



International Journal of Agriculture and Food Science

ISSN Print: 2664-844X

ISSN Online: 2664-8458

NAAS Rating (2026): 4.97

IJAFA 2026; 8(10): 159-167

www.agriculturaljournals.com

Received: 13-08-2026

Accepted: 24-09-2026

Published: 07-10-2026

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Aerobic petroleum hydrocarbon-degrading bacteria in oil spill bioremediation: mechanisms, microbial diversity, omics and emerging technologies

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DOI: <https://www.doi.org/10.33545/2664844X.2026.v8.i10c.2014>

ABSTRACT

Petroleum hydrocarbons (PHCs) contamination remains a major global environmental challenge due to its persistence, toxicity and widespread distribution. Aerobic bacterial bioremediation offers an eco-friendly and cost-effective alternative to conventional remediation methods by utilizing oxygen-dependent metabolic pathways to degrade hydrocarbons into non-toxic end products. Recent advances in genomics, metagenomics and other omics technologies have enhanced our understanding of hydrocarbon-degrading microorganisms, their functional genes and metabolic networks, enabling the development of more efficient bioremediation strategies. This review highlights the diversity of aerobic hydrocarbon-degrading bacteria, degradation mechanisms, biosurfactant-assisted remediation, environmental factors affecting biodegradation and emerging biotechnological approaches, emphasizing their potential for sustainable restoration of petroleum hydrocarbon-contaminated ecosystems.

Keywords: Petroleum hydrocarbons, Aerobic biodegradation, Bioremediation, Hydrocarbon-degrading bacteria, Biosurfactants, Monooxygenase, Dioxygenase, Metagenomics, *Microbial consortia*, Environmental biotechnology

1. Introduction

Petroleum is one of the most important natural resources supporting global industrial development, transportation, agriculture, manufacturing, and energy production (Speight, 2006) [1]. Despite the growing transition toward renewable energy, petroleum continues to supply a substantial proportion of the world's primary energy demand (IEA, 2024) [2]. However, extensive exploration, extraction, refining, transportation, storage, and utilization of petroleum have resulted in widespread environmental contamination through accidental oil spills, pipeline leakages, refinery effluents, offshore drilling accidents, and improper disposal of petroleum-derived wastes (National Research Council, 2003) [3]. Consequently, petroleum hydrocarbon pollution has become one of the most persistent and challenging environmental problems affecting terrestrial, freshwater and marine ecosystems worldwide (Varjani, 2017; Atlas *et al.*, 2011) [5, 4].

Petroleum hydrocarbons comprise a highly complex mixture of aliphatic, aromatic, cyclic, and heterocyclic compounds that differ considerably in their chemical structure, molecular weight, volatility, solubility, toxicity, and biodegradability (Speight, 2020; Wang *et al.*, 2023) [6]. Among these compounds, benzene, toluene, ethylbenzene, xylene (BTEX) and polycyclic aromatic hydrocarbons (PAHs) are of particular environmental concern because of their persistence, toxicity, mutagenicity, carcinogenicity, and tendency to accumulate in ecosystems (IARC, 2012; Kim *et al.*, 2013) [7, 8]. Once released into the environment, petroleum hydrocarbons adversely affect soil fertility, microbial diversity, nutrient cycling, plant productivity, aquatic biodiversity and overall ecosystem functioning, while posing significant risks to wildlife and human health (Sharma *et al.*, 2022) [9].

Conventional remediation technologies such as excavation, soil washing, thermal desorption, chemical oxidation, solvent extraction and incineration have been widely employed to remediate petroleum-contaminated environments (Vidali, 2001; Megharaj *et al.*, 2011) [10]. Although these methods often achieve rapid contaminant removal, they are generally associated with high operational costs, intensive energy consumption, incomplete degradation, generation of secondary pollutants and disruption of native microbial communities (Azubuike *et al.*, 2016) [11]. These limitations have stimulated increasing interest in environmentally sustainable and cost-effective biological remediation technologies (Das *et al.*, 2011; Varjani, 2017) [12, 5].

Bioremediation has emerged as one of the most promising approaches for the restoration of petroleum-contaminated environments because it exploits the natural metabolic capabilities of microorganisms to transform or completely mineralize petroleum hydrocarbons into carbon dioxide, water, and microbial biomass (Varjani and Upasani, 2017). Among the diverse hydrocarbon-degrading microorganisms, aerobic bacteria represent the most efficient degraders under oxygen-rich conditions owing to their remarkable metabolic

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versatility and possession of highly specialized oxygenase enzymes (Rojo, 2009; Das *et al.*, 2011) [13, 12]. Aerobic biodegradation begins with monooxygenase- and dioxygenase-mediated oxidation of hydrocarbons, producing oxygenated intermediates that subsequently enter central metabolic pathways for complete mineralization (Van Beilen and Rojo, 2009). Consequently, aerobic biodegradation constitutes the predominant natural attenuation mechanism operating in most contaminated terrestrial and aquatic ecosystems (Head *et al.*, 2006) [14]. Numerous bacterial genera, including *Pseudomonas*, *Acinetobacter*, *Alcanivorax*, *Marinobacter*, *Rhodococcus*, *Bacillus*, *Sphingomonas*, *Gordonia*, *Dietzia*, *Mycobacterium* and *Paracoccus*, have demonstrated exceptional capacities to degrade a broad spectrum of petroleum hydrocarbons ranging from short-chain alkanes to highly recalcitrant polycyclic aromatic hydrocarbons (Yakimov *et al.*, 2007; Ghosal *et al.*, 2016) [15]. These microorganisms possess diverse catabolic genes and enzyme systems, including alkane hydroxylases, cytochrome P450 monooxygenases, dioxygenases and aromatic-ring cleavage enzymes, enabling efficient degradation of structurally diverse hydrocarbons (Nie *et al.*, 2014) [16]. In addition, many hydrocarbon-degrading bacteria synthesize biosurfactants that increase hydrocarbon solubility and bioavailability, thereby significantly enhancing biodegradation efficiency (Ron and Rosenberg, 2002; Banat *et al.*, 2014) [17].

