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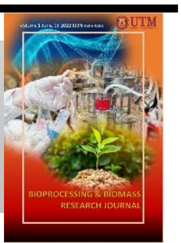

Research Article

Fungi as Agents of Hydrocarbon Biodegradation: A Review

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ABSTRACT

Despite the widespread reliance of petroleum-derived products in various industries, there is a significant environmental pollution issue arising from the improper disposal of oil products into the ecosystem. The toxicity, mutagenicity and carcinogenicity of petroleum hydrocarbons (PHs) and polycyclic aromatic hydrocarbons (PAHs) lead to threatening effects when they are introduced into the soil and aquatic ecosystems. As these hydrocarbon compounds resist natural degradation processes and will accumulate in biological systems, hence a sustainable and cost-effective solution needs to be approached. Recently, microbial bioremediation has gained recognition as an environmentally sustainable and cost-effective alternative to conventional remediation techniques such as incineration, excavation and chemical oxidation, which are often costly and ecologically disruptive. Microorganisms, particularly bacteria and fungi, have proven their degradation capability through their metabolic capacity to degrade PHs and PAHs into less harmful compounds. However, bacterial degradation systems are well explored, while fungal degradation remains underexplored in bioremediation research and field practice. This review discussed the fungi which are capable of degrading hydrocarbons related pollutants and recent research carried out related to the oil degradation fungi.

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INTRODUCTION

Environmental pollution caused by petroleum-derived products remains a critical global concern due to their extensive use in industrial and energy sectors (Chuah et al., 2023). Among these pollutants, used engine oil (UEO) represents a particularly hazardous waste as it contains complex mixture of petroleum hydrocarbons (PHs) and polycyclic aromatic hydrocarbons (PAHs), heavy metals, and engine-combustion derived by-products (Armioni et al., 2024). These contaminants are characterized by high hydrophobicity and persistence for degradation, which enables their accumulation in natural environment and posing significant risks to ecological systems, including human health (Premnath et al., 2021).

PHs consists of a broad class of organic compounds including saturated hydrocarbons (alkanes), aromatic hydrocarbons, resins, and asphaltenes with distinct chemical and physical properties (Wante et al., 2021). In particular, PAHs are highly recalcitrant due to their fused aromatic ring structures, low solubility, and strong bioaccumulation capabilities. These properties lead to a carcinogenic and mutagenic effects (Patel et al., 2020). Their

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persistence in the contaminated environments necessitates the development of efficient and sustainable remediation strategies.

Conventional remediation technologies, such as soil excavation, incineration, chemical oxidation, and thermal desorption are effective but often expensive, disruptive, energy-intensive and may produce secondary pollutants (Premnath et al., 2021). In contrast, bioremediation offers more reliable and sustainable alternative mechanism by utilizing microbial metabolic capabilities to convert complex hydrocarbons into simpler and less harmful substances (Suhaimi et al., 2021; Sayyed et al., 2020). Yet, the efficiency of microbial degradation is influenced by environmental factor including availability of nutrients surrounding temperatures as well as pollutants' bioavailability (Zhang et al., 2024). Most of the bacterial systems are limited by harsh and nutrient-deficient conditions (Dailin et al., 2020). Some microbes able to produced exopolysaccharides acting as a biodegradable biosorbent (Dailin et al., 2022).

Fungi have emerged as promising bioremediation agent for hydrocarbon pollutants due to their versatile metabolic capacities and abilities to secrete various oxidative enzymes extracellularly such as laccases and peroxidases (Sukmawati et al., 2020; Kadri et al., 2017). Their unique mycelial structure allows them to penetrate more deeply into the contaminated soil, enhanced interaction with hydrophobic pollutants, supporting degradation through enzymatic and biosorptive mechanisms (Kaur et al., 2024; Dinakarkumar et al. 2024). Several fungal species have demonstrated greater tolerance towards the acidic and nutrient poor conditions besides also less susceptible to heavy metal toxicity than many bacterial strains (Benguenab & Chibani, 2021; El Enshasy et al., 2018).

Despite the notable advancements, fungal-mediated degradation approaches for petroleum hydrocarbon pollutants, remains insufficiently understood and underutilized in practical applications. Reported degradation efficiencies show wide variations with limited mechanistic insights and lack of standardized methods for field scale application (Ghosal et al., 2016; Kadri et al., 2017). Therefore, this review aims to critically evaluate the role of fungi in the biodegradation of petroleum hydrocarbon pollutants, with particular emphasis on used engine oil contaminants. It synthesizes current knowledge on fungal degradation mechanisms, examines key fungal species and identifies factors influencing biodegradation efficiency.

HYDROCARBON CONTAMINANTS IN USED ENGINE OIL (UEO)

Chemical Composition and Environmental Impacts of UEO

Used engine oil (UEO) is a hazardous by-product generated during the operation of automotive and industrial machinery sectors. UEO is resulted from the physiochemical degradation of lubricating oil under high temperature and pressure conditions during engine operation. The lubricating oil undergoes oxidation, thermal breakdown, and further contaminated with combustion-derived residues that leads to the formation of a complex mixture of contaminants (Armioni et al., 2024). Consequently, the transformation of fresh oil into UEO leads to accumulation of various hazardous contaminants includes degraded base oil, heavy metals, PHs, and PAHs, which many of these exhibit high persistent and toxicity to the environment (Ratiu et al., 2022).

The composition and formation pathways of major UEO contaminants are summarized in **Table 1** which highlights the origin of the key pollutant groups. Fresh engine oil is primarily made up of petroleum-based oil, either mineral, synthetic or semi-synthetic and a wide range of performance-enhancing additives such as detergents, dispersants, antioxidants and anti-wear agents (Armioni et al., 2024). Upon the engine operations, the fresh engine oil were converted into UEO which contains a complex mixture of degraded base oils and contaminants. This complexity reflects the dynamic transformation of lubricating oil during engine operation and explains the increasing toxicity of UEO over the time. In particular, the enrichment of PAHs during usage is strongly associated with soot incorporation, unburned fuel residues, and thermally degraded additives resulting in compounds that are highly hydrophobic and resistant to natural degradation (Armioni et al., 2024).

Table 1 The type of contaminants and their formation pathways

Type of contaminants	Formation
Heavy metals (e.g.: Lead, Cadmium, Arsenic)	Originated from engine wear and additive breakdown.
Polycyclic aromatic hydrocarbons (PAHs)	Incomplete fuel combustion and thermal degradation of the lubricants.
Nitrogen oxides (NOx)	Reactions with nitrogen and sulfur compounds in the oil.
Sulfur oxides (SOx)	Prolonged exposure to high temperatures operating conditions.
Oxidation products	Incomplete combustion of fuels.

