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Review

Advancing Eco-Sustainable Bioremediation for Hydrocarbon Contaminants: Challenges and Solutions

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Abstract: In an era of rising population density and industrialization, the environment confronts growing challenges. Soil, agricultural land, and water bodies are becoming increasingly polluted by petroleum waste and hydrocarbons. While hydrocarbons are naturally present in crude oil, refining processes compound the complexity and toxicity of hydrocarbons. This is particularly evident in polycyclic aromatic hydrocarbons (PAHs) found in the air and soil, known for their carcinogenic, mutagenic, and teratogenic properties. In response, biodegradation emerges as an eco-friendly, cost-effective solution, especially in petroleum-contaminated settings. Biodiverse microbial communities play a pivotal role in managing hydrocarbon contamination, contingent on location, toxicity, and microbial activity. To optimize biodegradation, understanding its mechanisms is essential. This review delves into varied bioremediation techniques, degradation pathways, and the contributions of microbial activities to efficiently removing hydrocarbon pollutants. Recent research spotlights specific microorganisms like bacteria, microalgae, and fungi adept at hydrocarbon degradation, offering a contemporary perspective on petroleum hydrocarbon pollutant bioremediation. These microorganisms efficiently break down petroleum hydrocarbons, with enzymatic catalysis markedly accelerating pollutant breakdown compared to conventional methods. Given the intricate nature of hydrocarbon contamination, cooperative bacterial consortia are instrumental in effective cleanup, driven by specific genes guiding bacterial metabolism. For cost-effective and efficient removal from compromised environments, it is advisable to adopt an integrated approach that combines biostimulation and bioaugmentation.

Keywords: bioremediation; polycyclic aromatic hydrocarbons (PAHs); eco-friendly cleanup; microbial communities; metabolic pathways; enzymatic breakdown; sustainability

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1. Introduction

Hydrocarbons are prevalent organic contaminants in ecosystems [1,2], requiring thorough environmental impact assessment across various matrices. Hydrocarbons, primarily composed of carbon and hydrogen, are inherent constituents of crude oil, a complex mixture also containing oxygen, sulfur, nitrogen, and trace metals. Post-refining, petroleum products acquire altered physicochemical properties that enhance complexity and may impede their biodegradation [3]. Petroleum waste sludge from industries introduces pollutants like hydrocarbons, sulfides, and ammonia into soil environments [4]. Conventional physiochemical methods, such as incineration and solvent extraction, are expensive and environmentally disruptive [5]. The persistent presence of petroleum hydrocarbons in ecosystems, due to activities like oil spills and drilling, has adverse effects on aquatic life and public health [6–8]. Polycyclic aromatic hydrocarbons (PAHs), resulting from incomplete combustion of organic molecules, especially in fossil fuels [9], carry health risks including cancer, mutations, and congenital issues [10]. They infiltrate the environment via both natural and human activities, including forest fires, volcanic eruptions, and industrial processes [11].

Microorganisms play vital roles in natural ecosystems, encompassing organic matter decomposition, nutrient cycling, contaminant breakdown, and hydrocarbons. This microbial diversity and adaptability maintain ecosystem services, enabling the biodegradation of diverse aliphatic and aromatic hydrocarbons [1]. Bioremediation holds significant promise as an eco-friendly approach for degrading diverse hydrocarbon pollutants, involving intricate microbial processes that convert pollutants into simpler compounds [12]. Bioremediation employs microorganisms to naturally break down oil contaminants cost-effectively and sustainably [13].

Hydrocarbon compounds are a large and varied group of organic molecules. Each hydrocarbon molecule has its own unique chemical structure and properties. This diversity of hydrocarbon compounds means that different types of microorganisms use different methods to break them down [14]. Successful degradation depends on microbial populations and environmental factors like temperature, oxygen levels, pH, and nutrient availability [15]. Accordingly, recognizing the variability in hydrocarbon properties and bioavailability is pivotal in the realm of bioremediation. Although bioremediation shows promise for addressing organic pollutants like PAHs, robust solutions for the most toxic petroleum hydrocarbons remain underexplored [16,17]. Due to a lack of long-term efficacy evidence from field studies, comprehensive investigations into bioremediation methods' ecologically sustainable and functional features are imperative [18]. Bioremediation, involving bacteria, fungi, and plants, transforms contaminants into benign substances [19,20], with enzymes, biosurfactants, and metabolic products facilitating hydrocarbon degradation [6].

Microbial degradation of PAHs yields three main products: (a) enzymes like monooxygenases and dioxygenases break down hydrocarbons, forming alcohols [21,22]; (b) biosurfactants enhance biodegradation by emulsifying and releasing hydrocarbons [23]; (c) specific bacteria use hydrocarbons as an energy and carbon source, producing solvents that dissolve petroleum hydrocarbons [24,25]. Notably, *Acinetobacter*, *Bacillus*, *Clostridium*, *Micrococcus*, *Mycobacterium*, *Proteus*, *Pseudomonas*, *Rhodococcus*, and *Staphylococcus* species contribute to this process [26,27].

Complete petroleum hydrocarbon decomposition into carbon dioxide and water requires multiple microorganisms. Genetic engineering has enabled bacteria like *Pseudomonas* spp. to break down various petroleum compounds [28] concurrently. Given the challenges of traditional cleanup methods, biodegradation offers a promising solution for remediating sites contaminated by persistent organic pollutants like petroleum hydrocarbons [28].

This study aims to offer mechanistic insights into various bioremediation strategies, emphasizing the influence of microbial deployment in achieving eco-sustainable remediation [29]. In this context, understanding factors influencing bioremediation and microbial degradation is crucial. This research explores substrate bioavailability, microbial roles in petroleum hydrocarbon pollutant breakdown, molecular techniques for characterization, degradation processes in anaerobic and aerobic conditions, and bio-degradation variables [30].

2. Polycyclic Aromatic Hydrocarbons (PAHs) and Aliphatic Hydrocarbons

Hydrocarbons can be classified into two main groups: aliphatic hydrocarbons (saturated hydrocarbons) and aromatic hydrocarbons, which include both monocyclic aromatic hydrocarbons (MAHs) and (PAHs) [31]. Aliphatic hydrocarbons, or paraffins, are abundant in oil deposits and natural gas and consist of linear or cyclic structures [32]. They lack double bonds and possess low polarity, resulting in minimal water solubility and reactivity at room temperature [31].

On the other hand, aromatic hydrocarbons encompass compounds with benzene rings, subdivided into (MAHs) like BTEX (xylene, benzene, ethylbenzene, and toluene) and (PAHs). These hydrocarbons exhibit varying levels of aromaticity due to their benzene ring structures [33].

PAHs, arising from biological processes or incomplete combustion, whether natural (e.g., forest fires) or human-induced (e.g., vehicle emissions), are lipophilic organic pollu-

tants of substantial environmental concern due to their persistently ubiquitous presence in air, soil, and water and their detrimental effects on human health and ecosystems [34,35]. These pollutants encompass both low-molecular-weight forms (e.g., naphthalene, fluorene) with 2–3 benzene rings and their high-molecular-weight counterparts (e.g., pyrene, benzo(a)pyrene) featuring four or more benzene rings [33]. The former tends to evaporate into the atmosphere, while the latter can appear as liquids or solids, potentially partitioning into water [33]. The greater the increase in the number of benzene rings, the lower the solubility, leading to greater persistence and environmental risks [31].

The 'One Health' concept, promoted by the World Health Organization and outlined in numerous studies [36], underscores the intricate connections between human, animal, and environmental well-being. It serves as a vital framework for comprehending the far-reaching impacts of hydrocarbon contamination in our ecosystems. Hydrocarbons, such as polycyclic aromatic hydrocarbons (PAHs), are pervasive in diverse ecosystems, spanning water, soil, air, and sediment [37]. Their chemical properties and widespread presence significantly threaten human health and the delicate ecological equilibrium. As these hydrocarbon contaminants endure and accumulate across these contexts, they not only directly endanger human health, leading to a range of health issues such as respiratory problems, carcinogenic effects, and developmental disorders, but also challenge broader environmental stability by disrupting ecosystems, harming aquatic life, and altering soil composition [37]. Table 1 indicates the characteristics of priority physical-chemical contaminants among PAHs [38].

Table 1. Attributes of priority physical-chemical compounds among PAH pollutants [38–40].

PAH Name	Molecular Weight (g/mole)	Melting Point (°C)	Aqueous Solubility (mg/L)	Molecule Formula	Log KOW	Vapor Pressure (Pa, 25 °C)	Boiling Point (°C)
Pyrene	22	150–156	0.135	C16 H10	4.88	5.0×10^{-5}	360–404
Acenaphthene	154	90–96	3.9	C12H10	3.92	3.92	265–280
Acenaphthylene	152	92–93	16.1	C12H8	3.94	3.87	265–280
Fluorene	166	116–118	1.9	C13H10	4.18	1.66	293–295
Chrysene	228	252–256	0.002	C18H12	5.81	4.0×10^{-6}	441–448
Naphthalene	128	80.2	31.7	C10H8	3.30	11.14	218
Benzopyrene	252	177–179	0.00162	C20H12	6.13	6.0×10^{-8}	493–496
Benzofluoranthene	252	167–168	0.0008	C20H12	6.11	5.2×10^{-8}	481
Benzo(2)fluoranthene	252	198–217	0.0015	C20H12	5.78	5.0×10^{-7}	480–471
Phenanthrene	178	96–101	1.15	C14H10	4.46	1.06×10^{-1}	339–340

3. Hydrocarbon Toxicity and Ecosystem Impact

Hydrocarbons have intricate interactions with both living and non-living components of ecosystems. They can be categorized based on their carbon atom count. Fraction 2 (F2) comprises semi-volatile hydrocarbons with at least 10 carbon atoms (C10–C16), while fraction 1 (F1) contains volatile hydrocarbons with 6–10 carbon atoms (C6–C10). While fraction 4 (F4) includes the least volatile class with more than 35 carbon atoms (>C35), fraction 3 (F3) is made up of non-volatile hydrocarbons with 16 to 34 carbon atoms (C16–C34). This categorization based on carbon atom count helps us understand the diverse nature of hydrocarbons and their behavior in various environmental contexts. In general, toxicity rises with molecular weight, as demonstrated by the greater toxicity of large molecular-weight PAHs due to their higher boiling points [3,32].

Due to their complexity, light, volatile hydrocarbon fractions are released into the atmosphere, hydrophilic and amphipathic fractions dissolve in water, and lipophilic molecules bond to organic matter, soil, and sediment particles [3]. The level of toxicity is determined by bioavailability, a factor influenced by hydrocarbons' chemical and physical properties. Once absorbed, bioavailable chemicals can interact with cellular receptors, disrupting essential biological processes and potentially causing a range of lethal or sub-lethal impacts.

These impacts can include damage to cell membranes, interference with metabolic pathways, disruption of endocrine systems (EDCs), and the induction of oxidative stress [41]. Additionally, hydrocarbon contamination in the environment can lead to ecosystem disruptions, including reduced biodiversity, altered food chains, and habitat degradation, which can further affect human health and environmental stability [42]. The outcome of long-term exposure to hydrocarbon contaminants can vary based on exposure concentration and duration. For instance, acute oil spills in aquatic environments often lead to short-term exposure and lethality. In such cases, PAHs can damage organisms' central nervous systems by embedding in neuron cell membranes [3]. However, long-term exposure to PAHs in contaminated sediments can lead to bioaccumulation in aquatic organisms, disrupting their reproductive systems and immune responses. These long-term effects can have far-reaching consequences for both individual organisms and entire ecosystems [43].