Recent advances in molecular biology and omics technologies have substantially transformed petroleum bioremediation research (Bharagava *et al.*, 2023; Saxena *et al.*, 2022) [18, 19]. High-throughput sequencing, metagenomics, metatranscriptomics, metaproteomics, metabolomics, comparative genomics, and systems biology have significantly improved our understanding of microbial diversity, functional genes, metabolic pathways and microbial interactions involved in hydrocarbon degradation (Bharagava *et al.*, 2023; Varjani *et al.*,

2020) [18, 20]. Furthermore, emerging technologies such as synthetic biology, genome editing, artificial intelligence, machine learning and nanotechnology are creating new opportunities for developing highly efficient, predictive and sustainable bioremediation strategies capable of addressing increasingly complex environmental contamination (Saxena *et al.*, 2022; Bharagava *et al.*, 2023) [19, 18].

Despite remarkable scientific progress, several challenges continue to limit the large-scale application of microbial petroleum bioremediation. Environmental heterogeneity, low hydrocarbon bioavailability, nutrient limitation, fluctuating climatic conditions, toxicity of complex hydrocarbon mixtures, ecological competition, and regulatory constraints frequently reduce the effectiveness of field-scale remediation. Therefore, integrating microbial ecology, environmental engineering, molecular biology, computational modeling and systems biotechnology is essential for developing robust and site-specific remediation approaches.

This review provides a comprehensive and critical overview of aerobic petroleum hydrocarbon-degrading bacteria and their role in sustainable environmental bioremediation. It summarizes the classification and environmental impacts of petroleum hydrocarbons, mechanisms of aerobic microbial degradation, diversity of hydrocarbon-degrading bacteria, biosurfactant production, environmental factors influencing biodegradation, recent advances in omics technologies, artificial intelligence-assisted remediation, synthetic biology, representative case studies, current limitations, and future research directions. By integrating classical microbiological knowledge with modern biotechnological innovations, this review aims to provide a valuable resource for researchers, environmental scientists, engineers, and policymakers engaged in the sustainable management of petroleum-contaminated environments.

Table 1. Classification of petroleum hydrocarbons based on representative compounds, physicochemical properties and biodegradability

Hydrocarbon Class	Representative Compounds	Physicochemical Characteristics	Relative Biodegradability
Aliphatic Hydrocarbons	<i>n</i> -Alkanes, Isoalkanes, Cycloalkanes	Low molecular weight, non-polar, low water solubility	High
Monoaromatic Hydrocarbons (BTEX)	Benzene, Toluene, Ethylbenzene, Xylene	Volatile, toxic, moderately soluble in water	Moderate to High
Polycyclic Aromatic Hydrocarbons (PAHs)	Naphthalene, Phenanthrene, Anthracene, Pyrene, Benzo[a]pyrene	Hydrophobic, persistent, high molecular weight	Low to Moderate
Resins	Nitrogen-, sulfur- and oxygen-containing polar compounds	Polar, viscous, chemically complex	Low
Asphaltenes	High-molecular-weight polyaromatic compounds	Highly complex, insoluble, recalcitrant	Very Low

2. Sources and environmental impact of petroleum hydrocarbon pollution

Petroleum hydrocarbon contamination arises from both natural geological processes and anthropogenic activities associated with the exploration, extraction, processing, transportation, storage and utilization of crude oil and petroleum-derived products. Natural seepage is estimated to contribute approximately 40–50% of global crude oil inputs into marine environments, although anthropogenic releases account for most environmentally significant contamination events (Atlas *et al.*, 2011; Speight, 2006) [4, 1].

2.1 Sources of petroleum hydrocarbon pollution

Petroleum hydrocarbon (PHC) contamination originates from both natural and anthropogenic processes; however, anthropogenic activities are responsible for most environmentally significant contamination events worldwide (National Research Council, 2003; Fingas, 2018) [3, 21]. The rapid expansion of petroleum exploration, offshore drilling, refining, transportation, and petrochemical industries has substantially increased hydrocarbon releases into terrestrial and aquatic ecosystems (Speight, 2020; IEA, 2024) [2]. Continued urban-

ization and growing global energy demand have further intensified the spatial distribution and frequency of contamination events (United Nations Environment Programme [UNEP], 2021; IEA, 2024) [2]. Unlike naturally occurring hydrocarbon seeps, anthropogenic contamination often introduces petroleum at concentrations that exceed the natural biodegradation capacity of indigenous microbial communities, resulting in long-term ecological degradation and increased human health risks (Atlas *et al.*, 2011; Das *et al.*, 2011) [4, 12].

Recent global assessments indicate that chronic low-level petroleum contamination from industrial activities contributes substantially to cumulative environmental pollution because these continuous releases persist for extended periods and affect extensive geographical regions (National Research Council, 2003; Fingas, 2018) [3, 21].

Natural petroleum seepage represents one of the oldest mechanisms by which hydrocarbons enter the biosphere (Kvenvolden *et al.*, 2003; Etiope, 2015) [23, 22]. Geological fractures, tectonic faults, sedimentary basin migration, submarine vents, and natural bitumen seeps (including mud volcanoes) continuously release crude oil and natural gas into marine and terrestrial environments (Etiope *et al.*, 2002; Kvenvolden *et al.*, 2003) [24, 23]. These natural seeps have existed for millions of years and have played a fundamental role in the evolution

of indigenous hydrocarbon-degrading microorganisms (Head *et al.*, 2006; Yakimov *et al.*, 2007) [14, 15]. Consequently, microbial populations inhabiting seep-associated environments often possess highly specialized catabolic pathways that enable the efficient utilization of alkanes, cycloalkanes, and aromatic hydrocarbons as carbon and energy sources (Yakimov *et al.*, 2007; Rojo, 2009) [15, 13]. Although natural seepage contributes a measurable proportion of global hydrocarbon emissions, these releases generally occur gradually and permit long-term microbial adaptation, thereby limiting ecological disruption compared with sudden anthropogenic spills, although localized ecological impacts may still occur in sensitive environments (National Research Council, 2003; Fingas, 2018) [3, 21].