Upon release into natural environments, UEO contaminants demonstrate intense physicochemical interactions with soil and aquatic matrices, due to their non-polar and lipophilic characteristics. The hydrophobic PHs and PAHs in UEO, exhibit strong sorption capacity on soil organic matters and mineral surfaces (Ossai et al., 2020). Studies reported that sorption capacities of these pollutants, which with distribution coefficients (Kd) often exceeding 104 L per kg for high molecular weight PAHs (Armioni et al., 2024). This partitioning markedly reduces aqueous phase mobility and bioavailability, while promoting long-term sequestration and toxicity to terrestrial and aquatic ecosystems. Consequently, UEO also alters the microbial community structure and function which leads to inhibition of key remediation consortia (Ullah et al., 2025). Recent reviews summarize that persistent pollutants in soil environments alter taxonomic and functional shifts in the microbial communities. These pollutants also disrupt geochemical nutrient cycles by microorganisms such as nitrogen and phosphorus transformations, which in turn erode soil fertility, plant productivity and overall ecosystem stability (Hayat et al., 2025). In lentic and lotic aquatic systems, UEO may accumulate at the air-water interface, forming persistent surface microlayers that suppress gas exchange rates, reduce dissolved oxygen availability and contribute to hypoxic conditions that adversely affect aquatic systems. This ultimately cascading through food webs to impair the biodiversity and ecosystems (Adipah, 2018).

In parallel, UEO also poses acute and chronic risks to human health due to its repertoire of toxicants, notably PAHs benzo[a]pyrene and chrysene. These pollutants undergo trophic magnification through bioaccumulation and biomagnification in terrestrial and aquatic food chains (Abdel-Shafy & Mansour, 2016). Airborne emissions resulting from volatilization or improper combustion further contribute to atmospheric pollution and respiratory hazards (Rațiu et al., 2022).

Despite the use of existing management strategies, including the recycling of UEO for industrial applications, such practices may introduce secondary environmental risks under improper regulations (Ratiu et al., 2022). In addition, the complex composition of the UEO-derived contaminants limits the effectiveness of conventional remediation approaches. The co-existence of high-molecular-weight hydrocarbons and heavy metals poses a significant challenge, including low aqueous solubility, reducing the substrate bioavailability, high chemical persistence, and severe toxicity that inhibits indigenous microbial activity. Current knowledge remains fragmented and limited with comparison studies between cross-contaminants as well as scarce the integration of microbial taxonomy and functional data (Hayat et al., 2025; Ullah et al., 2025). These limitations underscore the need for alternative biological remediation strategies. To further understand the persistence and degradation challenges associated with UEO, it is important to examine the classification and environmental behaviours of its major constituents particularly PHs and PAHs.

Composition, Classification, and Environmental Behaviours of PHs and PAHs

The PHs mainly consists of hydrogen and carbon atoms arranged in varying structural forms. They can be categorised into aliphatic and aromatic fractions with varying structural complexity and environmental behaviour (Sharma et al., 2024). Their classifications include alkanes, alkenes, cycloalkanes, and aromatic hydrocarbons where each components exhibit district physiochemical properties that influence their degradability and persistence. In complements to this, **Table 2** summarizes the characterization of these hydrocarbon classes as well as highlighting the relationship between molecular structure and environmental fate.

Aliphatic hydrocarbons, particularly short chain, alkanes, are relatively less toxic and more susceptible for microbial degradation due their simpler structures. Alkenes are the unsaturated hydrocarbons with double bonds, showing a greater reactivity and prone to oxidation (Sharma et al., 2023; Ossai et al., 2020). In contrast, the branched and long-chain aliphatic exhibit greater resistance for degradation. Meanwhile, the complex aromatic hydrocarbons especially PAHs are significantly more persistent in the environment. This is due to their stable ring structures and low solubility (Al-Hawash et al., 2018). Their structural complexity greatly influences the efficiency of their degradation process and accounts for their persistence in the environment.

The PAHs are major subgroup of PHs, are formed primarily through incomplete combustion of organic materials and are commonly detected in soil, sediments, and water bodies (Baskaran & Byan, 2024). PAHs can be categorized into two classes, low molecular weight (LMW) PAHs such as naphthalene and phenanthrene with two to three aromatic rings, and high molecular weight (HMW) PAHs, such as benzo[a]pyrene and indeno[1,2,3-cd]pyrene which generally having four and above aromatic rings.

Table 2 Petroleum hydrocarbon classes and characteristics (Ossai et al., 2020)

Hydrocarbons	Characteristics	Examples
Aliphatics • Alkanes • Alkenes • Alkenes	• Less dense than water • Molecule size is inversely proportional to its volatility and water solubility	Methane, propane, butane (gas at room temperature); hexane, octane hexadecane (liquid at room temperature); eicosane, triacontane, pentacontane (solid at room temperature
Cycloaliphatics • Cycloalkanes	• Contains up to six carbon atoms in a ring • Fairly resistant to microbial degradation	Cyclohexane, methyl cyclohexane, methylcyclopentane, 1,2-dimethylcyclopentane
Aromatics • Monoaromatics BTEX • PAH	• Very volatile and relatively water-soluble • Have benzene ring • Some are resistant to microbial degradation	Benzene, ethylbenzene, naphthalene, toluene, xylene and phenanthrene
Other components • Asphaltenes • Waxes and tar • Resins • Non hydrocarbon compounds	• Soluble in aromatics and non-soluble in light alkanes • Contains about 18 to 65 carbon atoms	Phenols, fatty acids, ketones, esters, porphyrins, pyridines, quinolines, cardaxoles, sulphonates

The LMW have higher volatility and solubility compared to HMW, resulting in greater bioavailability and facilitating passive transport across microbial cell membranes. Consequently, LMW PAHs are typically degraded more rapidly by microorganisms. Meanwhile, the HMW possess greater structural complexity, hydrophobicity, and lower aqueous solubility, which limit enzymatic accessibility and microbial uptake, leading to increased environmental persistence and toxicity (Gundlapalli et al., 2024). Their hydrophobicity and affinity towards organic matter promotes adsorption onto soil particles, reducing bioavailability and limiting microbial access (Ossai et al., 2020).

In terms of environmental behaviours and remediation pathways of PHs, the biological approaches, especially bioremediation strategies, have gained increasing attention due to their sustainability and cost-effectiveness. However, the efficiency of the processes is strongly influenced by the structure of hydrocarbons, environmental conditions, and microbial carabiniers.

The presence of PHs and PAHs in the environment possess significant risks soil health, aquatic ecosystems, and human well-being. In soil systems, these contaminants reduce the microbial diversity, impair root development, and lower the soil fertility. This is due to their high hydrophobicity properties and affinity to organic matter. They will tend to adsorb to the soil particles and bind strongly, hence interfering with the nutrient cycle in the soil community (Ossai et al., 2020). Beyond the ecological impacts, long term exposure to PHs and PAHs contaminants also associated with a wide range of toxicological effects in human and animals, including carcinogenicity, genotoxicity, teratogenicity, and neurotoxicity (Ossai et al., 2020). These biotoxicity effects refers to the ability of PHs and PAHs contaminants to accumulate and interact with the biological system, at molecular levels (Patel et al., 2020). For instance, naphthalene has been proven to cause the breakdown of red blood cells and benzo[a]pyrene will cause skin irritations in animals and humans if exposed to high levels of PAHs (Patel et al., 2020). In addition, similar study also reported that phototoxicity may occurs due to formation of reactive intermediates when PAHs absorb ultra violet radiations. Genotoxicity of PAHs occurs when these reactive intermediates capable of damaging cellular genetic contents (Patel et al., 2020).