Exposure to hydrocarbons causes sub-lethal effects such as injuries, developmental defects, anoxia, and dietary and reproductive changes. Petroleum hydrocarbons in crude oil and their derivatives can cause immediate health impacts through inhalation or skin contact [44]. Inhalation can lead to respiratory irritation, coughing, and, in severe cases, chemical pneumonitis. Skin or eye contact can result in irritation or burns. Neurotoxic hydrocarbons can cause headaches, migraines, and dizziness by affecting the central nervous system. The severity depends on hydrocarbon type, concentration, and exposure duration, requiring prompt medical attention in acute cases [44]. The most studied PAHs for bioremediation procedures are shown in Figure 1.

PAHs significantly threaten health, affecting the nervous, immune, and excretory systems and potentially causing tumors and mutations [3,32]. Chronic PAH exposure can lead to cancer, and their cataractogenic properties are well documented, causing dermal and ocular alterations [45]. PAH exposure occurs via inhalation, ingestion, or dermal contact. Thanks to their higher fat solubility, they readily enter cells, accumulating in adipose tissue, kidneys, and the liver. This exposure can damage the blood and possibly suppress the immune system. Depending on exposure routes, PAHs, especially those with 3–7 aromatic rings, can trigger digestive, skin, or lung cancers. Their carcinogenic potential arises from liver metabolism, which converts them into reactive intermediates that bind to DNA and RNA, causing genetic damage. PAHs are known to interact metabolically, leading to synergistic and additive effects [31].

Hydrocarbons pose a significant threat to both living organisms and ecosystem functioning. Their pervasive presence has led to the extinction of multiple plant and animal species, resulting in detrimental ecological consequences [37]. These compounds contaminate various aquatic environments, such as freshwater, wastewater, and seawater, binding to sediments and particulates. Consequently, benthic organisms like invertebrates, fish, and filter feeders are exposed to hydrocarbons through the filtration of suspended petroleum [3]. The impact on aquatic ecosystems depends on the scale of hydrocarbon contamination. In acute cases, such as oil spills, immediate damage can occur, but the potential for recovery varies based on spill size, response, and environmental factors. Smaller spills may recover naturally over time, while larger ones can cause long-term harm if not mitigated [46].

Hydrocarbons profoundly influence sediment and soil properties, obstructing water and oxygen transfer. This impact on permeability, moisture levels, pH, nutrient availability, and redox conditions reverberates through ecosystems [47]. Notably, PAHs of higher molecular weight form persistent surface layers that impede both bioaccessibility and vegetation growth, affecting the ecosystem's vitality over extended periods [48]. Furthermore, direct exposure to hydrocarbons disrupts plant development by limiting light penetration and nutrient absorption, ultimately diminishing primary productivity and agricultural output [49]. These threats extend beyond the aquatic realm, as hydrocarbons can infiltrate subterranean ecosystems through percolation and atmospheric deposition, expanding their adverse influence on natural habitats [50].

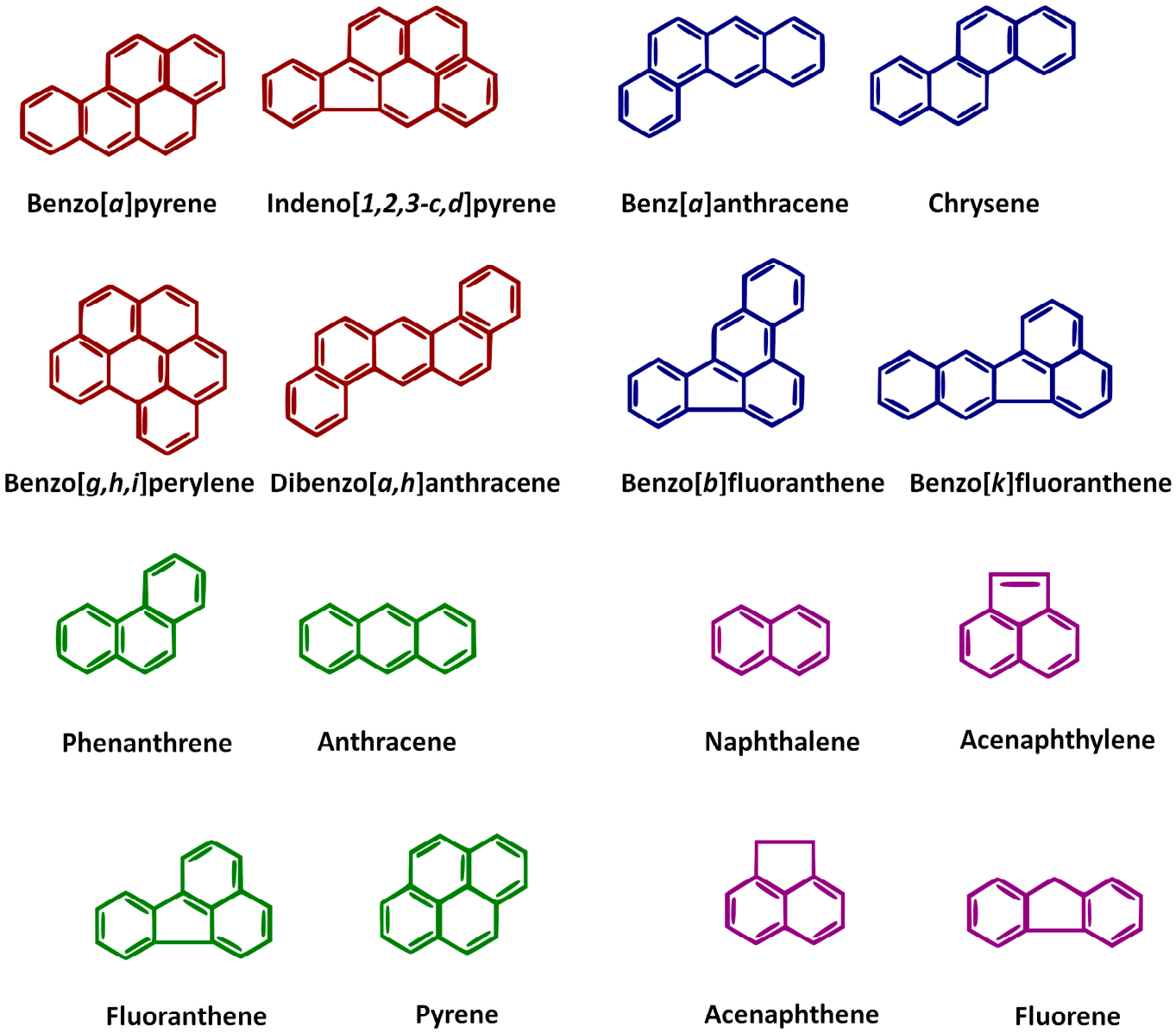

Figure 1. The most frequently examined PAHs are in the context of the bioremediation process [51].

Hydrocarbons can disrupt microbial communities, reducing diversity and altering population dynamics [49]. This can affect essential ecosystem functions and impact higher trophic levels through biomagnification [49]. For instance, hydrocarbons can hinder key soil bacteria like nitrifiers by competing with lighter hydrocarbons and inhibiting important enzymes [31], potentially impacting soil fertility. Certain hydrocarbons, including benzo(a)pyrene, have been classified as priority hazardous substances under the WFD (2000/60/EC). This classification is based on their potential to cause harm to aquatic ecosystems and human health, typically at higher concentrations due to their carcinogenic properties. Hydrocarbons shape microbial communities, with some species vulnerable and others employing mechanisms for removal [52]. The success of hydrocarbon biodegradation relies on diverse microbial metabolism in a contaminated environment, provided excessive levels do not inhibit microbial activity [49].

4. Variability in Hydrocarbon Properties: Implications for Bioremediation

Hydrocarbon compounds display remarkable diversity in terms of their chemical composition, biodegradability, and bioavailability. Hydrocarbon properties vary widely,

affecting their environmental behavior and biodegradability [53]. Notably, lighter hydrocarbons like methane and ethane are more amenable to microbial degradation than their heavier counterparts, such as crude oil and asphalt. In contrast, aromatic hydrocarbons like benzene and toluene often present greater resistance to biodegradation [54]. Moreover, the accessibility of hydrocarbons to microorganisms, known as bioavailability, is influenced by factors such as their physical state, association with organic matter or minerals, and solubility, impacting their suitability for bioremediation [55].

Microbes degrade hydrocarbon compounds through a variety of pathways, which vary depending on the hydrocarbon's structure and properties [56]. For example, methane and ethane are metabolized by different bacteria using different enzymes. Alkenes undergo oxidation processes, aromatic hydrocarbons are subject to ring cleavage, and PAHs are broken down via ring-cleaving enzymes [57]. Halogenated hydrocarbons, fatty acids, cyclic hydrocarbons, and other complex structures each follow their own specific enzymatic pathways [58]. Nitrogen- and sulfur-containing hydrocarbons undergo nitrogen ring cleavage and sulfur removal processes, respectively. Long-chain hydrocarbons are degraded through extracellular enzymes and biofilms, while highly branched alkanes require specialized pathways. Isoprenoids, phenolic compounds, polymeric hydrocarbons, and halocarbons have unique mechanisms. Additionally, alicyclic hydrocarbons, heterocyclic hydrocarbons, and halogenated aromatics undergo degradation through diverse enzymatic reactions [59,60].

As a result of this variability, bioremediation strategies must be tailored to specific hydrocarbon properties and environmental conditions. One approach involves combining different bioremediation technologies, such as biostimulation and bioaugmentation, for sites contaminated with mixed hydrocarbons [61]. Bioavailability, which pertains to the accessibility of hydrocarbons to microorganisms for degradation, relies on factors like the physical state of the contaminant, its interactions with environmental organic matter or minerals, and its solubility. Understanding these factors is essential for crafting effective bioremediation strategies for specific hydrocarbon contaminants. Overlooking the unique characteristics of hydrocarbon contaminants can lead to suboptimal outcomes, increased costs, and prolonged environmental impacts [55].

Furthermore, hydrocarbon properties can significantly influence the activity of microbial communities in hydrocarbon biodegradation. Microbes are central to breaking down hydrocarbons, and their effectiveness depends on the nature of the hydrocarbon substrate. Understanding this intricate relationship between hydrocarbon diversity and microbial communities is crucial for optimizing bioremediation processes [52,62]. Synergistic interactions within microbial communities are common, where some microbes produce metabolites or enzymes that benefit the degradation of specific hydrocarbons by other community members, leading to co-metabolic processes [63]. Environmental factors such as temperature, pH, oxygen availability, and nutrient levels further add to the complexity of the biodegradation process [15]. These factors influence which microbial species thrive and which degradation pathways are favored, making them critical considerations in real-world bioremediation applications. Other factors contributing to variability include the persistence and recalcitrance of certain hydrocarbon compounds, substrate preferences of microbial communities, temporal dynamics, and biodegradation limitations due to toxicity or chemical stability [64]. Recognizing and accommodating this variability is crucial for designing effective bioremediation strategies tailored to the specific contaminants present, the environmental conditions, and the potential for microbial adaptation.