Among anthropogenic sources, petroleum exploration and extraction activities represent major contributors to environmental petroleum hydrocarbon contamination worldwide (Speight, 2020; Fingas, 2018) [21]. Drilling operations generate drilling muds, drill cuttings, produced water, flowback water, lubricants, completion fluids, and may also result in accidental blowouts that introduce petroleum constituents into surrounding soils, groundwater, rivers, coastal environments, and marine ecosystems (Neff *et al.*, 2011; Lee and Page, 1997) [25]. Offshore drilling platforms present additional environmental risks because equipment failure, pipeline rupture, wellhead leakage, and uncontrolled pressure release can rapidly discharge large quantities of crude oil into marine environments (National Commission on the BP Deepwater Horizon Oil Spill and Offshore Drilling, 2011; Kingston, 2002). Even under normal operating conditions, routine maintenance activities, produced water discharge, and minor leakages contribute to chronic hydrocarbon inputs that may alter microbial community composition, reduce biodiversity, and affect ecosystem functioning in adjacent environments (Neff *et al.*, 2011; Cordes *et al.*, 2016).

Transportation of crude oil and refined petroleum products represents another major source of petroleum hydrocarbon release into the environment. Oil tankers, marine shipping, railway transport, road tankers, inland barges, pipelines, storage terminals and distribution facilities Support with the latest IEA (2024) [2] or Energy Institute Statistical Review (2024) [26]. Pipeline corrosion, mechanical damage, illegal tapping, natural disasters, operational errors and equipment fatigue frequently result in leakage of diesel, gasoline, kerosene, lubricating oil and crude petroleum into agricultural land and freshwater resources. Pipeline failures are particularly concerning because leaks often remain undetected for extended periods, allowing hydrocarbons to infiltrate subsurface soils and groundwater before remediation efforts begin. In many countries, particularly in developing countries where infrastructure maintenance may be limited.

Petroleum refining and petrochemical industries generate a wide range of hydrocarbon-containing wastes during crude oil processing, catalytic cracking, distillation, reforming, storage, blending, and product manufacturing (Speight, 2020; Wake, 2005) [27]. Refinery wastewater commonly contains dissolved hydrocarbons, phenolic compounds, polycyclic aromatic hydrocarbons (PAHs), sulfides, ammonia, suspended solids, heavy metals and various toxic organic compounds (Diya'uddeen *et al.*, 2011; Aljuboury *et al.*, 2017). Although modern refineries employ wastewater treatment systems, accidental bypasses, equipment malfunctions, overflow events, and inadequate treatment efficiency may still result in the discharge of residual petroleum contaminants into receiving water bodies (Diya'uddeen *et al.*, 2011; Varjani *et al.*, 2020) [20]. Long-term exposure to refinery effluents has been associated with deterioration of aquatic biodiversity, sediment contamination and alterations in microbial ecosystem functioning (Johnsen *et al.*, 2005; Cordes *et al.*, 2016).

Urban environments contribute substantially to diffuse petroleum pollution through stormwater runoff (Zgheib *et al.*, 2012) [28]. Vehicle-derived hydrocarbons originating from roads, parking areas, airports, railway stations, industrial zones, and residential neighbourhoods are transported into nearby aquatic ecosystems during rainfall events (Kayhanian *et al.*, 2012; Mahler *et al.*, 2019) [29]. Motor oil leakage, tire wear particles, brake pad residues, fuel spills at filling stations, at-

mospheric deposition of combustion products, and accidental discharge from automobile repair facilities collectively generate complex mixtures of petroleum hydrocarbons that accumulate within urban drainage systems (Wei *et al.*, 2018). During rainfall events, these contaminants are transported into rivers, lakes, wetlands, and estuaries, where repeated low-level inputs gradually produce chronic contamination despite the absence of major oil spill incidents (Mahler *et al.*, 2019; Wei *et al.*, 2018) [29]. Urban stormwater runoff is now recognized as one of the major non-point sources of petroleum hydrocarbon contamination in rapidly urbanizing regions (Mahler *et al.*, 2019; Sharma *et al.*, 2022) [29, 9].

Agricultural activities also contribute indirectly to petroleum hydrocarbon contamination through the extensive use of diesel-powered machinery, irrigation pumps, tractors, harvesters and fuel storage facilities (Aislabie *et al.*, 2004; FAO, 2022) [30]. Leakage from agricultural machinery, fuel storage tanks, improper disposal of lubricants, accidental diesel spills and inadequate storage practices may contaminate cultivated soils, particularly in regions characterized by intensive mechanized farming (Wu *et al.*, 2021) [31]. Although agricultural contamination events are generally localized, repeated hydrocarbon inputs may reduce soil fertility by altering microbial biomass, suppressing nitrogen cycling, impairing soil enzymatic activities and decreasing crop productivity (Megharaj *et al.*, 2011; Chaineau *et al.*, 2003) [10]. These adverse effects become more pronounced following prolonged or repeated petroleum inputs (Balseiro-Romero *et al.*, 2018) [32].