The persistence and limited bioavailability of PHs and PAHs necessitate the application of effective remediation strategies. The remediation approaches can be broadly categorized into containment, separation and destruction methods. They often associated with high costs, energy consumptions, and the risk of secondary pollutions (Ossai et al., 2020). In contrast, biological treatments to degrade these contaminants has raised a high attention as it offers a more sustainable, environmental friendly and cost effective alternative, compared to other physicochemical strategies such as soil excavation, incineration and chemical treatments. There are several biological treatment methods such as bioremediation, bio attenuation, and bioaugmentation has been exploited by utilizing microbial metabolism to degrade hydrocarbon pollutants into less harmful products (Ossai et al., 2020).

However, the efficiency of the microbial degradation is strongly influenced by the hydrocarbon structures and environmental conditions. In particular, the bacterial systems are often effective in degrading simple aliphatic hydrocarbons but show limited efficiency towards complex aromatic compounds such as HMW PAHs under nutrient-limited or environmentally-stressed conditions (& Adebayo, 2022). This limitation highlights a critical gap in current remediation strategies. Alao Consequently, there are increasing interest in alternative biological systems capable of overcoming these limitations. Fungal mediated biodegradation has emerged as a promising approach due to the ability of fungi to produce extracellular oxidative enzymes that can degrade structurally complex hydrocarbons, including recalcitrant PAHs. This positions fungi as key agents in advancing sustainable remediation strategies for hydrocarbon contaminated environments. Building on these challenges, the following section of this study reviews microbial bioremediation strategies, with particular emphasis on the mechanisms and limitations bacterial systems and the emerging role of fungi in hydrocarbon degradations.

MICROBIAL BIOREMEDIATION OF HYDROCARBONS: PRINCIPLES AND INFLUENCING FACTORS

Principles and Influencing Factors of Microbial Biodegradation

Bioremediation is a sustainable approach that utilizes microorganisms to degrade hydrocarbon pollutants into innocuous end-products such as carbon dioxide, water and biomass. Bioremediation strategies provide more sustainable, low-cost alternative to energy-intensive physiochemical methods such as incineration or soil washing (Karishma et al., 2024). Microbial degradation of hydrocarbons relies on their enzymatic processes and metabolic capabilities that can transform complex organic compounds into simpler intermediates, ultimately leading to mineralization. Microbial enzymes cascades oxidation of carbon-hydrogen bonding in the hydrocarbons, progressively yielding alcohols, aldehydes, carboxylic acids and proto-catechol for ring fission and eventual mineralization via Krebs cycle integration (Ławniczak et al., 2020; Xu et al., 2018).

Aerobic degradation predominates most of the microbial degradation of hydrocarbon pollutants. Oxygen utilized as substrate by oxygenises (mono- and dioxygenases) and peroxidases—that initiate oxidation, transforming complex structures into simpler intermediates, ultimately leading to mineralization (Karishma et al., 2024). Studies demonstrated that microbial dioxygenases such as naphthalene dioxygenase cleave aromatic rings of PAHs via cis-dihydrodiols achieving faster rates than anaerobic alternative reliant on fumarate addition or carboxylation strategies (Gundlapalli et al., 2024). Although slower than aerobic process, anaerobic degradation plays crucial role in oxygen-depleted environments like saturated soil, aquifers and marine sediments contaminated with PHs (Matturro et al., 2026; Bonifacio et al., 2023; Vigneron et al., 2021).

Under anoxic conditions, specialized syntrophic consortia which is typically composed of fermentative bacteria such as, *Syntrophus, Clostridium* spp.; sulfate-reducers such as *Desulfovibrio*; iron-reducers such as *Geobacter*; nitrate-reducers like *Thauera*; or methanogens like *Methanosaeta* (Matturro et al., 2026; Bonifacio et al., 2023; Vigneron et al., 2021). These consortia capable of activating inert alkanes and aromatics via fumarate addition, where benzylsuccinate synthase methylates toluene's methyl group to form a succinate adduct for β-oxidation. Aromatic rings of PAHs pollutants undergo carboxylation such as benzoyl-CoA pathway central to PAHs like naphthalene or undergo methyl group methylation. Anaerobic niches yielding carbon dioxide, methane, or acetate through degradation. Studies demonstrated that nitrate-dependent toluene degradation could reaches 50-70% efficiency in lab microcosms (Obuekwe & Al-Jadi, 2022). While less effective for HMW PAHs due to thermodynamic barriers, anaerobic pathways complement aerobic bioremediation in layered spills, sustaining long-term attenuation where O_2 diffusion fails.

In bioremediation, efficiency of microbial degradation hinges on environmental and physicochemical factors (Adedeji et al., 2022). Temperature can modulate the oil viscosity, volatility, and microbial physiology. In soil environments, peak degradation occurs at 30 – 40 ℃, meanwhile for water bodies varies as for freshwater at 20 – 30 ℃ and marine sediments at 15 – 20 ℃ (Obuekwe & Al-Jadi, 2022). Lower temperatures like below 10 ℃ increases oil viscosity which eventually reducing bioavailability and leads to slower enzymatic kinetics. In contrast, elevated temperatures especially above 40 ℃, volatizes LMW PHs fractions and disrupts the microbial consortia (Matturro et al., 2026; Bonifacio et al., 2023; Vigneron et al., 2021). Although temperature shows greater impacts on microbial degradation, studies reported enrichment of thermophile consortia in the elevated temperature niches and enrichment of psychrotolerant strains to sustain remediation activity in polar spills (Naranjo-Moran et al., 2026).

Emerging strategies for enhancing microbial degradation of petroleum hydrocarbons such as, bioaugmentation and biostimulation have been widely explored. Bioaugmentation involves the introduction of a specific microbial strains or consortia with high degradation potential to the polluted area (Ajona & Vasanthi, 2021; Alao & Adebayo, 2022; Pawan Baghmare et al., 2024). This could effectively enhance the bioremediation of hydrocarbons into less toxic compounds such as carbon dioxide and oxygen. Meanwhile, biostimulation is a strategy that amending limiting environmental factors, which eventually enhances indigenous microbial degradation in polluted areas (Alao & Adebayo, 2022; Karishma et al., 2024; Ajona & Vasanthi, 2021). Essential macronutrients such as carbon (C) nitrogen (N) and phosphorus (P) were supplemented to restore optimal C:N:P ratios, electron acceptors, and biosurfactants (Pawan Baghmare et al., 2024). Nutrient limitations remain the primary bottleneck in field bioremediation. Thus, site-specific biostimulation, a technique to accelerate the degradation of pollutants by adding limiting nutrients, electron acceptors, or carbon sources to native microbial communities, could precisely address rate-limiting microbial remediations (Alao & Adebayo, 2022; Pawan Baghmare et al., 2024).

