Africa could offer valuable insights into the bioactive potential of indigenous fungal species and contribute to the discovery of novel therapeutic agents. This will potentially revolutionize and influence many industrial advancements.

Anthropogenic threats to the mangrove ecosystem and opportunities for their conservation for sustainable exploitations.

Mangroves receive increasing global attention due to their ecological importance and crucial environmental role. They provide a protective shield for the coastlines against environmental catastrophes, constituting a vital entity for the well-being of coastal ecosystems. In addition, they have significant economic importance as they harbor microorganisms such as endophytic fungi, which have much significance. Despite the vast potential the mangrove ecosystem offers, it remains vulnerable to various threats. It is imperative to highlight the fundamental forces leading to mangrove losses at global and local levels.

Estimates of the current rate of mangrove decline are 2–8% loss per year (Chowdhury et al. 2017). Dynamic forces drive global mangrove losses, which vary dramatically across regional and local contexts. Death of these trees related to microorganisms such as fungi (Osorio et al. 2014), pollutants, oil spills, and mangrove-dependent subsistence economies, i.e., anthropogenic activities (Figure 1) deforestation and land reclamation (Teka et al. 2019), act as significant drivers of mangrove loss.

With about 40% of the world's population inhabiting coastal zones (Chowdhury et al. 2017), anthropogenic activities in these ecosystems are apparent. These populations rely mainly on coastal and marine ecosystems for food, fishing, and other economic activities. As this population increases, the risk of inflicting devastating changes to these coastal and marine ecosystems is becoming very apparent. However, it should be noted that an increase in population can come with potential benefits, such as an increase in local economies and participation in biodiversity conservation (Alongi 2002). Hence it is imperative to put in place systems that will continuously evaluate this ecosystem's status.

Development and management plans should be implemented for these mangroves' current and future sustainable use. Implications for mangrove health, diversity, and value arising from pollution, over-harvesting, and other coastal development should be communicated to the local communities in direct contact with these communities, i.e., participatory approaches (Teka et al. 2019). Information should be publicly available for all stakeholders, including managerial bodies, to enable priority setting and the development of clear policies and guidelines.



Fig. 1 – Human activity has become a significant challenge to mangrove conservation. (a and b) Charcoal production and firewood collection inside mangrove forest;(c) Feeding livestock inside the mangrove conservation area. (Photo by first author 2022 along Indian Ocean, Tanzania)

Conclusions and prospects

African mangrove holds a great diversity of marine fungi yet to be explored. Bioactive compounds from mangrove fungi can be used in medicine, pharmaceutical, bioprospecting, and bioremediation. Furthermore, some of these fungi can withstand extreme environments making them more potential for unique bioactive compound production. A better understanding of the enormous diversity harboring beneficial bioactive compounds is crucial as they remain undervalued. Mangrove ecosystems are reported to be at risk worldwide due to natural phenomena and anthropogenic activities. Some mangrove fungi are used for medicinal purposes and are overexploited. Established mangrove fungal metabolites of therapeutic importance will add value and eventually enhance the conservation of the mangroves. More studies on African mangrove fungi should be done, including modern techniques such as omics-based studies enabling uncover of none cultivable fungi with other conventional methods. This will enhance the comprehensive survey of mangrove fungal diversity from Africa.

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