5. Bioremediation of Petroleum Hydrocarbons: A Green Solution

Traditional physical and chemical cleanup methods, involving costly drilling and transportation of contaminated materials, have limitations due to expenses and inefficiencies [65]. These techniques encompass soil washing, chemical deactivation (e.g., hydrogen peroxide (H_2O_2) and potassium permanganate ($KMnO_4$)), and various other processes [65]. To address these shortcomings, green technologies reliant on the natural regenerative properties of plants and microorganisms have emerged [28].

Microorganisms, such as bacteria, are used as bioremediation agents to convert hazardous organic pollutants into harmless compounds. This process can be efficient, cost-effective, and environmentally friendly [28]. Microbes significantly enhance catalytic capabilities, aiding in pollutant removal and microbial oil extraction [21]. Microbial bioremediation is commonly used to combat contamination of agricultural and marine habitats by petroleum hydrocarbons [58,66]. Microbes like bacteria, fungi, and algae, with their genetic adaptations to petroleum-contaminated environments, play pivotal roles in degrading petroleum pollutants [58]. Bacterial strains such as *Pseudomonas* and *Rhodococcus* and fungi like *Aspergillus* and *Penicillium* have been widely used in biodegradation due to their proficiency in breaking down hydrocarbons [67]. Additionally, microalgae such as *Chlorella* and *Scenedesmus* have the potential to absorb and metabolize hydrocarbons in aquatic environments, offering a versatile bioremediation approach [68]. A summary of the fundamental bioremediation techniques employed by different microbial groups is shown in Figure 2.

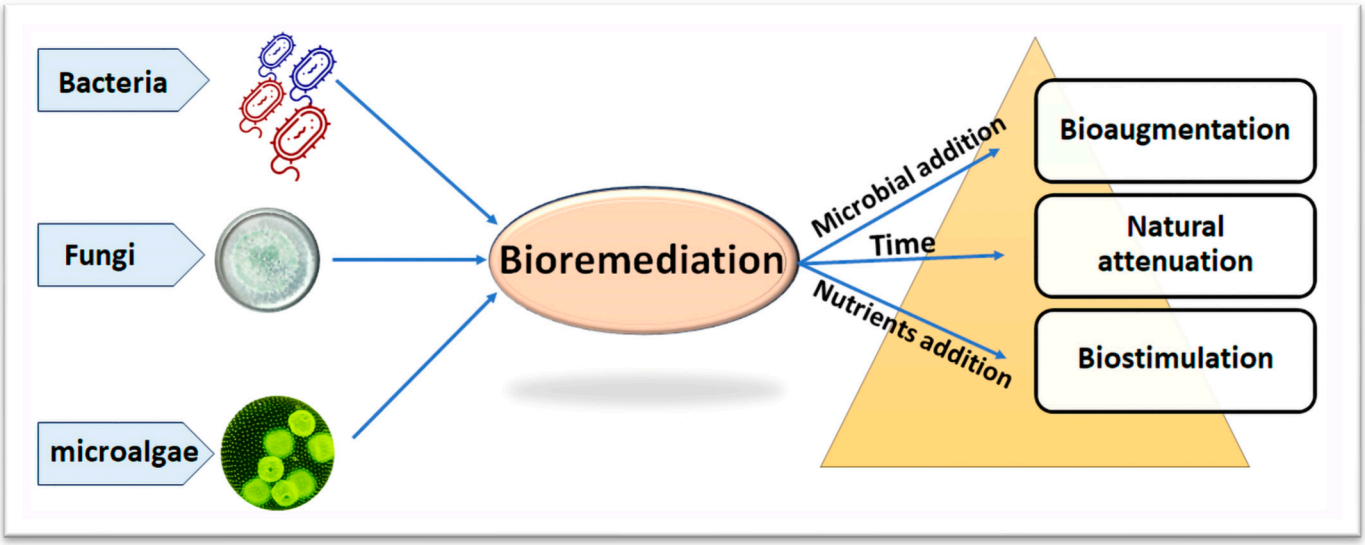

Figure 2. A basic outline of the bioremediation approaches employed by various groups of microorganisms.

This biodegradation process involves a succession of enzymatic metabolic steps, primarily encoded on plasmids [69,70]. Plasmids are essential for breaking down complex hydrocarbon molecules [71]. Diverse enzyme systems orchestrate the degradation of petroleum hydrocarbons, typically initiated by (a) microbial cell attachment to substrates and (b) the synthesis of biopolymers, acids, solvents, and gases [72]. Hydrocarbons can act as electron donors in the metabolic processes of microorganisms and, at times, as their sole carbon source [73]. Oxidation, catalyzed by oxygenases and peroxidases, is the initial intracellular defensive mechanism against organic contaminants [38]. Environmental degradation mechanisms then sequentially transform these contaminants into central mediators, culminating in the creation of cell biomass by producing precursor metabolites, including acetate, succinate, and pyruvate [74].

Numerous degradation methods and catabolic genes were identified for different hydrocarbon families, with enzyme requirements varying based on hydrocarbon chain length and type [49,75]. A promising advancement in environmental microbiology involves metaproteomics and metabolomics, offering insights into PAH biodegradation by revealing metabolites and protein involvement [35]. This includes enzymes like cytochrome P450 monooxygenases and dioxygenases that catalyze key reactions in the breakdown of PAHs. Metabolomics has revealed the presence of metabolites like catechols and dihydrodiols, which are intermediates in the PAH degradation pathway [76]. Although metabolomics can precisely identify the metabolites generated through PAH biodegradation, proteomics

is a robust method for detecting proteins and their involvement in the breakdown of PAHs [35]. These techniques, functional metagenomics, metatranscriptomics, and DNA microarrays, are becoming indispensable for understanding PAH biodegradation processes, even involving uncultured organisms [35,38].

6. Microbial Involvement in the Biodegradation of Hydrocarbons

Hydrocarbon degradation involves intricate microbial processes that transform complex hydrocarbons into simpler forms (Figure 3). Predominantly anaerobic and aerobic microorganisms engage in catalysis and enzymatic activation to achieve this transformation under controlled conditions. *Acinetobacter radioresistens* KA2, isolated from oily waste sludge, exhibited effective two-stage bioremediation, achieving up to 80% removal of total petroleum hydrocarbons (TPH) over 16 weeks [7]. Similarly, *Enterobacter hormaechei* KA6 and *A. radioresistens* KA5, derived from petroleum waste sludge, showcased a significant TPH reduction of 84% within three months, with an 80% removal rate in a four-month in-vessel experiment [8]. Rapidly growing bacteria like *E. hormaechei* KA3 and *Staphylococcus equorum* KA4, isolated from heavy oil sludge, displayed promising TPH removal efficiency of up to 89% over a sixteen-week bioreactor study [77]. In addition, anaerobic BTEX degradation is the microbial breakdown of benzene, toluene, ethylbenzene, and xylene in oxygen-depleted environments. Microbes transform BTEX compounds into simpler forms through anaerobic respiration, potentially producing methane [78]. This process is crucial for bioremediation but can be slow and influenced by environmental factors such as electron acceptors, temperature, and pH [79].

Notably, fungal species such as *Fomitopsis pinicola*, *Daedalea dickinsii*, and *Gloeophyllum trabeum* exhibited substantial DDT contamination reduction in soil through bioremediation [80]. The isolation and assessment of *E. hormaechei* KA6 and *A. radioresistens* KA5 from petroleum waste sludge involved various tests for strain identification [81]. Additionally, fungi like *Scedosporium apiospermum* H16 and *Aspergillus ochraceus* H2, along with various microorganisms (*Proteobacteria* (α, β, γ), *Actinobacter*, *Thermobifida*, and *Streptomyces*), demonstrated successful biodegradation of diverse hydrocarbons and PAH contaminants [16]. The extent of removal can be influenced by various factors, including the specific hydrocarbon, or PAH, the environmental conditions, and the duration of the biodegradation process. In some instances, complete removal may be achieved, while in others, removal rates of 70% or 50% may still be considered successful based on the context of the contamination and the goals of the bioremediation effort. Therefore, the success of biodegradation can range from partial removal to near-complete elimination, depending on the specifics of each case. Experimental studies using hydrocarbon-contaminated drill mud waste, cow bile, and indigenous bacteria such as *Brevibacterium casei* and *Bacillus zhangzhouensi* resulted in impressive TPH removal of up to 90% [82]. Notably, *Acinetobacter radioresistens* KA2 achieved a 90% removal efficiency in a two-stage, 8-week process for oily sludge [83]. For hydrocarbon-contaminated drill mud waste, *Brevibacterium casei* and *Bacillus* sp. achieved an impressive 99% removal efficiency in a composting bioreactor process spanning six weeks [77]. Furthermore, algae, particularly when used in consortia, can be powerful agents for bioremediation due to their versatility and ability to harness solar energy for metabolic processes. Therefore, considering the most efficient bioremediation approach, a consortium of various species, including algae, may offer enhanced capabilities and adaptability to different environmental conditions [84]. The comprehensive insights gathered from these experiments are pivotal for guiding large-scale hydrocarbon bioremediation studies, with a focus on physical parameter optimization and scaling considerations.

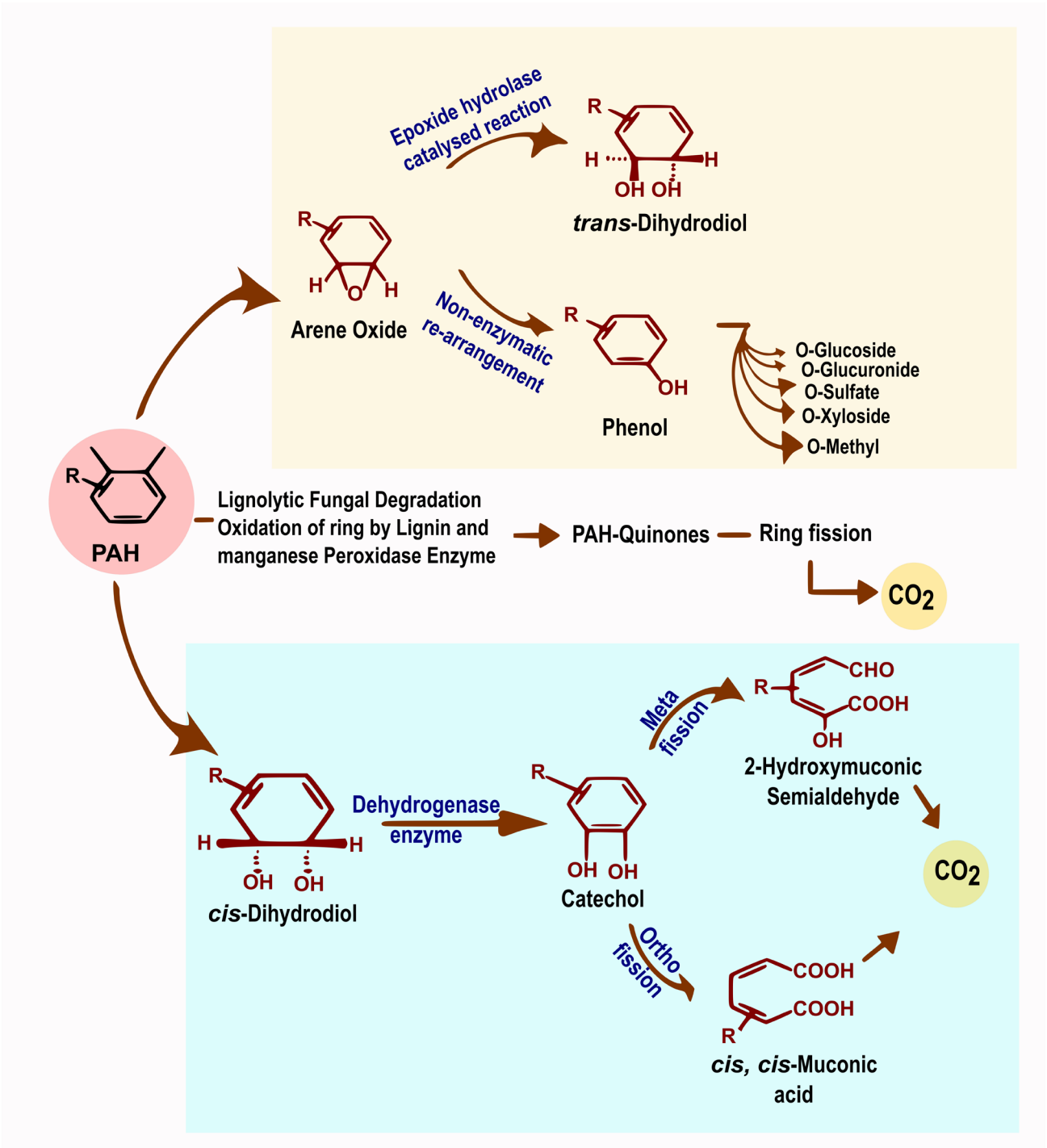

Figure 3. There are three primary pathways through which bacteria and fungi degrade polycyclic aromatic hydrocarbons (PAHs) [38,85].