Biodegradation of PHs and PAHs is a complex but essential process for environmental cleanup. While natural microbial communities are effective, optimizing bioremediation will require deeper studies of microbial ecology, genetics and field-scale applications. Interdisciplinary strategies such as nano-bioremediation and electrokinetics, bioremediation should be implemented to mitigate the hydrocarbon pollution (Sharma et al., 2023). Nano-bioremediation utilizes engineered nanoparticles to increase pollutant bioavailability and stimulate microbial degradation (Gupta et al., 2024), while electrokinetics applies low-level electrical currents to improve the transport of nutrients and microbes in low-permeability soils (Porcino et al., 2024). While microbial biodegradation provides an effective framework of hydrocarbon removal, the efficiency of degradation varies significantly on the type of the microorganisms employed and the structural complexity of the pollutants. In particular, simpler hydrocarbons are more readily degraded whereas complex PAHs persists in environment due to microbial accessibility and enzymatic capabilities. These variations highlight the importance of selecting appropriate microbial systems for the effective remediation. Therefore, the following section focusses on bacterial degradation system with emphasis on their mechanism and inherent limitations as a basis for exploring alternative biological approaches.

Bacterial Remediation: Mechanisms and Limitations

Bacteria serve as primary agents utilized in bioremediation of hydrocarbons due to their high metabolic capabilities, rapid proliferation and ability to utilize wide range of hydrocarbons as sole sources of carbon and energy sources (Alao & Adebayo, 2022; Hamouda et al., 2022). Bacterial groups often employ a number of intracellular enzymatic systems, especially oxygenases, to catabolize aliphatic and simple aromatic PHs (Zhang et al., 2024; Ansari et al., 2023; Ghosal et al., 2016). These intracellular pathways typically involve terminal hydroxylation followed by beta-oxidation or ring-cleavage through ortho- or meta-pathways, which will yield central intermediates like acetyl-CoA for mineralization (Obuekwe & Al-Jadi, 2022; Ławniczak et al., 2020). To overcome the low aqueous solubility of PHs, many bacterial species capable of secreting rhamnolipid or trehalolipid biosurfactants, to lower the surface tension and promote oil emulsification. This effectively increasing the bioavailability of organic pollutants for internal enzymatic breakdown (Wei et al., 2026). Furthermore, bacterial consortia often outperform than monocultures as the mix cultures utilize synergistic interactions for sequential or simultaneous breakdown of complex hydrocarbon mixtures (Zhang et al., 2024; Ansari et al., 2023; Hamouda et al., 2022).

Bacterial genera that are frequently isolated from hydrocarbon contaminated sites degrading potential include *Pseudomonas* (Varjani & Upasani, 2016), *Acinetobacter* (Li et al., 2025), *Alcanivorax* (Dong et al., 2024), *Bacillus* (Shokranian et al., 2025), *Rhodococcus* (Wei et al., 2026), and *Actinomycetes* (Parejiya et al., 2026). Certain bacterial groups play a specialized and dominant role in oxygen limited oil-spill remediation, particularly in marine sites (Alao & Adebayo, 2022). The obligate hydrocarbonoclastic bacteria (OHCBs) such as *Alcanivorax borkumensis* and *Thalassolituus oleivorans*, are typically present in low abundance in pristine ecosystems but bloom rapidly upon oil exposure. This property contributes significantly to the attenuation of organic pollutants, hence able to be degraded (Sharma et al., 2026; Hayat et al., 2025; Ansari et al., 2023; Ghosal et al., 2016).

In addition, recent studies highlight significant degradation efficiencies for various potent isolates under optimized laboratory conditions. For instance, the novel strain *Enterobacter kobei* DH7 has demonstrated an 84.6% degradation potential for petroleum hydrocarbons (Nawaz et al., 2023), while an *Alcaligenes* sp. has achieved an even higher efficiency of 92.5% (Ishaya et al., 2023). Furthermore, specific remediation targets like the high-molecular-weight PAH benzo[a]pyrene have been successfully addressed by *Stutzerimonas stutzeri* strain LOBP-19A, which exhibited an 87.95% degradation potential (Kumari & Chandra, 2023). These findings underscore the critical contribution of both specialized hydrocarbonoclastic populations and surfactant-producing isolates to the effective attenuation of hydrocarbon contamination (Zhang et al., 2024; Ansari et al., 2023). Despite their efficiency with low-molecular-weight aliphatic PHs, the bacterial degradation systems face significant, multi-faceted limitations that frequently impede field-scale remediation efforts. A primary metabolic bottleneck is their inability to efficiently degrade high-molecular-weight PAHs. Bacterial catabolic system relies mostly on specific intracellular enzymatic complexes, specifically monooxygenases and dioxygenases which initiate the degradation of various organic contaminants. Most of bacterial strains lack of extracellular and non-specific oxidative enzymes that able to "attack" the sterically hindered, multi-ring aromatic structures found in weathered used engine oil (Hadibarata & Hadibarata, 2025). Bacterial systems are restricted to the uptake of smaller, more soluble molecules, rendering them largely ineffective against the most recalcitrant, complex fractions of petroleum (Hadibarata & Hadibarata, 2025; Zhang et al., 2024).

Furthermore, bacterial degradation system is frequently plagued by extreme sensitivity to the environmental stress and toxicity at polluted sites. Many potent hydrocarbon-degrading strains often reported with sensitive to extreme salinity, pH or presence of co-contaminants like heavy metals. During degradation process, the metabolic intermediates produced are toxic as these intermediates accumulates in the cell or in the external environment where it can inhibit bacterial respiration process and growth (Alao & Adebayo, 2022). Additionally, most of the bacterial candidates are structurally limited by their unicellular nature which prevents them from actively penetrating the complex or compacted soil environments (Gundlapalli et al., 2024). Bacterial degradation of oil-contaminated soil is largely confined to the surface or the outer edges of soil particles. Degrading bacteria unable to reach pollutants which trapped within the internal mineral pores or bound tightly to clay particles in the contaminated soil. Consequently, bacterial remediation is only effective at the easily accessible contact points on the surface, potentially could leave a substantial number of sequestered pollutants untreated deep within the soil matrix (Gundlapalli et al., 2024; Karishma et al., 2024; Ansari et al., 2023; Ajona & Vasanthi, 2021).

Moreover, ecological pressures also severely impact the effectiveness of bacterial remediation, as the field conditions are more robust and challenging (Karishma et al., 2024). One of the failures in bioaugmentation strategies would be the aggressive resource competition encountered by introduced bacterial strains, from the native and indigenous microflora which are mostly non-degrading type but well adapted to the site's environmental, nutritional, and also mineral conditions (Hamouda et al., 2022). This competition further worsened by protozoa, which graze on the introduced bacteria, rapidly reducing the bacterial population before they can effectively degrade the pollutants (Hadibarata & Hadibarata, 2025).