Military operations, airports, ports, and defense installations represent additional anthropogenic sources of petroleum contamination (Cachada *et al.*, 2018; Anderson *et al.*, 2012) [33]. Aviation fuel, jet fuel, hydraulic fluids, lubricants, diesel, gasoline, and bunker fuel are extensively handled within these facilities, increasing the probability of accidental releases during storage, transportation, fueling operations, equipment maintenance and emergency response activities (ITOPF, 2023; Fingas, 2018) [21]. Historical military sites frequently exhibit persistent petroleum hydrocarbon contamination, often accompanied by co-contaminants such as per- and polyfluoroalkyl substances (PFAS) (Anderson *et al.*, 2016; Brusseau *et al.*, 2020) [34]. Such contaminated sites often require integrated remediation strategies combining physicochemical treatment with microbial biodegradation to achieve effective environmental restoration (Khan *et al.*, 2022).

Improper management of petroleum wastes further exacerbates environmental contamination (Khan *et al.*, 2022; Wake, 2005) [27]. Illegal dumping of used engine oil, waste lubricants, oily sludge, refinery residues, drilling wastes and contaminated industrial wastewater introduces complex hydrocarbon mixtures into landfills, vacant land, drainage channels and watercourses (El Naggar *et al.*, 2018; Wake, 2005) [35, 27]. Waste engine oil is particularly hazardous because, in addition to petroleum hydrocarbons, it frequently contains heavy metals, combustion-derived polycyclic aromatic hydrocarbons (PAHs), additives and oxidation products that increase environmental toxicity while simultaneously inhibiting microbial degradation (ATSDR, 1997; El Naggar *et al.*, 2018) [35]. These mixed contaminants complicate remediation efforts because microorganisms must tolerate multiple environmental stressors simultaneously (Khan *et al.*, 2022; Varjani *et al.*, 2020) [20].

Climate change has emerged as an additional factor influencing petroleum pollution dynamics (Field *et al.*, 2014; NASEM, 2022) [36]. Increasing frequency of hurricanes, cyclones, floods, coastal erosion and extreme precipitation events elevates the probability of infrastructure damage, pipeline rupture, storage tank overflow, and accidental release of petroleum products into surrounding ecosystems (Jonkman, 2005; Dawson *et al.*, 2020) [38, 37]. Rising sea levels may also accelerate the corrosion of coastal petroleum infrastructure, while thawing permafrost in Arctic regions poses additional risks to pipelines and drilling facilities (AMAP, 2021; Hjort *et al.*, 2022) [39, 40]. Consequently, the spatial distribution and persistence of petroleum contamination are expected to be increasingly influenced by climate-

driven environmental disturbances, emphasizing the need for resilient remediation strategies capable of maintaining effective performance under changing environmental conditions (NASEM, 2022; Schaefer *et al.*, 2023).

Conceptual overview of the major natural and anthropogenic sources of petroleum hydrocarbon pollution, their transport pathways and their impacts on terrestrial and aquatic ecosystems, biodiversity, ecosystem functioning and human health.

2.2 Environmental impact of petroleum hydrocarbon pollution

2.2.1 Impact on soil

Soil is a fundamental natural resource supporting agricultural productivity, ecosystem functioning, nutrient cycling and biodiversity. Petroleum hydrocarbon contamination has represented a major threat

to soil quality due to increasing industrialization, accidental oil spills, leakage from pipelines, refinery discharges, transportation accidents and improper disposal of petroleum products. Once released into soil, petroleum hydrocarbons (PHCs) alter the physical, chemical and biological properties of the soil, leading to long-term environmental degradation. The extent of damage depends on the composition of hydrocarbons, contamination level, soil type, climatic conditions and the indigenous microbial community. High concentrations of total petroleum hydrocarbons (TPHs) often persist for years depending on climate, soil characteristics and microbial activity because several hydrocarbon fractions, particularly polycyclic aromatic hydrocarbons (PAHs), resins and asphaltenes, exhibit high hydrophobicity and resistance to natural degradation, thereby complicating remediation efforts. (Das *et al.*, 2011; Xu *et al.*, 2018; Mekonnen *et al.*, 2024) [12, 41, 42].

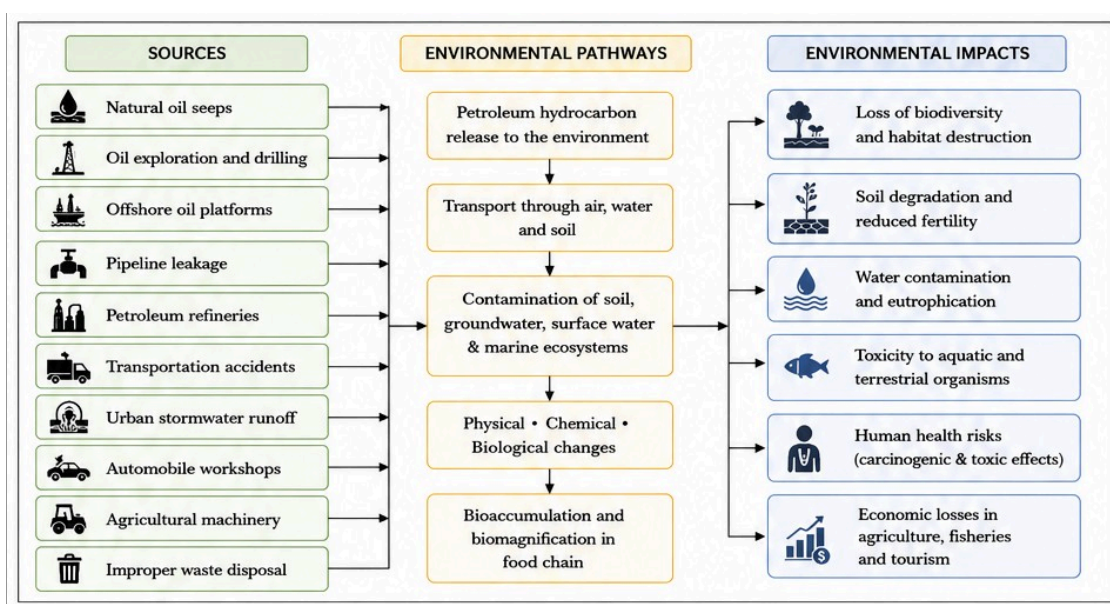


Figure 1. Major Sources, Environmental Transport Pathways and Ecological Impacts of Petroleum Hydrocarbon Pollution