Microorganisms exhibit diverse utilization modes for petroleum hydrocarbons, including chemotrophic, hypoxic, phototrophic, aerobic, and anaerobic strategies. The initial step in the interaction between microorganisms and oil pollution involves direct contact, facilitated by the water-repellent nature of cell wall surfaces [86]. Hydrocarbons, entering microorganisms as minute droplets upon direct contact, interact with surfactant activity and hydrophobicity, overcoming diffusion limitations and enhancing substrate delivery to cells. Microbes proficient in oil decomposition and surfactant utilization demonstrate heightened efficiency in anoxic conditions, promoting in situ methanogenesis in oil reservoirs. The breakdown of petroleum hydrocarbons by microorganisms leads to the generation of vari-

ous substances with a physiological effect, either adhering to cell surfaces or being released as extracellular molecules that contribute to the environment [87]. Various microorganisms, including bacteria, algae, and fungi, react differently to hydrocarbon contaminants. For example, hydrocarbonoclastic bacteria are efficient at oil decomposition and surfactant utilization, particularly in anoxic conditions that promote methane generation [88]. Algae, due to their photosynthetic capabilities, focus on removing hydrophobic contaminants from aquatic systems [89]. Fungi excel at breaking down complex hydrocarbons like PAHs. Each group possesses unique mechanisms, metabolic pathways, and environmental preferences for interacting with hydrocarbon contaminants [52]. Bioactive molecules are key factors influencing hydrocarbon bioavailability, microorganism activity, interaction, and transport. Bioactive surfactants, capable of significantly reducing interfacial tension and oil viscosity at contamination sites, prove effective in degrading up to 77% of hydrocarbons in crude oil [28]. Enzyme-catalyzed metabolic processes mediate the role of microorganisms in petroleum hydrocarbon degradation, with oxygenases, peroxidases, reductases, hydroxylases, and dehydrogenases playing significant roles. Microorganisms involved in hydrocarbon degradation exhibit varying enzyme production rates. Specialized hydrocarbonoclastic bacteria are known for their high oxygenase and reductase production, enabling fast hydrocarbon breakdown. Algae and fungi also contribute, but their enzyme production varies by species. These differences highlight that different microbial groups have distinct enzyme production levels, with bacteria typically reacting more quickly due to their specialization in hydrocarbon degradation [90].

6.1. Bacterial Degradation of Hydrocarbons

Methane, the simplest hydrocarbon, is a source of energy and carbon for a specific group of bacteria known as methanotrophs. However, these bacteria cannot grow on hydrocarbons with more carbon atoms [91]. Pyrene, a complex, high-molecular-weight hydrocarbon, is hydrophobic and poorly soluble in water, making it resistant to biodegradation [92]. Mycobacterium, among other genera, has been found to mineralize pyrene and utilize it as a special carbon and energy source [93]. Various pyrene-degrading bacteria, including species from *Stenotrophomonas*, *Bacillus*, *Rhodococcus*, *Pseudomonas*, *Sphingomonas*, *Mycobacterium*, *Burkholderia,* and *Cycloclasticus*, have been identified [92,94].

In the case of oil spills, volatile hydrocarbons evaporate rapidly, leaving longer aliphatic chains and aromatic compounds. Hydrocarbon-oxidizing bacteria attach to petroleum droplets, facilitating oil degradation [31]. These bacteria are crucial in shifting microbial communities toward hydrocarbonoclastic species capable of utilizing hydrocarbons as carbon and energetic resources. These hydrocarbonoclastic bacteria adapt to hydrocarbon exposure through various mechanisms, including the production of biosurfactants that enhance hydrocarbon bioavailability [95].

Microorganisms produce biosurfactants, amphiphilic molecules that uptake and detoxify hydrocarbons [3]. These compounds, like rhamnolipids, have been shown to improve the desorption of PAHs in contaminated soil, promoting faster biodegradation [96]. Bacteria like *Pseudomonas* and *Delftia* can synthesize biosurfactants, improving their capability of degrading several different hydrocarbons [97]. Some species, such as *Achromobacter*, produce bioemulsionants that reduce surface tension, aiding the degradation of hydrocarbons like pyrene [98].

Hydrocarbons can influence bacterial chemotaxis, allowing them to migrate toward contaminated areas [3]. For instance, the strain *Pseudomonas putida* G7 can absorb and participate in the cometabolism of pyrene, making it available for biodegradation [99]. *Stenotrophomonas* sp., isolated from crude oil-contaminated soil, has grown on various PAHs as a carbon and energy source, with specific genes involved in PAH degradation [100]. Additionally, *Actinobacteria*, including *Rhodococcus* strains, exhibit hydrocarbon-degrading abilities [95]. *Rhodococcus* sp. P14, for example, can metabolize high-molecular-weight PAHs and aliphatic hydrocarbons by altering its cell membrane composition to enhance hydrophobicity [101]. Overall, various bacterial genera play vital roles in hydrocarbon

degradation, as shown in Table 2. Many bacteria mentioned in Table 2, such as *Acinetobacter*, *Pseudomonas*, and *Enterobacter*, are commonly found in various environmental niches. They are often called "ubiquitous bacteria" because they exist in various habitats, including soil, water, and sediments. This ubiquity is one of the reasons they are frequently utilized in bioremediation efforts. For example, Acinetobacter species are known to thrive in various environments, and this adaptability makes them valuable for breaking down hydrocarbons in different settings.

Table 2. Some bacterial species have the ability to bioremediate hydrocarbons.

Bacterial Species	Hydrocarbon	Mechanism of Action	References
Pseudomonas putida	Pyrene	Cometabolism	[102]
Pseudomonas W10	Phenanthrene		[31]
Pseudomonas aeruginosa	n-alkanes (C16–C19), fluorene, phenanthrene, and pyrene	Biosurfactant production	[96]
Delftia sp. *NL1*	diesel		[97]
Rhodococcus sp. *P14*	phenanthrene, pyrene, benzo(a)pyrene	Change in fatty acid composition of the cell membrane/biofilm formation/	[101]
Acinetobacter	naphthalene, acenaphthene, and acenaphthylene	Biosurfactant production	[35]
Enterobacter cloacae	crude oil		[103]
Stenotrophomonas sp. *Pemsol*	biphenyl, anthraquinone, phenanthrene, naphthalene, phenanthridine	Horizontal gene transfer	[104]
Achromobacter (AC15)	Pyrene	Biosurfactant production	[105]
Alcanivorax borkumensis	Alkanes	Alkane hydroxylase	[106]
Rhodococcus erythropolis	Alkanes	Cytochrome P450	[107]
Rhodococcus sp. BCP1, and *R. opacus* R7	Alkanes, fatty acids, aromatic compounds, and (PAHs)	Cytochrome P450 and dioxygenase systems	[108]
Sphingomonas sp.	(PAHs)	Dioxygenase	[109]
Sphingobium yanoikuyae B1	(PAHs) and phenanthrene derivatives	Dioxygenase and monooxygenase systems	[110]
Mycobacterium sp.	(PAHs)	Dioxygenase	[111]
Gordonia sp.	Alkanes	Cytochrome P450	[112]
Acinetobacter sp.	Alkanes	Alkane hydroxylase	[113]
Micrococcus sp., *Bacillus* sp., *Corynebacterium* sp., *Flavobacterium* sp., *Pseudomonas* sp., *Acinetobacter* sp., *Moraxella* sp. and *flavobacterium* sp.	xylene, benzene, hexane, crude oil, kerosene, gasoline, diesel and olive oil	Biosurfactant production	[114]
Moraxella sp., *Pseudomonas* sp., members of Enterobacteriaceae, Vibrionaceae	Resins	employ versatile enzymatic and metabolic processes, including biofilm formation and adaptation.	[115,116]
B. stereothermophilus, *Pseudomonas* sp., *Corynebacterium* sp., *Vibrio* sp., *Nocardia* sp., *Bacillus* sp., *Achromobacter* sp.	Monocyclic aromatic hydrocarbons	*B. stereothermophilus* thrives at high temperatures for thermophilic hydrocarbon degradation; the other strains employ a variety of enzymatic and metabolic mechanisms.	[115,116]
Alcaligenes sp., *Arthrobacter* sp., *Xanthomonas* sp., *Pseudomonas* sp., *Mycobacterium* sp., *Bacillus* sp., *Burkholderia cepacia*, *Anabaena* sp.,	Polycyclic aromatic hydrocarbons	employ various enzymatic and metabolic processes to effectively break down hydrocarbons, contributing to bioremediation	[115,116]

Versatile bacterial consortia are essential for breaking down complex and diverse hydrocarbons, like pyrene, into inorganic compounds, nutrients, and cellular biomass. The composition and percentages of efficiency depend on various bacterial species and environmental conditions [117]. At the same time, naphthalene and benzo[a]pyrene were

biodegraded using bacterial inocula enriched with wheat straw due to structural similarities with lignocellulosic biomass [118].

Phulpoto et al. [119] extracted bacterial consortia from various depths of a lake and evaluated their bioremediation potential in lab tests. The dominant hydrocarbon-degrading genera differed by depth, with *Stenotrophomonas*, *Acinetobacter*, and *Pseudomonas* prevalent in surface water, *Pseudomonas*, *Acinetobacter*, *Sphingobacterium*, and *Aeromonas* in sediment, and *Flavobacterium*, *Pseudomonas*, *Comamonas*, *Enterobacter*, and *Acinetobacter* in deep water. Biodegradation efficiency was highest when consortia comprised 3–5 bacterial species, particularly in sediment (67.60% in 12 days) and deep water (59.70% in 12 days), attributed to increased biosurfactant production.