Another biggest challenge in bacterial remediation will be the metabolic specialization of an individual strain against contaminant heterogeneity. Most of the bacterial degradation pathways are often highly substrate-specific, meaning that the proposed candidate may efficiently degrade one fraction of the pollutant while other fractions of the pollutants are not degraded (Hamouda et al., 2022). They lack of the metabolic versatility needed for cleaning up complex mixtures. With the current advancement, microbial engineering could be employed to address this. Yet, a balanced groups are incredibly difficult to maintain at unpredictable changes in environmental conditions and shifting of contaminations (Ansari et al., 2023).

As discussed above, bacterial remediation strategies are frequently hindered by a varies factors including metabolic, environmental, and ecological constraints that limit their success in field applications. These inherent challenges underscore the necessity of identifying more resilient and versatile biological agents capable of overcoming the limitation of bacterial remediation strategies.

FUNGAL-MEDIATED HYDROCARBON DEGRADATION (MYCOREMEDIATION)

Mycoremediation is a form of bioremediation that utilised a specific fungal strain to degrade, transform ore remove environmental pollutants. Fungi are capable of breaking down a wide range of complex organic compounds through the secretion of extracellular enzymes and the production of diverse metabolic intermediates. Consequently, mycroremediation has emerged as a transformative strategy for addressing complex and persistent organic pollutants, including PHs and PAHs (Kaur et al., 2024; Akhtar & Mannan, 2020). Unlike bacterial candidates, which may be limited by the structural complexity of pollutants and low bioavailability of certain contaminants, fungi possess a unique biological characteristic that enables them to thrive in challenging environments and degrade complex organic molecules (Dinakarkumar et al., 2024; Pawan Baghmare et al., 2024). Their superior remediation capability is attributed to a combination of metabolic versatility, resilience to environmental stress, and specialised extracellular enzyme systems (Kaur et al., 2024; Roy et al., 2025). These attributes allow various fungal strains to overcome the bioavailability barriers that frequently limit the bacterial remediators. As a result, mycoremediation is a critical component in the next generation of sustainable, site-specific bioremediation technologies (Roy et al., 2025; Akhtar & Mannan, 2020).

Mechanisms of Fungal Remediation

Unlike bacterial degradation which often rely on intracellular degradation pathways, unparalleled ability of fungi to mineralize recalcitrant hydrocarbons is fundamentally rooted in their aggressive enzymatic reactions and mechanical substrate colonization. These two prolonged degradation approaches allow fungi to function not merely as biochemical reactors but also as an active, invasive remediation force that physically and chemically recondition the polluted environment (Dinakarkumar et al., 2024; Kaur et al., 2024; Roy et al., 2025; Akhtar & Mannan, 2020).

The fungal strategy functions as a highly coordinated interface between chemical modification and physical exploration. Unlike many bacterial strains that preferentially utilize readily available low-molecular-weight organic compounds, fungi can obtain nutrients from complex organic substrates through extracellular digestion. Fungi secrete a wide range of extracellular enzymes that depolymerize recalcitrant organic matter into smaller molecules, which are subsequently absorbed and metabolized by the fungal cells (Alao & Adebayo, 2022). The fungal cell walls composed of polysaccharides, lipids and amino acids facilitate the production of powerful oxidative enzymes such as laccases, peroxidases, proteases, and chitinases (Hadibarata & Yuniarto, 2020). This external digestive system breakdown massive and insoluble hydrocarbon molecules into smaller and more accessible fragments. These breakdowns then being absorbed into fine network of hyphae for further catabolic reactions by internal enzymes (Kaur et al., 2024; Hadibarata & Yuniarto, 2020; Kadri et al., 2017; Bonugli-Santos et al., 2015). Simultaneously, the mechanical growth of the hyphal and mycelial network also exerts physical pressure on soil aggregates, effectively cracking them open to create new pathways for flow of air, water and enzymes (Hamad et al., 2021; Dhar et al., 2014; Jawhari, 2014). This synergy is critical in extreme environmental sites where pollutants have become deeply locked within the soil dense mineral structure. Together with chemical degradation with structural expansion, fungi bypass the transport limitations that typically trap and neutralize bacterial efforts. Essentially, fungi transform the soil from an impenetrable storage zone into a porous, biologically active environment (Kaur et al., 2024; Hadibarata & Yuniarto, 2020). This holistic approach ensures that sequestered hydrocarbons which typically remain untouched for decades are continuously exposed, fragmented, and eventually mineralized.

Extracellular Enzymatic System

The core of fungal-mediated hydrocarbon degradation lies on the sophisticated extracellular enzymatic systems that operates independently and enables the transformation of structurally complex and recalcitrant organic pollutants. Filamentous fungi, particularly lignin-degrading species such as the white-rot fungus *Phanerochaete chrysosporium* and *Pleurotus* spp. are evolutionarily adapted to breakdown the lignin, which is a chemically complex, irregular and recalcitrant biopolymers that shares similar structure with complex hydrocarbon pollutants. To achieve this, lignin-degrading fungi secrete high-redox potential lignin-modifying enzymes (LMEs), such as laccases, lignin peroxidases (LiP), and manganese peroxidases (MnP), directly into their immediate surroundings (Kaur et al., 2024; Hadibarata & Yuniarto, 2020; Kadri et al., 2017; Bonugli-Santos et al., 2015). These oxidative enzymes are non-specific and catalyse free-radical mediated oxidation, generating highly reactive species that can attack the stable and fused aromatic rings of HMW PAHs. As the catabolic activity occurs extracellularly, this allows fungi to bypass the need for transporting insoluble and bulky pollutants across the cell membrane like bacterial agents (Kaur et al., 2024; Hadibarata & Yuniarto, 2020).

In addition to this extracellular oxidative activity, fungal degradation of hydrocarbons typically proceeds through a coordinated two-phase catabolic process. During the initial extracellular phase, lignin-modifying enzymes partially oxidize complex hydrocarbons, resulting in the formation of intermediate compounds such as quinones, alcohols, and organic acids. These intermediates are generally more polar and water-soluble, which enhances their bioavailability and facilitates subsequent uptake by fungal cells (Vaksmaa et al., 2023; Hamad et al., 2021). Once transported into the intracellular environment, these compounds undergo further enzymatic transformation through the action of intracellular enzymes, particularly cytochrome P450 monooxygenases, which catalyze additional oxidation and structural modification reactions (Roy et al., 2025; Pawan Baghmare et al., 2024; Roshandel et al., 2021; Ławniczak et al., 2020).

This sequential degradation pathway ultimately leads to the breakdown of complex hydrocarbons into simpler molecules that can be assimilated into central metabolic pathways, such as the tricarboxylic acid (TCA) cycle, thereby supporting fungal growth and energy production. By effectively decoupling the degradation process into an extracellular "pre-treatment" phase and an intracellular "mineralization" phase, fungi demonstrate remarkable metabolic versatility and adaptability. This dual-phase mechanism enables them to thrive in contaminated environments where the dominant carbon sources are structurally complex, hydrophobic, and potentially toxic, such as weathered petroleum hydrocarbons and used engine oil residues (Vaksmaa et al., 2023; Hamad et al., 2021).