Petroleum hydrocarbons profoundly modify the physicochemical characteristics of soil. Oil forms a hydrophobic coating around soil particles, reducing pore space, limiting water infiltration, decreasing hydraulic conductivity and restricting gaseous exchange between the atmosphere and soil. Consequently, oxygen availability declines, creating unfavorable conditions for aerobic microorganisms and plant root respiration. Soil bulk density generally increases, whereas soil porosity and aggregate stability decrease, resulting in poor soil structure and reduced root penetration. These changes impair the soil's capacity to retain moisture and nutrients, ultimately reducing agricultural productivity and ecosystem resilience (Varjani, 2017; Saxena *et al.*, 2020; Mekonnen *et al.*, 2024) [5, 42].

Petroleum hydrocarbons influence soil pH, electrical conductivity, cation exchange capacity and organic carbon content. total organic carbon (TOC) often increases soil organic carbon because of the addition of hydrocarbon-rich compounds; however, these compounds are largely unavailable to plants and microorganisms as nutrients. This reduction results from microbial immobilization, altered nutrient cycling, reduced mineralization and changes in soil physicochemical

properties. Nitrogen immobilization frequently occurs because indigenous microorganisms consume available nitrogen during hydrocarbon degradation, leading to nutrient deficiency and reduced fertility. One of the major ecological consequences of petroleum contamination is the alteration of soil microbial community structure and function. Soil harbors diverse microorganisms responsible for decomposition, nutrient mineralization, nitrogen fixation, phosphorus solubilization and organic matter recycling. Petroleum contamination also alters fungal communities, including mycorrhizal fungi, thereby influencing nutrient uptake and plant-microbe interactions. As a result, overall microbial diversity and community evenness generally decline, despite temporary enrichment of specialized hydrocarbon-degrading microorganisms. This shift in microbial community composition alters ecosystem functioning and reduces the ecological stability of contaminated soils. High-throughput sequencing studies have demonstrated significant reductions in bacterial richness and evenness following long-term petroleum contamination, particularly in soils containing high concentrations of aromatic hydrocarbons and PAHs (Xu *et al.*, 2018; Wang *et al.*, 2023; Mekonnen *et al.*, 2024) [41, 6, 42].

Table 2. Major anthropogenic and natural sources of petroleum hydrocarbon pollution, associated pollutants, affected environments and environmental impacts

Source	Representative Petroleum Contaminants	Primary Affected Environment	Major Environmental Consequences
Natural oil seeps	Crude oil, methane, light alkanes	Marine sediments, terrestrial seeps	Long-term microbial adaptation, localized contamination
Oil exploration and drilling	Crude oil, drilling fluids, produced water	Soil, groundwater, offshore waters	Habitat disturbance, sediment contamination
Offshore oil platforms	Crude oil, lubricants, production chemicals	Marine ecosystems	Fish mortality, coral damage, coastal pollution
Pipelines	Diesel, gasoline, crude oil	Agricultural soils, groundwater	Chronic leakage, groundwater contamination
Petroleum refineries	Mixed hydrocarbons, PAHs, phenols	Rivers, soils, sediments	Toxic wastewater discharge, biodiversity loss
Transportation accidents	Crude oil, refined fuels	Marine and terrestrial environments	Acute ecological damage, long-term soil contamination
Urban stormwater runoff	Fuel residues, lubricants, PAHs	Rivers, lakes, estuaries	Diffuse chronic hydrocarbon pollution
Automobile workshops	Waste oil, grease, diesel	Urban soils	Persistent localized contamination
Agricultural machinery	Diesel, lubricants	Agricultural land	Reduced soil fertility and microbial activity
Improper waste disposal	Waste engine oil, oily sludge	Landfills, open land	Mixed organic and metal contamination

Petroleum hydrocarbons also interfere with essential soil biochemical processes by inhibiting enzyme activities. These enzymes are widely used as sensitive bioindicators of soil biological health and microbial activity. indicators of soil biological health because they regulate nutrient cycling and organic matter decomposition. Although most studies report reduced enzyme activities, temporary increases in dehydrogenase activity have occasionally been observed during the early stages of biodegradation owing to increased microbial metabolism. Reduced enzyme activity decreases carbon, nitrogen, phosphorus and sulfur cycling, thereby limiting nutrient availability for plants and slowing ecosystem recovery. Nevertheless, during successful bioremediation, gradual restoration of enzyme activities is frequently observed and is considered a reliable indicator of soil rehabilitation (Das *et al.*, 2011; Sharma *et al.*, 2022; Dvořák, 2024) [12, 9, 43].

Plant growth is significantly impaired in petroleum-contaminated soils because hydrocarbons interfere with seed germination, root elongation, nutrient uptake, chlorophyll synthesis and photosynthetic efficiency. Oil-coated soil particles reduce oxygen diffusion within the rhizosphere, resulting in root hypoxia and impaired water and nutrient uptake. Excessive ROS production causes lipid peroxidation, membrane damage, protein oxidation, DNA damage and chloroplast dysfunction, ultimately reducing plant growth. Consequently, contaminated plants often exhibit chlorosis, necrosis, reduced biomass accumulation, delayed flowering, poor reproductive development and significant yield reduction. Crop species such as wheat, maize, rice, soybean and vegetables have shown considerable sensitivity to petroleum hydrocarbon contamination, particularly during early growth stages (Varjani, 2017; Saxena *et al.*, 2020; Mekonnen *et al.*, 2024) [5, 42].