Seawater has also harbored bacterial consortia effective in degrading spilled oils. One consortium featured *Burkholderia*, *Rhodanobacter*, and *Pseudomonas aeruginosa* for diesel (>C12) removal, while another primarily contained *A. calcoaceticus*, *Flavobacterium* sp., and *P. aeruginosa* to biodegrade engine/lubricating oil (C9–C16) [120]. Bacosa et al. [121] isolated a consortium (*Achromobacter* sp., *Cupriavidus* sp., and *Alcaligenes* sp.) from seawater, showing a preference for aromatic hydrocarbon degradation. Jamal et al. [122] isolated *Marinobacter* spp. from the Red Sea, effectively degrading phenanthrene (72% in 16 days) and pyrene (86% in 12 days).

Microbial metabolism can be enhanced for environmental cleanup through biostimulation or bioaugmentation. For instance, Chinese soil contaminated with petroleum was bioremediated using an indigenous bacterial consortium and a sophorolipid biosurfactant [123]. Bioremediation is more efficient when combined with plants (bio-assisted phytoremediation) [124]. Vasilyeva et al. [125] combined an adsorbent and a hydrocarbon-degrading bacterial biopreparation to reduce petroleum hydrocarbons in contaminated soil. Fahid et al. [126] achieved diesel-polluted water cleanup by planting wetlands with *Phragmites australis* and introducing a hydrocarbon-degrading bacterial consortium, indicating its natural ability to enhance bioremediation efficiency. Sánchez-Jiménez et al. [127] emphasize the promise of bioremediation and phytoremediation in addressing challenging environmental issues like heavy metal contamination. They highlight the unique capabilities of hyperaccumulating plants and heavy metal-resistant microbes to absorb and improve polluted soils.

6.2. Fungi with Hydrocarbon Degradation Capabilities

Fungi and bacteria play essential roles as soil microorganisms due to their abundance and ecological functions. Their significance lies in the decomposition of organic pollutants [128]. Recently, filamentous fungi (molds) have gained prominence in the realm of PAH degradation research, surpassing bacteria in this aspect. These fungi excel at breaking down a range of PAHs, facilitated by enzymes such as laccase and dioxygenase [129]. Certain fungi that degrade aromatic hydrocarbons can reach populations ranging from 1.28×10^3 to 9.6×10^6 CFU/g. Among the 150 studied white rot fungi, 55 species have demonstrated tolerance to PAHs, including pyrene [130]. Initially, research on PAH degradation by fungi centered on white rot fungi in the Basidiomycete class, or Zygomycetes. However, it is evident that various species from classes like Micromycetes, Ascomycete, Mucoromycota, Rozellomycota, Glomeromycota, and Mortierellomycota can also effectively break down organic pollutants when the right conditions are available [131]. There is evidence of micromycetes' ability to metabolize pyrene since they were identified from PAH-contaminated sediment, and ten isolated strains exhibited substantial pyrene degradation, exceeding 2.4 mg/g dry weight [132]. Genera like *Cladosporium*, *Aspergillus*, *Penicillium*, *Rhizochaete*, *Bjerkandera*, *Phanerochaete*, *Dentipellis*, *Mycoaciella*, *Phlebia*, *Ceriporia*, *Peniophora*, *Papulospora*, *Phlebiella*, *Pseudochaete*, *Trichaptum*, *Heterobasidion*, and *Phillotopsis* exhibit notable proficiency in PAH degradation [133]. Table 3 shows some examples of common fungi engaged in the biodegradation of hydrocarbons.

Table 3. Some fungal species are involved in hydrocarbon biodegradation.

Fungal Species	ID	Degradation Rate %	Hydrocarbons	References
Aspergillus ficuum	MB#5058	54.6	Aromatic hydrocarbons	
A. fumigatus	MB#352615	59.6	Aromatic hydrocarbons	[134]
A. flavus	MB#347788	59.8	Aromatic hydrocarbons	
Cladosporium sp.	CBMAI 1237	62	Aromatic hydrocarbons	[135]
Coriolopis byrsina	APC5	96.1	(PAHs)	[136]
Crinipellis campanella	MB#285848	39		
C. perniciosa	MB#500896	95	Aromatic hydrocarbons	[137]
C. stipitaria	MB#100767	94		
Fusarium sp.	FJ613115.1	18.2–74.6	Aromatic hydrocarbons	[138]
Rhizoctonia zeae	SOL3	42	Aromatic hydrocarbons	[139]
Marasmiellus sp.	CBMAI 1062	98.8	(PAHs)	[140]
Merulius tremellosus	KUC9161	83.6	(PAHs)	[141]
Polyporus sp.	S133	71	(PAHs)	[142]
Armillaria sp.	FO22	63	(PAHs)	[143]
Peniophora incarnata	KUC8836	82.6, 97.9	(PAHs)	[144]
Trichoderma sp.	F03	78	(PAHs)	[129]
Pleurotus pulmonarius	FO43	99	(PAHs)	[142]
Scopulariopsis brevicaulis	PZ-4	64	Aromatic hydrocarbons	[145]
Phlebia brevispora	KUC9045	63.3	(PAHs)	[144]
Phanerochaete chrysosporium		92.2	(PAHs), chlorinated compounds	[146]
Pseudotrametes gibbasa		28.33	(PAHs)	[143]

The scientific interest in the involvement of white rot fungi in PAH metabolism arises from their innate capacity to break down lignin. They generate intricate extracellular enzymes, such as laccase, lignin peroxidase, and manganese peroxidase, which culminate in the complete conversion of PAHs into CO_2 [130]. These lignolytic fungi employ three primary enzyme groups: lignin peroxidase (LiP), manganese-dependent peroxidase (MnP), and phenol oxidase (laccase and tyrosinase), accompanied by enzymes that produce H_2O_2 [147]. The initial assault on PAHs by these fungi hinges on two central enzymes: cytochrome P450 monooxygenase and lignin peroxidase. Cytochrome P450 integrates an oxygen molecule into the PAH structure, forming an arene oxide that subsequently rearranges into phenol [144]. Preliminary PAH oxidation is facilitated by extracellular peroxidases, with lignin peroxidase and manganese peroxidase contributing to subsequent oxidation stages. While peroxidases play a direct role in oxidation, manganese peroxidases have an indirect influence through enzyme-mediated lignin peroxidation. Notably, the performance and synthesis of these enzymes are heavily influenced by environmental factors such as temperature, pH, and salinity [144].

The breakdown of PAHs by aerobic fungi relies on oxygenase enzymes that activate the fungi by reducing oxygen, enabling their entry into substrates. Pyrene oxidation by fungi begins with dihydrodiol formation via dioxygenases, following either the meta or ortho pathway and yielding intermediates like catechol and protocatechuate [148]. Aerobic circumstances result in converting electron acceptors with low standard reduction potential into forms with lower Gibbs free energies. It is crucial to note that fungi breaking down PAHs, including pyrene, are categorized as lignolytic and non-lignolytic. For initial degradation, lignolytic fungi use enzymes like lignin peroxidase and cytochrome P450 monooxygenases. Similarly, non-lignolytic fungi like *Aspergillus*, *Penicilium*, and others can create cytochrome P450 monooxygenase by breaking 2–5-ring PAHs [149]. The lignolytic fungus *P. ostreatus* can metabolize various PAHs, such as pyrene. Enzymes such as MnP, laccase, and LiP oxidize organic compounds, creating transient PAH diphenols that auto-oxidize to form quinones [150]. Laccase oxidizes PAHs in the presence of mediators like aniline or phenol, initiating a process leading to quinones, polymers, high-molecular-weight products, and some CO_2 without requiring direct enzyme contact [144,151].

6.3. Microalgae Role in Petroleum Remediation

Microalgae is vital in addressing water contamination from hydrocarbons and crude oil. Several principal genera of microalgae and cyanobacteria play crucial roles in bioremediation. These include *Spirulina*, *Chlorella*, *Spirogyra*, *Scenedesmus*, *Oscillatoria*, *Chlorococcum*, *Synechocystis*, *Nannochloropsis*, and *Selenastrum* [152]. Ugya et al. assessed the potential of biofilm-grown microalgae to eliminate petroleum contaminants like PAHs and total petroleum hydrocarbons (TPH). Their findings indicated significant reductions in various phytochemical parameters, including sulfate, chloride, nitrates, total suspended solids (TSS), chemical oxygen demand (COD), and total dissolved solids (TDS), with TPH removal reaching 15% after 14 days [153]. Kuttiyathil et al. investigated how the mechanical action of sea waves contributes to emulsifying crude oil, enhancing its removal by the microalga *Chlorella* spp. Within five days, *Chlorella* gets rid of 80% of emulsified oil [89]. Özhan et al. explored water mixing's impact on bioremediation, revealing altered crude oil bioavailability and increased alkanes and PAHs under physical mixing [154].

Chlorella spp. garnered attention due to its ability to thrive in contaminated environments. Also, *Chlorella* spp. successfully removed phosphorus and reduced nitrogen and COD in petroleum effluent, but long-term exposure inhibited cell growth [155]. The crude oil's nature and concentration influence *Chlorella*'s performance. Xaaldi Kalhor et al. [156] demonstrated *Chlorella vulgaris*'s successful removal of low- and heavy-molecular-weight hydrocarbons in varying concentrations and time intervals. They tested different concentrations of crude oil (10 and 20 g/L) over two time frames (7 and 14 days). The most effective removal of low-molecular-weight hydrocarbons (LW), reaching 100%, was achieved at 10 g/L for 14 days. However, at higher concentrations (20 g/L) and the same duration, LW removal decreased to 82%. A similar pattern was observed for heavy molecular weight hydrocarbons (HW), with the best reduction of around 78% occurring over 14 days at a concentration of 10 g/L. Notably, *Chlorella*'s hydrocarbon removal success is attributed to its mixotrophic and heterotrophic mechanisms, enabling it to efficiently degrade hydrocarbons by using organic carbon from pollutants while consuming organic compounds to enhance its growth. These dual mechanisms offer adaptability and versatility, which are the keys to *Chlorella*'s effectiveness in bioremediation and hydrocarbon removal [65,157]. This aligns with Das et al.'s findings, showing *Chlorella*'s substantial biomass yield and nitrogen removal in mixotrophic conditions with petroleum-derived produced water [158].

Green microalgae, particularly Chlorophyceae, show promise in eliminating crude oil pollutants. Notably, pyrene degradation ranging from 34% to 100% was achieved in seven days using green microalgae (*Chlamydomonas*, *Scenedesmus*, *Chlorella*, and *Selenastrum*) or cyanophytes (*Synechocystis*) [159]. Likewise, studies demonstrated the effectiveness of *Nitschia* sp. and *Skeletonema costatum* in eliminating fluoranthrene and phenanthrene [160]. Furthermore, marine cyanobacteria like *Microcoleus chthonoplastes*, *Phormidium corium*, and *A. quadruplicatum* can remove phenanthrene [161]. Another *Phormidium* species from coastal environments in Todoa Santos Bay, Mexico, effectively removed 45% of hexadecane and 37% of diesel oil from seawater in 10 days [162]. Additionally, *Isochrysis galbana* and *Nannochloropsis oculata* are promising candidates for eliminating hydrocarbons from contaminated seawater, achieving an impressive 80% removal rate [163].