Another advantage of these powerful oxidative systems is that most fungal strains used in bioremediation produce multiple types of degradative enzymes, rather than relying on a single enzyme for pollutant degradation. Breakdown of pollutants will be initiate in the extracellular phase where the LMEs combinations destabilize the aromatic structures to produce partially oxidized intermediates like quinones and organic acids. Subsequently, these water-soluble intermediates are actively transported into the cell, where they undergo further catabolic degradation mediated by intracellular oxygenases, including cytochrome P450 monooxygenases. This sequential breakdown ensures that even the most complex hydrocarbon contaminants are progressively dismantled into simpler forms of organic acids, which then can be safely channeled into their primary metabolic pathways, such as the Krebs cycle, to support fungal growth and energy production (Kaur et al., 2024; Vaksmaa et al., 2023; Hadibarata & Yuniarto, 2020). **Figure 1** illustrates the biodegradation pathway of PAHs fungi using the enzymatic system.

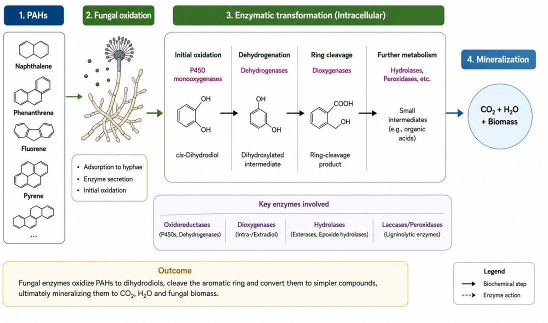

Figure 1 Biodegradation pathway of PAHs by fungi using the enzymatic system

Mycelial Colonization and Bioavailability Enhancement

Mycelial colonization provides fungal strains with a major physical advantage in bioremediation strategies, especially in hydrocarbon remediation (Hamad et al., 2021; Dhar et al., 2014; Jawhari, 2014). Their filamentous growth form, known as hyphae, allows them to move through soil in a way that single bacterial cells cannot. As hyphae extend, they can follow pores, cracks, and moisture pathways, and this root-like exploration allows them to reach pollutants trapped inside compacted aggregates or partially sealed soil zones. This ability is particularly important in contaminated sites because hydrocarbons are often heterogeneously distributed, where they may adsorb onto mineral surfaces, become embedded within organic matter, or accumulate in low-permeability pore spaces where diffusion is limited and bacterial access is restricted (Vaksmaa et al., 2023). Fungal mycelia also help restructure the soil itself by binding particles together, creating channels, and improving aeration and water movement, which can indirectly support contaminant weathering and the activity of other microbes. In this way, fungi do not only contact pollutants more effectively, but they also improve the physical conditions of the contaminated matrix, making the site more accessible for enzymatic attack and long-term biodegradation (Vaksmaa et al., 2023; Hamad et al., 2021).

Fungal growth also supports persistence in harsh environments. Even when nutrient levels are low, fungi can continue to extend their hyphae and search for new carbon sources. Their filamentous form allows them to survive under spatially heterogeneous conditions where nutrients and pollutants are unevenly distributed. This is important in contaminated soils because the pollutant may be concentrated in only a few zones (Rafin et al., 2023). By exploring the environment in multiple directions, fungi increase the probability of finding and degrading these isolated pollutant pockets. This exploratory behavior gives fungi a distinct advantage over microorganisms that depend on close and direct contact with accessible substrate. This structural advantage is further enhanced by fungal surface chemistry, especially the production of hydrophobins and other amphipathic compounds that help fungi attach to oil-water interfaces (Zhang et al., 2026). Hydrophobins reduce interfacial tension, so oil droplets disperse more readily and become easier for fungal hyphae and enzymes to access. That means fungi can "open up" hydrophobic pollutants that are otherwise difficult to emulsify in soil, increasing the contact area between the contaminant and the degrading biomass. Some fungi also release surfactant-like metabolites that complement this effect by increasing solubility and mobility of hydrocarbons within the contaminated zone. Combined with hyphal penetration, this makes fungal remediation especially effective for old, weathered, or deeply buried contamination where pollutants are no longer freely available at the surface (Rafiq & Baig, 2023; Silva et al., 2021).

Overall, mycelial colonization contributes to hydrocarbon bioremediation in both direct and indirect ways. Directly, it increases the physical reach of the fungus and improves access to buried pollutants. Indirectly, it enhances soil porosity, aeration, water movement, and pollutant dispersion. Together with hydrophobin production and surfactant-like activity, these features help fungi overcome the main limitation of hydrocarbon bioavailability. For this reason, fungal remediation is often more effective than bacterial remediation in deep, compacted, and weathered contaminated soils (Rafin et al., 2023; Rafiq & Baig, 2023; Silva et al., 2021).

Biosorption and Bioaccumulation

Finally, fungi contribute to hydrocarbon remediation through passive but highly effective sequestration processes known as biosorption and bioaccumulation (Claudia et al., 2025; Rafin et al., 2023). These mechanisms are important because they allow fungi to remove contaminants even before complete enzymatic degradation occurs. The fungal cell wall is composed of chitin, glucans, lipids, and proteins, and this structure contains many functional groups such as carboxyl, phosphate, sulfate, hydroxyl, and amine groups (Vaksmaa et al., 2023). These groups provide negatively and positively charged binding sites that can attract and retain hydrocarbon molecules, oil residues, and associated heavy metals from the surrounding environment (Kaur et al., 2024). As a result, fungi can reduce contaminant mobility and lower the immediate availability of pollutants in the contaminated matrix.

Biosorption occurs mainly at the surface of the fungal biomass and does not require active metabolism. This makes it especially useful in harsh environments where fungal growth may be slowed by low nutrients, high pollutant loads, or adverse physicochemical conditions. Because the contaminants are held on the cell wall surface, they remain in close contact with fungal enzymes, which increases the chance that they will later be oxidized and broken down. In this way, biosorption acts as an initial capture step that concentrates pollutants near the fungal biomass and improves the overall efficiency of degradation. It also helps reduce the toxicity of the surrounding soil or water by preventing free movement of hydrocarbons (Claudia et al., 2025).

In addition to surface adsorption, some fungi are capable of bioaccumulation, where smaller pollutant fragments enter the cell and are stored temporarily in vacuoles or lipid-rich compartments. This process helps protect the fungal cytoplasm from toxic interference and prevents reactive intermediates from damaging cellular structures. Bioaccumulation therefore serves as an internal detoxification mechanism that complements external biosorption. Together, these two processes allow fungi to function as both a passive filter and an active detoxification system. This is particularly valuable in long-term remediation of weathered oil-contaminated sites, where pollutants are strongly retained in soil and are not easily removed by bacterial systems alone (Pawan Baghmare et al., 2024; Vaksmaa et al., 2023; Hamad et al., 2021).