Agricultural productivity declines substantially following petroleum contamination because soil fertility, microbial activity, nutrient cycling and plant physiological processes are simultaneously disrupted. Hydrocarbon-induced reductions in crop yield not only threaten food security but also impose significant economic losses on farming communities. Contaminated agricultural soils may remain unsuitable for cultivation for several years, depending on hydrocarbon composition, contamination intensity, soil properties and remediation practices. Long-term studies conducted in oil-producing regions have demon-

strated persistent reductions in grain yield, soil organic matter turnover and nutrient use efficiency, emphasizing the need for integrated remediation approaches involving bioaugmentation, biostimulation, phytoremediation and microbial consortia to restore agricultural land (Atlas and Hazen, 2011; Saxena *et al.*, 2020; Mekonnen *et al.*, 2024) [4, 42].

Recent advances in molecular ecology and multi-omics technologies have substantially improved understanding of soil microbial responses to petroleum contamination. Metagenomic and metatranscriptomic analyses have revealed that hydrocarbon-contaminated soils are enriched with functional genes involved in alkane oxidation (*alkB*), aromatic hydrocarbon degradation (*nah*, *catA*, *xylE*) and stress adaptation pathways. These findings indicate that indigenous microbial communities rapidly adapt to hydrocarbon stress by activating specialized catabolic pathways. However, successful biodegradation depends on adequate oxygen availability, balanced nutrient supply, suitable moisture content and favorable temperature conditions. Therefore, maintaining optimal environmental conditions remains essential for enhancing microbial degradation and accelerating soil restoration (Sharma *et al.*, 2022; Wang *et al.*, 2023; Dvořák *et al.*, 2024) [9, 6, 43].

2.2.2 Impact on groundwater and freshwater ecosystems

Groundwater and freshwater resources constitute essential components of the global hydrological cycle and are indispensable for drinking water supplies, agricultural irrigation, industrial processes and ecosystem sustainability. Petroleum hydrocarbon contamination of groundwater and freshwater ecosystems has become an increasingly significant environmental concern due to accidental oil spills, leakage from underground storage tanks (USTs), pipeline failures, refinery effluents, landfill leachates and industrial wastewater discharge. Once petroleum hydrocarbons infiltrate subsurface environments, they exhibit prolonged persistence because of limited oxygen availability, reduced microbial activity and slow groundwater movement. Consequently, contamination of groundwater aquifers represents one of the most

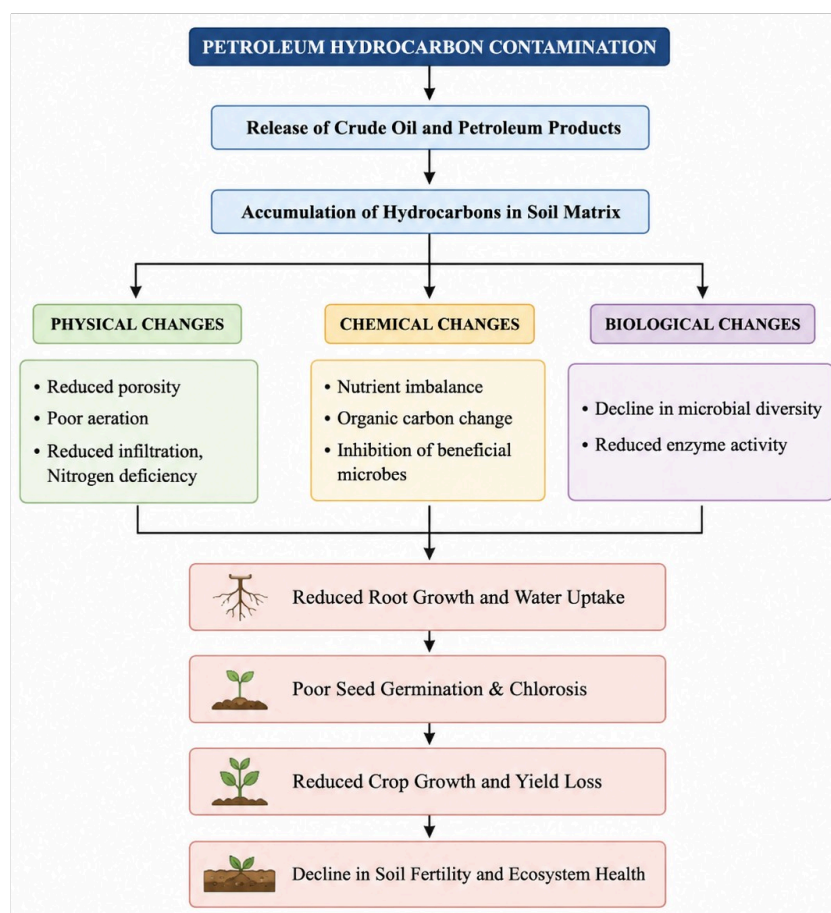


Figure 2. Impact of Petroleum Hydrocarbon Contamination on Soil

difficult environmental problems to remediate, often requiring several years or even decades for complete restoration (Das *et al.*, 2011; Varjani, 2017; Xu *et al.*, 2018) [12, 5, 41].

Groundwater contamination generally occurs when petroleum products migrate downward through the unsaturated (vadose) zone and eventually reach the saturated aquifer. The movement of contaminants depends on soil texture, porosity, permeability, groundwater flow velocity and the physicochemical properties of individual hydrocarbon compounds. Light non-aqueous phase liquids (LNAPLs), such as gasoline and diesel fuel, tend to float on the groundwater table because of their lower density than water, whereas dense non-aqueous phase liquids (DNAPLs) may penetrate deeper into aquifers, creating persistent contamination sources. Dissolved hydrocarbons such as benzene, toluene, ethylbenzene and xylene (BTEX) are highly mobile and frequently migrate considerable distances from the original spill site, increasing the risk of contaminating drinking water wells and irrigation systems (Atlas and Hazen, 2011, Speight, 2020) [4].