The exact mechanism is not fully understood, but two main hypotheses suggest microalgae utilize organic carbon from hydrocarbons or treat hydrocarbons as contaminants for defense [164]. Ugya et al. [153] explored both hypotheses, observing increased saponins after petroleum treatment. These compounds lower surface tension, enhancing bioavailability due to their amphipathic and surfactant properties. Elevated ROS production and increased alkaloids, flavonoids, and carotenoids post-treatment indicated microalgae's detoxification of hydrocarbons [153]. The accumulation of elements like silicon, aluminum, and iron was facilitated by extracellular polymeric substances (EPS) associated with functional groups. Another explanation for the remediation ability of microalgae may be explained by the presence of diverse heterotrophic microbes in cultures of marine phototrophs, which could be responsible for hydrocarbon degradation [165]. Chernikova

et al. [166] supported this idea by showing that hydrocarbon-degrading bacteria, such as *Marinobacter* sp. and *Alcanivorax* sp., dominated when crude oil was incubated with two marine microalgae (*Pavlova lutheri* and *N. oculata*).

Ghodrati et al. investigated genetic aspects, suggesting that LOXs may aid PAH degradation. Exposure to 1% crude oil induced LOX gene expression, facilitating hydrocarbon breakdown and generating growth-promoting compounds [167]. SureshKumar et al., suggested a similarity between microalgae and prokaryotes in PAH degradation mechanisms, focusing on the CYP450 oxidative system. Low-molecular-weight PAHs can interact with CYP450, potentially forming hydrogen bonds [168]. An antioxidant mechanism for petroleum degradation emerges, removing toxins and generating growth-supporting nutrients. Microalgae can continue removing contaminants even after cell death by adsorbing oil micro-droplets [89,164].

6.4. Genetically Modified Organisms (GMOs) for Bioremediation

Advanced scientific methods allow for creating genetically modified organisms or artificial consortia with bioremediation capabilities. By transferring genetic information from external microbes to native microorganisms using molecular biology techniques, genetically modified organisms can be developed in the laboratory [169,170]. These engineered microbes show potential for remediating petroleum hydrocarbon-contaminated sites [171]. Unlike immobilized microbial consortia, free microorganisms exhibit higher tolerance to extreme pH, variable NaCl concentrations, and low temperatures, resulting in a 47% greater degradation of crude oil [172,173]. Since free microorganisms have the advantage of adapting more flexibly to a wide range of environmental conditions, despite these advantages, concerns remain regarding their stability and functional consistency between laboratory conditions and real-world environments after treatment [174]. Given recent advancements, employing immobilized microbial cells to address oil sector pollutants has gained attention among researchers and industry experts. Immobilization techniques can enhance the stability and longevity of the microbial consortium and improve its performance in challenging conditions, including extreme pH, variable salinity, and low temperatures.

Additionally, immobilized cells can be used continuously, making them suitable for large-scale and long-term bioremediation efforts in industrial settings. According to Lou et al. [175], immobilized cells and enzymes play a crucial role in bioremediation technologies, significantly enhancing the efficiency of the remediation process. Their multifaceted role contributes to improved stability, operational control, reusability, targeted degradation, and compatibility with engineered systems. Using immobilization techniques, microbial cells or enzymes are trapped within matrices or carrier materials, protected from harsh environmental conditions, and targeted precisely in order to eliminate harmful microorganisms. Moreover, immobilized systems can be reused, reducing operational costs and waste [175]. These attributes make immobilized cells and enzymes essential for effective and sustainable contaminant remediation in bioremediation applications.

6.5. Synergistic Approaches for Sustainable Hydrocarbon Contaminant Remediation

Phytoremediation is an eco-friendly method that utilizes plants to address hydrocarbon contamination by absorbing, accumulating, and sometimes degrading these pollutants in soil, water, or air. It is a versatile and sustainable approach suitable for various contaminated sites [176]. While it is effective, phytoremediation can be influenced by plant selection and environmental conditions [177]. Integrating bioremediation with phytoremediation creates a comprehensive strategy, combining the abilities of microorganisms to break down contaminants at the molecular level with the capacity of plants to absorb and stabilize pollutants [178]. This integrated approach widens the range of contaminants addressed and enhances degradation by promoting the growth of hydrocarbon-degrading microorganisms in the plant's rhizosphere [179]. Additionally, it mitigates contaminant mobility, is cost-effective, and offers a sustainable, long-term solution for diverse sites [175].

This integration holds significant promise as an environmentally friendly solution for remediating hydrocarbon pollutants and contributing to environmental restoration [175].

7. Influences on Petroleum Hydrocarbon Degradation

7.1. Factors Influencing Degradation

Optimal growth and biodegradation rates are attainable when these microorganisms—bacteria; fungi; and algae—are present; provided there is sufficient nutrient concentration, oxygen availability, and an ideal pH. Physical and chemical oil properties, coupled with environmental conditions like temperature, oxygen, nutrients, pH, bioavailability, photooxidation, alkalinity, soil moisture, acidity, water content, and oil absorption effects, are pivotal for biodegradation success [180]. Additionally, nutrient availability, temperature, oxygen levels, and moisture content in the soil influence the bio-degradation process [181].

Hydrocarbon-degrading organisms (bacteria) thrive within a specific temperature range, generally between 20 and 300 degrees Celsius, ensuring optimal biodegradation. Temperature influences soil moisture and retention capacity, with higher temperatures accelerating biodegradation rates, while lower temperatures lead to reduced rates [182]. Microorganisms rely on different nutrient categories for hydrocarbon degradation, including macro-, micro-, and trace elements. The primary macronutrients—carbon, phosphorus, and nitrogen—constitute 14% of the microbial dry weight. Certain micronutrients like cobalt, manganese, zinc, iron, and copper are unnecessary for HC-degrading organisms. Hydrocarbon-containing oils can limit soil nutrient accessibility for plant growth, but HC-contaminated sites often offer nutrients for microbial growth and organic substrates as electron donors for bioremediation [183].

Hydrocarbon degradation is most effective within pH ranges of 6 to 8. Suboptimal pH levels hinder microbial and bacterial growth rates. The enzymatic degradability of HC compounds is pH-dependent, influencing the degradation process [38]. The ability of algae to degrade hydrocarbon contaminants is influenced by a combination of factors related to the algal species, the specific hydrocarbon type, and the environmental conditions in which they are deployed [72]. Specific fungi exhibit better hydrocarbon biodegradation at pH 7 than bacteria, which excel at pH 5 [181]. Both anaerobic and aerobic conditions influence hydrocarbon degradation. Oxygen is the final electron acceptor in aerobic respiration, while anaerobic respiration produces nitrate, iron, sulfate, and carbon dioxide. Both aerobic and anaerobic degradation can be affected by many physical, chemical, and biological conditions that influence the overall pollutant degradation efficiency. Several factors, such as pollutant concentration, temperature, pH, availability of inorganic nutrients, and microbial adaptation, influence the rate and extent of biodegradation of BTEX [79,184]. Hydrocarbon compounds degrade rapidly under aerobic conditions, leading to non-toxic byproducts like CO_2 and water. Consequently, elevated oxygen levels facilitate bioremediation [181].

7.2. Enhancement of Bioremediation Conditions

Bioremediation's effectiveness is influenced by diverse factors, including biological elements (microbial populations) and non-biological factors (aeration, moisture, and temperature) [185]. Selecting the right approach is crucial, and advanced sequencing techniques aid in discovering novel microbes in extreme environments [8]. Genome sequencing accelerates microbial identification and strain characterization [37].

Microbial population composition strongly impacts efficiency; however, the optimal composition can vary depending on the type of hydrocarbon contaminants and environmental conditions. Maintaining moisture levels around 50–55% is crucial, with a near-neutral pH for optimal microbial performance. A minimum of 40% organic content and a C/N ratio below 50 facilitate swift biodegradation, ideally at 65–70 °C [186].

7.2.1. Soil Conditions

Chemometrics techniques enhance conditions and efficacy by analyzing input-output relationships, pinpointing factors like pH, temperature, and nutrient concentration that

impact efficiency, and enabling tailored optimization. Data sets encompassing microbial shifts and metabolite production guide progress assessments [187]. Common methods like DoE, RSM, ANN, PCA, and GA aid in this optimization [188]. Leveraging bioinformatics and data analytics, chemometrics offers efficient, cost-effective, and sustainable bioremediation solutions.

7.2.2. Bioreactors

The biodegradation process involves the maturation stage (mesophilic and thermophilic phases) and the curing stage (second mesophilic phase). The mixing ratio significantly influences success, with two-stage methods common for petroleum contaminants. In-vessel reactors are widely used for laboratory experiments on petroleum sludge bioremediation [77]. Successful in situ bioremediation of olive mill waste (OMW) utilized various techniques like biowaste, animal waste, and vermicomposting, effectively degrading phenol compounds [189]. An evaporation pond bioremediation experiment employed a microbial-fungal consortium isolated from OMW [8]. Additional time was needed for in-vessel pyrene-contaminated soil remediation. Various methods, like open-vessel and static pile, yielded efficient results in removing contaminants [189].

Choosing the inoculation method depends on substrates, contaminants, and prevailing conditions. Effective growth of isolated microorganisms or consortia is crucial before introduction into bioreactors, piles, or windrows [77]. Microbial consortia often prove more effective than single population types [144,164].

8. Hydrocarbon Degradation Pathways

The variability within hydrocarbon compounds and microbial communities plays a pivotal role in the biodegradation pathways of these organic molecules. Hydrocarbons constitute a diverse group of compounds, encompassing alkanes, alkenes, aromatics, halogenated hydrocarbons, esters, and more. Each class of hydrocarbon possesses unique chemical properties that directly affect their biodegradability. This variability extends to microbial communities, composed of a wide array of bacteria, archaea, fungi, and other microorganisms, each with distinct enzymatic capabilities for hydrocarbon degradation. These microbial communities utilize specific enzymes tailored to the chemical structures of the hydrocarbons they target, resulting in a highly specialized breakdown process.

Moreover, the metabolic pathways involved in hydrocarbon degradation can differ significantly between microbial groups and individual species, with preferences for aerobic, anaerobic, or facultative anaerobic pathways. Microbial populations exhibit adaptability and evolutionary potential, responding to changes in hydrocarbon contaminant availability and leading to shifts in predominant degradation pathways. Complex mixtures of hydrocarbon compounds in contaminated sites add to the intricacy of biodegradation processes, as different compounds may be degraded by different microbial groups or through distinct pathways.

Microbial populations use diverse pathways for hydrocarbon degradation, which is a complex process. The challenge of breaking down hydrocarbons like petroleum and PAHs arises from their hydrophobic nature. Biosurfactants, containing both polar elements like phosphates and alcohol products as well as non-polar residues like fatty acids, enhance interactions due to their amphiphilic properties, reducing surface and interfacial tensions [190]. For instance, a *Bacillus methylotrophicus* biosurfactant reduces water surface tension by 40% and degrades 92% of crude oil [191]. Another *Bacillus* strain's biosurfactant enhances oil sludge solubilization, bioavailability, emulsification, and biodegradation [192]. Thus, increasing PAHs bioavailability and solubility aids their degradation. A biosurfactant's efficacy depends on its bioavailability, reduced surface tensions, oxygen, and nutrients [190]. The main pathways, aerobic and anaerobic, involve enzymatic activation followed by catalysis. Understanding these mechanisms is vital for efficient bioremediation strategies.