Overall, biosorption and bioaccumulation enhance the ability of fungi to reduce pollutant bioavailability, limit toxicity, and support gradual degradation over time. These mechanisms also improve the persistence of fungi in contaminated environments by allowing them to tolerate and manage exposure to hydrocarbons and co-contaminants. In this sense, fungal biomass acts not only as a degradative agent but also as a temporary sink that captures and stabilizes pollutants before their eventual transformation. This dual function makes fungi especially promising for the remediation of complex hydrocarbon-contaminated environments (Claudia et al., 2025).

Comparative Performance of Fungal Genera in Hydrocarbon Biodegradation

Mycoremediation has been widely recognized as an effective and sustainable approach for the remediation of hydrocarbon-contaminated soil and aquatic environments. Numerous fungal genera and species have been exploited with the metabolic versatility and adaptive capabilities to degrade PHs, PAHs, and total petroleum hydrocarbon contaminants. Most of these identified strains were coordinating remediation activity through extracellular enzymatic oxidation, mycelial colonization, biosorption, and intracellular detoxification mechanisms. **Table 3** summarizes the biodegradation performance of various fungal species reported for petroleum hydrocarbons, crude oil, used engine oil, and PAHs under different experimental conditions. The reported degradation efficiencies vary widely depending on pollutant type, hydrocarbon concentration, nutrient availability, environmental conditions, and fungal metabolic activity. Overall, fungal genera such as *Aspergillus, Penicillium, Pleurotus*, and other white-rot fungi consistently exhibit significant hydrocarbon degradation capabilities due to their ligninolytic enzyme systems and environmental adaptability.

Several studies have demonstrated the effectiveness of the fungal strains in degrading structurally complex hydrocarbon contaminants. Study by Daâssi et al. (2023) has reported several strains includes *Aspergillus* niger, *Tubingensis, Syncephalastrum sp.*, *Paecilomyces Formosus*, *Fusarium chlamydosporum* and *Coniochaeta sp.* were capable of degrading PAHs from contaminated soil. Similarly, the study of Roshandel et al. (2021) has observed an average TPH remediation efficiency at 55% after 30 days by white-rot fungi *Pleurotus florida*.

In addition, Sari et al. (2019) reported that *Aspergillus* sp. LBKURCC151 and *Penicillium* sp. LBKURCC153 achieved PAHs degradation efficiencies of 61% and 45%, respectively after 16 days of incubation. Besides, study by Benguenab and Chibani (2021) demonstrated that the two fungal isolates from UEO contaminated soil including, *Aspergillus ustus* and *Purpureocillium lilacinum*, have been proven their ability to degrade crude oil and diesel hydrocarbon contaminants.

Table 3 Mycoremediation of hydrocarbons using fungal strains

Fungal Strains	Pollutants	Biodegradation Efficiency (%)	References
Pycnoporus sanguineus	PAHs: Naphthalene Acenaphthene Fluorene Anthracene Pyrene	 12.0 7.0 17.6 15.6 4.4	Arun et al. (2008)
Coriolus versicolor	Naphthalene Acenaphthene Fluorene Anthracene Pyrene	27.4 2.0 23.0 22.4 42.0	
Pleurotus ostreatus	Naphthalene Acenaphthene Fluorene Anthracene Pyrene	29.4 20.6 20.6 19.0 32.0	
Fomitopsis palustris	Naphthalene Acenaphthene Fluorene Anthracene Pyrene	19.5 7.5 7.0 31.7 7.3	
Daedalea elegans	Naphthalene Acenaphthene Fluorene Anthracene Pyrene	35.8 5.9 5.9 2.4 26.1	
Aspergillus niger *P. documbens*	Crude oil	8.6 7.9	Nasrawi, (2012)
Aspergillus sp. *Candida spp.* *P. chrysogenum*	Engine oil	35.01 33.09 43.33 (within 30 days)	Umanu & Dodo, (2013)
Mixed fungal consortia *Aspergillus sp.* *Penicillium sp*	TPHs	up to 90 (28 days of incubation)	Jawhari (2014)
Penicillium sp.	Crude oil	55%	Dirisu et al. (2018)
Aspergillus sp. RFC-1	Crude oil Naphthalene Phenanthrene Pyrene	60.3 97.4 84.9 90.7	Al-Hawash et al. (2018)
Aspergillus sp. LBKURCC151 *Penicillium* sp. LBKURCC153	Crude oil	61 46	Sari et al. (2019)
Coriolopsis caperata	PAHs: Phenanthrene Anthracene Pyrene	All > 65	Hadibarata & Yuniarto (2020)
Fomes fomentarius	PAHs: Phenanthrene Anthracene Pyrene	All > 75	
Pluteus chysophaeus	PAHs: Phenanthrene Anthracene Pyrene	 95.6 85.2 89.5	
Aspergillus ustus	Crude oil Diesel Used engine oil	30.43 21.27 16.00	Benguenab & Chibani, (2021)
Purpureocillium lilacinum	Crude oil Diesel Used engine oil	44.55 27.66 14.39	
Pleurotus florida (P.Kumm)	Total petroleum hydrocarbons	55% (30 days)	Roshandel et al., (2021)
Aspergillus terrus isolate Shu1	Total petroleum hydrocarbons	Normal: 57 ± 2	Othman et al. (2022)
Aspergillus fumigatus isolate Shu2		Enhanced nutrients: 63 ± 2	
Purpureocillium lilacinum	TPHs Cycloalkanes n-alkanes aromatics iso-alkanes	15.3 100 21.2 15.1 14.5	Yang et al. (2023)
Penicillium chrysogenum	TPHs Cycloalkanes n-alkanes aromatics iso-alkanes	7.6 +82.6 (increase) -1.3 (degrade) +10.2 +11.9	
Aspergillus niger [MW699896] KBR 1	Petroleum hydrocarbons	22.68	Daâssi et al. (2023)
Tubingensis [MW699895] KB8		20.34	
Syncephalastrum sp. [MZ817958] KBR1-1		12.3	
Paecilomyces formosus [MW699897] KB4		29.32	
Fusarium chlamydosporum [MZ817957] KB2		13.54	
Coniochaeta sp. [MW699893] LB3		16.21	
Aspergillus tubingensis FA-KSU5	Wastewater: Petroleum Hydrocarbons	 90.80 - 98.58	Ameen et al. (2024)
	Soil: TPHs PAHs	 93.15 - 98.48 88.11 - 97.31	
Aspergillus niger FU-KSU69	Wastewater: Aromatic Hydrocarbons	 93.17 - 96.0	
	Soil: TPHs PAHs	 90.37 - 94.90 95.13 - 98.15	
Aspergillus spp. CA3(2) CB4(3) CB3(3) CA4(2) *Penicillium spp.* CB3(1) CA2(2)	Spent engine oil	 Day 15: 55 Day 15: 48 Day 15: 34.9 Day 15: 78.9 Day 15: 72.1 Day 15: 70	Victor Ekwebelem - et al. (2025)

Strain *A. ustus* able to degrade 30.43% of crude oil, 21.27% of diesel and 16.00% of UEO, meanwhile *P. lilacinium* able to degrade 44.55% of crude oil, 27.66% of diesel and 14.39% of UEO. These studies have extensively shown the hydrocarbon degradation potential of fungi under normal conditions or enhanced growth conditions.