Among petroleum constituents, benzene is considered one of the most hazardous groundwater contaminants because of its relatively high solubility, mobility and well-documented carcinogenicity. Long-term consumption of benzene-contaminated groundwater has been associated with haematological disorders, bone marrow suppression, leukaemia and immune system impairment. Similarly, other BTEX compounds adversely affect the nervous system, liver, kidney and respiratory tract following prolonged exposure. Polycyclic aromatic hydrocarbons (PAHs), although less soluble than BTEX compounds, persist in groundwater for extended periods because of their strong adsorption to organic matter and slow biodegradation rates, posing chronic health risks through continuous low-level exposure (IARC, 2019; ATSDR, 2022; WHO, 2022) [44].

Petroleum hydrocarbon contamination significantly alters the physicochemical and biological quality of groundwater, affecting its suitability for domestic, agricultural and industrial use. Petroleum contamination generally increases total organic carbon (TOC), chemical oxygen demand (COD) and, where biodegradable hydrocarbons are

present, biochemical oxygen demand (BOD), while decreasing dissolved oxygen concentrations. The depletion of dissolved oxygen limits aerobic microbial activity and promotes anaerobic conditions, thereby slowing the natural attenuation of contaminants. In addition, petroleum contamination may alter groundwater pH, electrical conductivity and concentrations of dissolved metals through complex geochemical interactions. Such changes can substantially impair groundwater quality, frequently necessitating treatment before domestic, agricultural, or industrial use. (Varjani, 2017; Sharma *et al.*, 2022) [5, 9].

Freshwater ecosystems, including rivers, lakes, ponds, reservoirs and wetlands, are highly vulnerable to petroleum hydrocarbon pollution because contaminants are readily transported through surface runoff, industrial discharge, stormwater drainage and accidental spills. Once petroleum enters freshwater bodies, lighter hydrocarbon fractions spread rapidly across the water surface, forming a thin oil film that restricts atmospheric oxygen transfer and decreases light penetration. This physical barrier reduces photosynthetic activity of phytoplankton and submerged aquatic vegetation, leading to decreased primary productivity and disruption of aquatic food webs. Simultaneously, dissolved hydrocarbons exert direct toxic effects on aquatic organisms, resulting in reduced biodiversity and ecological imbalance (Head *et al.*, 2006; Xu *et al.*, 2018; Mekonnen *et al.*, 2024) [14, 41, 42].

Aquatic microbial communities are among the earliest biological components to respond to petroleum hydrocarbon contamination. Indigenous microbial populations responsible for organic matter decomposition, nutrient cycling and ecosystem functioning, nutrient cycling and ecosystem functioning often decline immediately following contamination because of hydrocarbon toxicity. However, specialized hydrocarbon-degrading bacteria such as *Pseudomonas*, *Acinetobacter*, *Rhodococcus*, *Alcanivorax* and *Marinobacter* rapidly proliferate and initiate biodegradation under favorable environmental conditions. Although this microbial succession contributes to natural attenuation, complete recovery of microbial diversity may require several years

and depends on contamination severity, ecosystem type and environmental conditions (Das *et al.*, 2011; Xu *et al.*, 2018) [12, 41].

Table 3. Effects of petroleum hydrocarbon contamination on soil physicochemical properties, biological characteristics and agricultural productivity.

Soil Parameter	Effect of Petroleum Hydrocarbon Contamination	Environmental Consequence	Selected References
Soil porosity	Decreases because hydrocarbons clog soil pores	Poor aeration and reduced root penetration	Das and Chandran (2011); Xu <i>et al.</i> (2018)
Water infiltration	Reduced due to hydrophobic coating	Water stress and poor seed germination	Varjani (2017); Mekonnen <i>et al.</i> (2024)
Soil pH	May increase or decrease depending on oil composition	Alters nutrient availability and microbial activity	Saxena <i>et al.</i> (2020)
Organic carbon	Initially increases due to petroleum carbon	Limited availability of usable nutrients	Atlas and Hazen (2011)
Nitrogen and phosphorus	Depleted because of microbial utilization during degradation	Reduced soil fertility	Sharma <i>et al.</i> (2022)
Microbial diversity	Sensitive microorganisms decline while degraders increase	Ecological imbalance	Wang <i>et al.</i> (2023)
Soil enzyme activity	Dehydrogenase, urease and phosphatase activities decrease	Disrupted nutrient cycling	Dvořák <i>et al.</i> (2024)
Plant growth	Root inhibition, chlorosis and reduced biomass	Lower agricultural productivity	Mekonnen <i>et al.</i> (2024)

Fish and other aquatic organisms exhibit varying degrees of susceptibility to petroleum hydrocarbon toxicity depending on species, developmental stage and hydrocarbon composition. Exposure to dissolved hydrocarbons damages fish gills, impairs respiration, reduces reproductive success, alters swimming behavior, suppresses immune responses and increases mortality. Eggs and larval stages are particularly sensitive because hydrocarbons interfere with embryonic development and cause developmental abnormalities. Crustaceans, mollusks, amphibians and aquatic insects similarly experience reduced growth, impaired reproduction and population decline following chronic hydrocarbon exposure. These biological effects ultimately disrupt trophic interactions and reduce freshwater ecosystem resilience (Saxena *et al.*, 2020; WHO, 2022).