Bacteria use aerobic or anaerobic metabolism for hydrocarbon degradation, with oxygen being more efficient as the terminal electron acceptor in aerobic conditions. Anaerobic scenarios rely on nitrate, sulfate, or iron molecules as acceptors, leading to slower degradation [3,32]. Aerobic degradation converges on the tricarboxylic acid (TCA) cycle, resulting in complete oxidation to CO_2 and NADH. Oxygen is the final electron acceptor, supporting energy production for biosynthesis and bacterial growth [33]. Aerobic hydrocarbon biodegradation involves diverse reactions grouped into peripheral and central metabolic pathways. Oxygenases facilitate oxygenation by introducing hydroxyl groups (-OH) from molecular oxygen (O_2) into the substrate. Monooxygenases introduce one oxygen atom, while dioxygenases introduce both atoms.

Oxygenation reactions require the reduced coenzymes NADH or NADPH, limiting them to intracellular environments due to rapid degradation outside bacterial cells. Monooxygenases target aliphatic and aromatic hydrocarbons, while dioxygenases primarily focus on aromatics. Dioxygenases include ring-activating and ring-opening types, both incorporating oxygen atoms into the substrate. Ring-opening dioxygenases do not require reduced pyridine nucleotides [33].

Bacteria degrade alkane compounds classified by aliphatic hydrocarbon content: low (C8–C16), medium (C17–C28), and high (C29–C35) [193]. Enzymes activate alkane breakdown, oxidized by monooxygenase and dioxygenase, forming alcohols, acids, or CO_2. Alkenes with double bonds are more reactive and oxygenated by monooxygenase to potentially form epoxides. Branched alkanes yield hydroxy and dioic acids, while cycloaliphatic compounds may degrade to adipic acid. Anaerobic bacteria use respiration (e.g., nitrate, sulfate), fermentation, and even anoxygenic phototrophy. Anaerobic hydrocarbon biodegradation occurs via fumarate addition. Key processes include oxygen-independent hydroxylation, carboxylation, saturated bond hydration, reverse methanogenesis, and certain anaerobic fermentation processes [5,194].

Bacterial hydrocarbon degradation relies on enzymes, crucial biological catalysts. Enzymes break down complex hydrocarbons into simpler compounds for microbial metabolism, reducing activation energy. They act on carbohydrates (amylase, cellulase), lipids (lipase), and proteins (protease). Enzymes are further classified based on function: hydrolase, dehydrogenase, isomerase, esterase, oxygenase, and decarboxylase [8,92,194]. Enzymes in hydrocarbon degradation vary based on hydrocarbon type and microbial community. Oxygenase and peroxidase enzymes initiate intracellular oxidation by activating and combining oxygen [58]. Monoxygenases incorporate an oxygen atom into the substrate while removing another from water, with polyaromatic hydrocarbon biodegradation affected by their low solubility and strong adsorption [195]. Dioxygenases couple oxygen molecules (O_2) to form reaction products [195]. Petroleum hydrocarbon susceptibility to microbial degradation follows a descending order: n-alkanes, branched alkanes, low-molecular-weight aromatics, and cyclic alkanes [115].

Anaerobic hydrocarbon breakdown follows two pathways: respiration-driven oxidation with alternate electron acceptors like sulfate or nitrate and fermentation processes [38]. Bacteria utilize electron acceptors such as sulfate, nitrate, iron, manganese, and carbon dioxide for anaerobic petroleum hydrocarbon degradation [180]. Challenges exist for certain bacteria degrading branched alkanes and higher-molecular-weight polyaromatic hydrocarbons [196]. Various enzymes facilitating hydrocarbon compound decomposition are listed in Table 4.

Aerobic aliphatic hydrocarbon degradation involves sub-terminal or terminal oxidation pathways. Sub-terminal oxidation starts with the oxygenation of a sub-terminal methyl group, forming a secondary alcohol that progresses to a ketone and an ester. Ester hydrolysis generates fatty acids and alcohols, both of which are oxidized to their corresponding forms. Terminal oxidation, used by most bacteria, oxygenates the terminal methyl group, yielding an aldehyde and, eventually, a carboxyl group. Fatty acids enter β-oxidation for acetyl-CoA production in the TCA cycle [33]. While aerobic organisms also metabolize aromatic hydrocarbons, naphthalene degradation involves intermediate formation with

a single aromatic ring bearing two hydroxyl groups (dihydroxylate), forming catechol (ortho-diphenol). Catechol 1,2 dioxygenase cleaves the ring at the ortho position, incorporating oxygen atoms into hydroxyl-linked carbon atoms. The bond between carbon atoms at positions 1 and 2 is broken, yielding cis-cismuconic acid, which is converted into succinate and acetyl-CoA. Catechol 2,3 dioxygenase initiates ring cleavage in the meta position, causing the ring to open between a hydroxylated carbon atom and an adjacent non-hydroxylated one. This forms a hydroxymuconic semialdehyde, which is converted through reactions into pyruvate and acetaldehyde.

Table 4. Various enzymes are implied in the bioremediation of pollutants.

Enzyme Name	Organism	Degraded Pollutants	References
Peptidase, Hydrolase	*Pseudoalteromonas*	PAHs	[164,197]
Hydrolase, Peptidase	*Colweillia*		[164,198]
Peptidase, Hydrolase	*Cyclocasticus*		[164]
Cytochrome P450	*Haematococcus pluvialis*		[164]
Hydroperoxidase	*Chlorophyceae* (*Dunaliella tertiolecta*)		[199]
Lipoxygenase			[164,200]
Methane monooxygenase	*Methylomirabilis oxyfera*	Methane	[201]
Cytochrome P-450 dependent alkane monooxygenase	*Alcanivorax* spp.	cycloalkanes	[166,202]
Hydrolase (AlkB1 and AlkB2)		n-alkanes	
Laccase	*Trametes versicolor*, *Pleurotus ostreatus*	Phenolic compounds, dyes, and lignin	[203]
Dehalogenases	*Burkholderia xenovorans*, *Trametes versicolor*	Halogenated compounds, e.g., chlorinated solvents	[204]
Nitroreductase	*Pseudomonas* spp.	Nitroaromatic compounds and nitramine-type explosives	[205]
Alkaline Phosphatase	*Pseudomonas putida*	Phosphorous-containing pollutants, like organophosphates	[206]
Naphthalene Dioxygenase	*Pseudomonas putida*, *Pseudomonas* sp. KK1	(PAHs)	[207]
Methane Monooxygenase	*Methylosinus trichosporium*, *Methylococcus capsulatus*	Methane and other hydrocarbons	[208]
Urease	*Bacillus* sp., *Klebsiella* sp.	Urea and related compounds	[209]
Xylanase	*Aspergillus niger*, *Bacillus* sp., *Trichoderma viride*	Xylan and lignocellulosic materials	[210]
Phosphotriesterase	*Pseudomonas diminuta*, *Agrobacterium radiobacter*	Organophosphates and pesticides	[211]
Glutathione S-Transferase	*Ganoderma* sp.	(PAHs)	[212]
Oxidoreductases	*Pleurotus ostreatus*	Organic compounds, including phenolic pollutants and lignin	[213]
Xanthine oxidase	*Pseudomonas putida*	Purine compounds	[214]
Monooxygenase binding flavin (AlmA)	*Gammaproteobacteria*	Long C_{22} and C_{36} n-alkanes	[164]
	Chlorophyceae		

Microbes enhance degradation through biosurfactants that emulsify hydrocarbons, making them accessible. *Candida sphaerica* and *Candida tropicalis* use biosurfactants like sophorolipids for impressive removal (75% to 97%) [77]. Other biosurfactants, including glucolipids and lipopeptides, effectively remove contaminants [57,66,67]. Understanding microbial roles helps grasp metabolic processes [215]. Further research is needed to uncover complexities involving non-biological agents [8,215].

8.1. Enzymatic Responses and Hydrocarbon Degradation Genes

8.1.1. Hydrocarbon Degradation Enzymes

Aromatic organic compounds pose challenges to rapid biodegradation due to their low solubility, toxic byproducts, and preferred substrates, leading to slower degradation rates

than other compounds [181]. To overcome these limitations, enzyme-based biocatalysis, known as white biotechnology, emerges as a promising alternative. Enzymes offer advantages in bioremediation: they work under adverse conditions, resist metabolic inhibitors, remain active with antimicrobial agents, exhibit mobility, and function intracellularly or extracellularly [216]. Notably, hydrolases, dehalogenases, transferases, and oxidoreductases from bacteria, fungi, and plant-associated microbes play key roles in breaking down ester, amide, and peptide bonds [216]. Enzymes like naphthalene dioxygenase and cytochrome P450 facilitate hydrocarbon degradation [58]. Analyzing enzymes like leucine aminopeptidase, B-glucosidase, and alkaline phosphatase allows for degradation rate calculation [38]. The widespread co-thiolate monooxygenase superfamily, including cytochrome P450 alkane hydroxylase, plays a pivotal role in the microbial degradation of various substances, with enzyme systems required for substrate oxygenation and biodegradation initiation [217]. Cytochrome P450 enzyme systems significantly contribute to petroleum hydrocarbon biodegradation.

Certain aromatic hydrocarbons, like BTEX, are present in petroleum, with naphthalene being the simplest form of PAHs containing two rings. Although co-metabolic activities have been noticed, it is still difficult for bacteria to use large molecular-weight aromatic molecules, such as benzopyrene, as their exclusive energy source [38]. Aerobic bacteria employ dioxygenase enzyme systems to catalyze the oxidation of arenes, generating vicinal cis-dihydrodiols as the initial intermediate in aromatic hydrocarbon degradation. These dihydroxylation byproducts undergo ring cleavage via intra- or extra-diol ring-cleaving dioxygenases, following either an ortho- or meta-cleavage pathway. This process produces intermediates like protocatechuate and catechols, which, when using benzene as an example, enter the TCA cycle to provide the cell with carbon and energy via metabolite breakdown [181].

PAHs undergo molecular degradation or structural transformation through enzymatic reactions involving various metabolic pathways. This intricate process comprises sequential cascade enzymatic reactions and multiple gene involvement. The main mechanisms are hydroxylation and oxidation, particularly effective for low molecular weight (LMW) PAHs due to the increased hydroxylation sites as the ring count rises [144,218,219]. Ligninolytic fungi have unique enzyme production capabilities, particularly tailored for their substrates. These fungi could oxidize PAHs through extracellular peroxidases, mainly facilitated by enzyme-mediated lignin peroxidation. Fungal lignin peroxidases directly oxidize several PAHs, while manganese peroxidases in fungi cooxidize themin. Although fungi may not degrade PAHs as rapidly or effectively as bacteria, their versatility enables them to target a wide range of xenobiotics. Fungi in soil litter can contribute to PAH removal by infiltrating soil and spreading throughout the solid matrix, underscoring their ecological importance in bioremediation. Furthermore, numerous fungal enzymes, including MnP, LiP, and laccase, participate in PAH degradation [220].

8.1.2. Hydrocarbon Degradation Genes

The genes responsible for enzymes engaged in peripheral metabolic pathways for aliphatic hydrocarbons include alkB, acmAB, prmABCD, and ladA. The alkB gene encodes alkane 1-monooxygenase, an integral membrane protein that initiates hydroxylation of n-alkanes (C5–C12) to form 1-alkanols. This enzyme is present in *Pseudomonas* spp. and *Rhodococcus* spp. [4,61]. Meanwhile, the ladA (long-chain alkane monooxygenase) gene contributes to the terminal oxidation of long-chain alkanes, catalyzing oxygen insertion. This gene was identified in *Acinetobacter*, *Pseudomonas*, *Delftia*, and *Achromobacter* [221,222].