Among numerous fungal genera reported, *Aspergillus* sp. strains have shown high efficiency in degrading PAHs such as 84.6% of naphthalene, 51.3% phenanthrene, and 55.1% of pyrene in controlled conditions (Al-Hawash et al., 2018). In engine oil contaminated media, degradation rates up to 78.9% within 15 days have been reported (Victor-Ekwebelem et al., 2025). Besides, their high tolerance towards harsh environments also supports their degradation capabilities. For example, according to the review of Bonugli-Santos et al. (2015), certain fungi species under the genera of *Aspergillus* sp. that are marine derived isolates are salt tolerant and able to withstand nutrient deficient contaminated areas.

Similar to *Aspergillus* spp., *Penicillium* species secrete a range of hydrocarbon degrading enzymes, including laccases, lipases, monooxygenase, peroxidase, and esterases. These enzymes allow the occurrence of oxidative cleavage of hydrocarbon chains and aromatic rings (Balaji et al., 2014). Study by Umanu and Dodo (2013) has demonstrated ability of *Penicillium chrysogenum* to degrade 43.33% of engine oil within 30 days which is comparatively higher than 35.01% of *Aspergillus* sp.. In addition, Victor-Ekwebelem et al., (2025 also reported that isolated *Penicillium* spp. strains able to degrade up to 72.1% of UEO within 15 days. To be noted, the mixed fungal culture with *Aspergillus* spp. and *Penicillium* spp. able to degrade hydrocarbons up to 90%. This suggested a synergistic interaction between mixed fungal actions (Ameen et al., 2024). Moreover, *Penicillium chrysogenum* are capable of producing high levels of laccase at 79 U/mL and lipase at 112 U/mL, showing strong enzymatic responses to hydrocarbon exposure (Balaji et al., 2014).

Analysis of **Table 3** further indicates that fungal biodegradation efficiency is strongly influenced by hydrocarbon composition, environmental conditions, incubation period, and fungal metabolic capability (Kaur et al., 2024). In general, low molecular weight hydrocarbons are more readily degraded due to their higher bioavailability, whereas high molecular weight PAHs exhibit greater resistance because of their hydrophobicity and fused aromatic ring structures (Ghosal et al., 2016). Nevertheless, fungi possessing strong ligninolytic enzyme systems, particularly white-rot fungi and filamentous genera such as *Aspergillus* and *Penicillium*, demonstrate enhanced degradation of recalcitrant hydrocarbons through extracellular oxidative mechanisms involving laccases, manganese peroxidases, lignin peroxidases, and cytochrome P450 monooxygenases (Kadri et al., 2017; Bonugli-Santos et al., 2015). Beyond enzymatic degradation, extensive mycelial growth and fungal biosorption mechanisms further improve pollutant accessibility and contaminant sequestration, thereby enhancing overall remediation efficiency.

In addition to species-specific enzymatic capability, environmental and operational factors significantly influence fungal degradation performance. Parameters such as nutrient availability, pH, temperature, aeration, moisture content, and pollutant concentration directly affect fungal growth and extracellular enzyme production (Atlas, 1981; Adedeji et al., 2022). Several studies summarized in **Table 3** reported improved degradation efficiencies following nutrient supplementation and optimized incubation conditions, indicating the importance of environmental regulation in maximizing fungal biodegradation potential. Mixed fungal consortia have also demonstrated superior degradation performance compared to single isolates due to synergistic metabolic interactions and broader enzymatic diversity. Jawhari (2014), for example, reported degradation efficiencies approaching 90% for petroleum hydrocarbons using mixed fungal cultures following extended incubation periods.

Collectively, the findings summarized in **Table 3** demonstrate that fungal-mediated biodegradation represents a highly promising strategy for the remediation of hydrocarbon-contaminated environments. The ability of fungi to combine extracellular enzymatic degradation, extensive substrate colonization, biosorption, and intracellular detoxification provides a significant ecological and functional advantage over many conventional microbial systems, particularly in the treatment of structurally complex and weathered petroleum contaminants. Furthermore, the broad adaptability of fungal species under environmentally stressed conditions highlights their potential for future large-scale and field-level bioremediation applications.

CONCLUSION AND FUTURE PERSPECTIVE

Fungal-mediated hydrocarbon biodegradation has emerged as a highly promising and sustainable approach for the remediation of petroleum hydrocarbon-contaminated environments, particularly those polluted with used engine oil, crude oil, and polycyclic aromatic hydrocarbons (PAHs). The findings discussed throughout this review demonstrate that fungi possess several unique ecological and biochemical advantages over many conventional microbial systems, including extensive mycelial colonization, extracellular oxidative enzyme production, biosorption capability, and intracellular detoxification mechanisms. These attributes enable fungi to effectively degrade structurally complex and recalcitrant hydrocarbon compounds that are often resistant to bacterial degradation. Genera such as *Aspergillus, Penicillium, Pleurotus, Trichoderma*, and other white-rot fungi consistently exhibit strong degradation performance under diverse environmental conditions, highlighting their broad applicability in hydrocarbon remediation. Furthermore, the ability of fungi to simultaneously reduce pollutant toxicity, improve contaminant bioavailability, and mineralize complex hydrocarbons underscores their significant potential as environmentally friendly bioremediation agents for contaminated soil and aquatic systems.

Despite these advantages, several limitations continue to restrict the large-scale implementation and long-term effectiveness of fungal-mediated remediation technologies. Variability in environmental conditions, pollutant composition, nutrient availability, and fungal strain performance can significantly influence degradation efficiency under field conditions. Therefore, future research should focus on developing integrated and optimized remediation strategies capable of improving fungal adaptation, enzymatic stability, and pollutant accessibility in complex contaminated environments. In particular, the application of mixed fungal consortia, fungal–bacterial synergistic systems, biosurfactant-assisted remediation, and immobilized fungal biomass represent promising strategies for enhancing degradation performance and environmental resilience. Advances in genomics, transcriptomics, proteomics, and metabolic engineering may further facilitate the identification and development of highly efficient fungal strains with enhanced hydrocarbon degradation capabilities. In addition, future studies should prioritize pilot-scale and field-scale investigations to evaluate the long-term ecological stability, scalability, and practical feasibility of fungal remediation systems under real environmental conditions. Collectively, the integration of advanced biotechnological approaches with fungal-based remediation strategies may significantly advance the development of sustainable, efficient, and economically viable solutions for the treatment of hydrocarbon-contaminated environments in the future.

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Conflicts of Interest

The author declares that there is no conflict of interest regarding the publication of this paper.

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