Furthermore, petroleum contamination significantly influences aquatic vegetation. Oil films reduce sunlight penetration, thereby inhibiting photosynthesis in algae and submerged macrophytes. Reduced oxygen production, coupled with hydrocarbon toxicity, contributes to hypoxic conditions that further stress aquatic organisms. Wetland vegetation, which plays an essential role in shoreline stabilization, nutrient cycling and wildlife habitat, is particularly vulnerable because petroleum accumulates within sediments surrounding plant root systems. Consequently, degradation of aquatic vegetation often initiates cascading ecological effects throughout freshwater ecosystems (Head *et al.*, 2006; Mekonnen *et al.*, 2024) [14, 42].

Table 4. Ecological effects of petroleum hydrocarbon contamination of groundwater and freshwater ecosystems

Environmental Component	Representative Petroleum Contaminants	Primary Effects	Ecological Consequences	Representative References
Groundwater	BTEX, TPH, dissolved hydrocarbons	Reduced water quality, increased TOC and COD	Contamination of drinking water aquifers	Das and Chandran (2011); Xu <i>et al.</i> (2018)
Lakes	PAHs, refinery effluents	Reduced light penetration, eutrophication	Decline in aquatic vegetation	Varjani (2017)
Wetlands	Mixed petroleum hydrocarbons	Sediment contamination	Loss of habitat and ecological services	Mekonnen <i>et al.</i> (2024)
Aquatic Microorganisms	BTEX, PAHs	Shift in microbial community structure	Reduced nutrient cycling	Xu <i>et al.</i> (2018)
Fish and Amphibians	Aromatic hydrocarbons	Gill damage, reproductive impairment	Population decline	WHO (2022); ATSDR (2022)

Groundwater contamination by petroleum hydrocarbons is particularly persistent because subsurface environments are characterized by limited oxygen availability and slow natural attenuation processes. Freshwater ecosystems rapidly respond to hydrocarbon pollution through oxygen depletion, reduced photosynthetic activity, microbial community shifts and toxicity to fish, amphibians and aquatic inverte-

brates. The mobility of BTEX compounds further increases the risk of widespread contamination of drinking water resources and agricultural irrigation systems. Consequently, integrated monitoring and sustainable bioremediation strategies are essential for protecting freshwater resources.

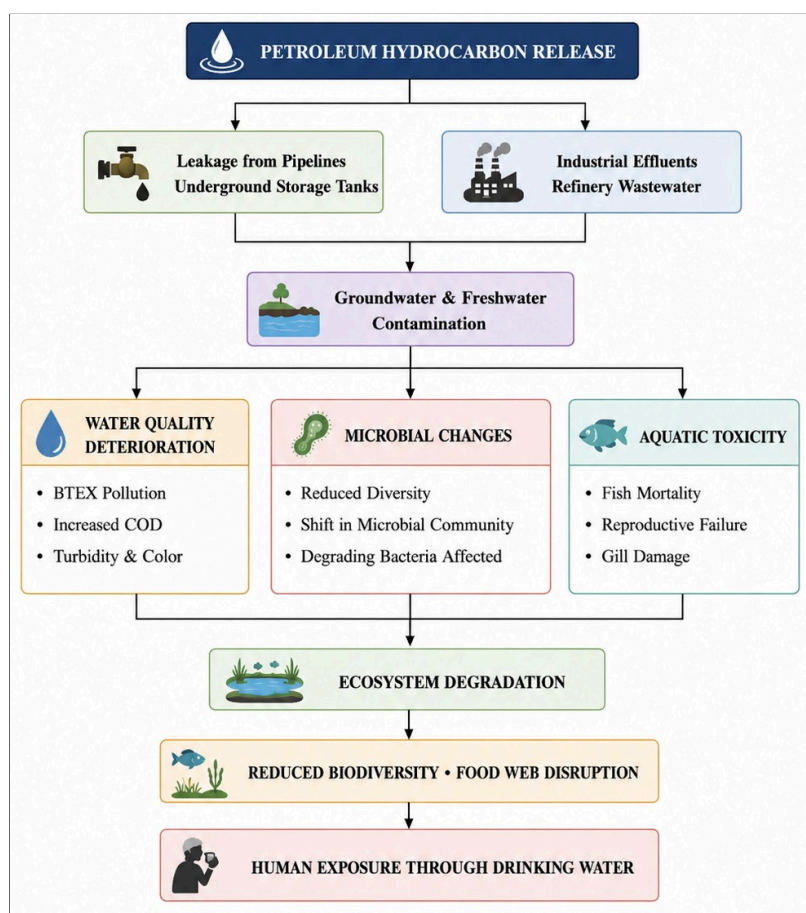


Figure 3. Major Natural and Anthropogenic Sources of Petroleum Hydrocarbon Contamination

Conclusion

Petroleum hydrocarbon pollution remains a major environmental challenge due to its persistence, toxicity and widespread occurrence. Aerobic petroleum hydrocarbon-degrading bacteria provide an effective, eco-friendly and sustainable solution by degrading hydrocarbons through oxygen-dependent metabolic pathways. Genera such as *Pseudomonas*, *Alcanivorax*, *Acinetobacter*, *Rhodococcus* and *Marinobacter* play key roles in the biodegradation of diverse hydrocarbon compounds. Recent advances in omics technologies, synthetic biology, artificial intelligence and nanotechnology have improved our understanding of microbial degradation mechanisms and enhanced bioremediation strategies. However, challenges such as limited hydrocarbon bioavailability, environmental variability and insufficient field-scale validation remain. Integrating advanced molecular tools with sustainable bioremediation approaches will further improve the efficiency and practical application of petroleum hydrocarbon remediation in contaminated environments.

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How to cite this article: Chaudhari FN, Nair NB, Bhuariya U, Sharma S. Aerobic petroleum hydrocarbon-degrading bacteria in oil spill bioremediation: mechanisms, microbial diversity, omics and emerging technologies. *International Journal of Agriculture and Food Science*. 2026;8(10):159-167. doi: <https://www.doi.org/10.33545/2664844X.2026.v8.i10c.2014>