Typically encoding ring-hydroxylating dioxygenases and monooxygenases, these genes break down aromatic rings. For instance, bphAa encodes biphenyl 2,3-dioxygenase, transforming biphenyl to benzoate [223]. The peripheral metabolic pathways for aliphatic hydrocarbon degradation in various bacteria are also linked to genes like nahAa, nagG, phtAa, pht3, mhpB, hcaE, bphAa, etbAa, cmtAb, cmtC, carAa, phdF, nidA, tphA2, antA, benA, bphC, pobA, nahAb, nahC, and poxA [31]. These genes encode specific enzymes

and proteins involved in the breakdown of aliphatic hydrocarbons. In central metabolic pathways, intermediates from peripheral pathways are further processed to yield fatty acid molecules, eventually entering β-oxidation and the tricarboxylic acid cycle (TCA) [224]. Genes such as chqB, pcaG, catAE, badA, ligA, hmgA, and the boxABCD cluster genes are involved in hydrocarbon central pathways for aromatic degradation by certain bacterial species. The boxABCD genes encode benzoyl-CoA 2,3 epoxidase, converting benzoate to intermediates for the Krebs cycle [223]. Intermediates undergo oxidative phosphorylation following entry into the Krebs cycle (TCA cycle).

Genes coding for enzymes in xenobiotic substance degradation and metabolism are typically found in plasmids [32], allowing for a swift response to hydrocarbon contamination. However, the simultaneous presence of aerobic and anaerobic conditions and high- and low-molecular-weight hydrocarbons in the same environment is rare in natural ecosystems. Consequently, most hydrocarbons tend to persist. To address this, biostimulation and bioaugmentation methods are needed for effective hydrocarbon removal.

The *M. vanbaalenii* PYR-1 strain employs dual pathways for pyrene metabolism. One route involves C1 and C2 deoxygenation, generating o-methylated derivatives leading to pyrene 1-2-diol [225]. The alternative pathway focuses on C4 and C5 deoxygenation in the K-region, culminating in comprehensive degradation. NidA/B genes act as indicators of pyrene-degrading microorganisms, encoding subunits (A and B) of ring hydroxylating oxygenase responsible for distinct deoxygenation events [219]. The C1 and C2 deoxygenation tasks are managed by the NidA3B3 genes, yielding 1-2 dihydroxypyrene [219]. Catechol o-methyl transferase, coded by MT1743, drives the conversion of 1-hydroxy-2-methyloxypyrene into 1-2 dimethylpyrene [218]. In terms of metabolic genes, PdoA2B2 encodes phenanthrene ring-hydroxylating oxygenase (A2 and B2), orchestrating the conversion of 4-phenanthroate to cis-3-4-dihydroxyphenanthrene-4-carboxylate [226]. NidD, a catabolic gene, is in charge of aldehyde dehydrogenase, which facilitates the transformation of 2-carboxylbenzaldehyde into phthalate [227]. Phthalate undergoes conversion to phthalate 3-4 dihydrodiol by PhtAaAb-encoded phthalate 3-4 dioxygenase (α-subunit Aa and β-subunit Bb) [228]. Subsequently, the conversion of phthalate 3-4 dihydrodiol to 3-4 dihydroxy phthalate is executed by phthalate 3-4 dihydrodiol dehydrogenase, encoded by PhtB [229].

9. Recent Advances in Biodegradation and Bioremediation Research

Recently, several advancements have been made in biodegradation and bioremediation research. Some important techniques used to study these processes include isotope monitoring, modeling, and multi-omics approaches [230]. Isotope monitoring is a valuable tool for biodegradation and bioremediation research. By providing insights into the microbial pathways responsible for biodegradation, the effectiveness of bioremediation treatments, and the fate and transport of pollutants in the environment, isotope monitoring can help to develop new and more effective bioremediation strategies [231]. This technique utilizes stable isotopes, such as carbon-13 (13C) or nitrogen-15 (15N), or radioisotopes, like tritium (3H) and carbon-14 (14C), to track the movement and transformation of specific elements or compounds [232]. This technique involves the application of stable and radioactive isotopes to follow the fate of contaminants in ecosystems [233]. Researchers can monitor their dispersion, transformation, and biodegradation processes by labeling contaminants with specific isotopes. Isotope monitoring is instrumental in quantifying the rate of contaminant degradation and identifying the microbial communities responsible for these processes [234]. Moreover, it aids in assessing the success of bioremediation efforts, evaluating the bioavailability of contaminants to microorganisms, and comparing the efficiency of various remediation technologies [235].

Modeling serves as an indispensable and multifaceted tool in biodegradation and bioremediation research, playing a pivotal role in understanding, optimizing, and tracking environmental cleanup processes [236]. It enables the prediction of contaminant behavior and the refinement of cleanup strategies. Models help comprehend complex microbial

interactions, quantify biodegradation kinetics, and support risk assessments [237]. By simulating various remediation techniques, they assist in identifying the most effective approach for specific contaminants and sites. Additionally, mathematical models offer insights into degradation rates, metabolic pathways, and factors influencing the process [238]. They facilitate estimates of the potential impact of contaminants on human health and the environment while guiding decision-making for appropriate remediation strategies. Furthermore, modeling leads to cost savings and a reduced environmental footprint associated with cleanup efforts [239].

Multi-omics approaches have revolutionized biodegradation and bioremediation research, significantly advancing our comprehension of complex environmental processes. These methodologies encompass various omics disciplines, including genomics, metagenomics, proteomics, and metabolomics, to comprehensively analyze microbial communities and their interactions with contaminants [230]. In bioremediation, multi-omics techniques are invaluable for optimizing treatment strategies. Metagenomics helps identify novel biodegradation pathways and select appropriate microbial consortia for specific contaminants [240]. Proteomics provides insights into the expression of key enzymes involved in pollutant transformation, aiding in the design of efficient bioremediation processes [241]. In the context of biodegradation, multi-omics approaches offer a comprehensive perspective on the microbial communities responsible for pollutant degradation. Genomic analysis aids in the identification of specific genes and metabolic pathways involved in contaminant breakdown, thereby revealing the genetic potential of microbial communities [242]. Metagenomic sequencing enables the exploration of entire microbial populations, unveiling the diversity of species engaged in biodegradation processes [240]. Proteomics and metabolomics illuminate the proteins and metabolites generated during biodegradation, facilitating a deeper understanding of microbial community functionality [241]. Accordingly, the multi-omics approaches enhance our knowledge of biodegradation and bioremediation and improve our ability to monitor and control these processes. They empower researchers to develop more effective and sustainable environmental cleanup strategies by deciphering the molecular mechanisms underlying microbial interactions with contaminants.

10. Challenges and Future Prospects in Bioremediation

Persistent petroleum hydrocarbon pollutants, recognized for their resistance to degradation, inflict lasting harm on ecosystems. Due to their hydrophobic and insoluble properties, these pollutants remain largely inaccessible to microbes. Nonetheless, biodegradation faces constraints stemming from contaminant properties, microbial limitations, and limited bioavailability. Noteworthy microorganisms like *Pseudomonas* sp., *Micrococcus* sp., *Nocardiopsis* sp., *Bacillus* sp., and *Acinetobacter radioresistens* display competence in hydrocarbon degradation [243–245]. Strategies vary based on contaminant type, duration, and site-specific conditions, encompassing in situ, ex situ, or in-vessel methods. Validation on larger scales and in-field settings is vital beyond lab-scale experiments [246]. Translating successful enhanced removal techniques from lab to practical treatment systems presents a challenge that needs to be addressed for the field's advancement. Biodegradation emerges as a promising solution in the quest to address pollution [247]. However, bridging the gap between lab success and real-world application poses a significant challenge, demanding innovative strategies. Despite successful lab outcomes, applying enhanced removal techniques practically remains a hurdle, necessitating inventive approaches to bridge the gap. Integrating lab-derived insights into field-scale implementation is crucial for ensuring consistent and efficient remediation in complex real-world settings.

Employing Bushnell-Haas medium with 1% crude oil or kerosene and a 0.5 McFarland isolate solution aids in isolating petroleum-degrading bacteria, achieving up to 90% removal of total petroleum hydrocarbons (TPHs) [77,248]. Successful bioremediation hinges on substrate selection, ratios, microbial profiles, biogeochemical transformations, and physical parameters. Pre-treatments, engineering interventions, and numerical simulations optimize efficiency [246]. Costs vary based on site location, contamination severity,

and treatments. Immobilized enzyme approaches on iron oxide surfaces offer an innovative solution for enhancing hydrocarbon degradation. Modified enzymes, microbial adsorption methods, and site-specific mutations show promise in boosting oxidation and biodegradation rates [215,249,250]. By reshaping enzymatic reactions through these methods, bioremediation efficiency is bolstered, contributing to sustainability by conserving resources and protecting ecosystems [8].

Further investigation is warranted regarding the anaerobic elimination and transformation of PAHs, particularly high-molecular-weight ones. Understanding anaerobic removal pathways, kinetics, enzyme regulations, and genetic aspects of wastewater and sludge treatment requires attention [38]. Various soil treatment strategies have been developed for PAH-contaminated industries, effective on a field scale and contingent on site-specific factors [251]. While each method has strengths and weaknesses, no universal approach for PAH removal exists. Future research can integrate tailored remediation methods for different soil types to enhance PAH degradation efficacy, requiring thorough site assessments [252]. Amidst conventional methods' technical and economic challenges, biodegradation emerges as a promising pollution mitigation strategy [247]. Offering eco-friendly and cost-effective benefits, biodegradation is adaptable to specific contaminants. Despite challenges in terms of contaminant properties, microbial performance, and bioavailability, biodegradation remains an appealing avenue for pollution remediation, contributing to sustainable environmental restoration efforts [38].

11. Conclusions

Hydrocarbon contaminants raise ecological and health concerns and pose challenges due to their low reactivity and hydrophobic nature, requiring solvents for bacterial degradation. Bioremediation offers a practical, cost-efficient chemical control alternative, relying on interdisciplinary teams such as microbiology, ecology, chemistry, geology, and engineering. Two main approaches provide substrates: direct cell contact and biosurfactant interaction. Individual microorganisms, or consortia, can regulate polluted environments by degrading these pollutants. Removing hydrocarbon contamination from the environment typically demands bacterial consortia rather than single species. Bacterial metabolism depends on genes encoding key enzymes in peripheral and central pathways for breaking down aliphatic and polycyclic aromatic hydrocarbons. The involved aerobic and anaerobic catabolic routes aid in designing effective bioremediation for petroleum hydrocarbon pollutants. Understanding catabolic routes aids in designing pollutant removal solutions. Advanced techniques such as enzyme modification, microbe alteration, and microbial adsorption require scaling for practical application. This comprehensive approach speeds up bioremediation by optimizing enzyme and microbial activity, while insights into mechanisms improve reaction rates. Immobilized enzymes and altered binding processes notably boost biodegradation. Advanced tools speed up bioremediation, and understanding microbial action aids target enhancement. Considering unique ecosystem conditions during transition, advancing field-scale understanding is crucial for real-world use. So, there is an ongoing necessity to investigate and enhance bioremediation methods for efficiently cleaning hydrocarbon-contaminated sites and promoting eco-sustainable development.

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