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Review

# Microbial Enzymatic Pathways for Petroleum Biodegradation in Aquatic Environments: Molecular Mechanisms and Environmental Perspectives

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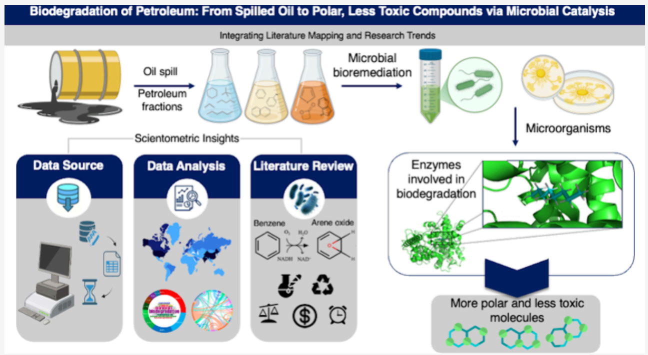


**ABSTRACT:** The growing global energy demand and extensive use of petroleum have led to recurrent environmental incidents—particularly oil spills—that pose severe ecological risks. Microbial biodegradation has emerged as a promising biocatalytic strategy for remediation of environments contaminated by petroleum hydrocarbons. This review provides an integrative analysis of microbial degradation pathways, highlighting key enzymatic mechanisms, catalytic efficiencies, and environmental and operational factors influencing biodegradation. Prominent microbial agents include *Pseudomonas aeruginosa* and *Alcanivorax borkumensis* (bacteria), *Aspergillus niger* and *Trametes versicolor* (fungi), and yeasts such as *Yarrowia lipolytica* and *Candida tropicalis*, each with distinct enzymatic systems involved in the transformation of alkanes, aromatics, and polycyclic hydrocarbons. A scientometric analysis covering 2005−2025 reveals a substantial rise in research activity, with China and the United States leading in publications and citations. High-impact journals, such as *Chemosphere* and *Journal of Hazardous Materials*, dominate the dissemination of findings in this field. Additionally, the study discusses the ecological impacts of petroleum pollution, compares conventional and biological remediation techniques, and explores the molecular basis of microbial catalysis. Emerging approaches—including nanobioremediation, metabolic engineering, and omics-driven modeling—are highlighted as future directions for enhancing catalytic performance and environmental sustainability. Overall, this review underscores the potential of microbial biocatalysis as a scalable and ecoefficient approach to address the environmental challenges posed by petroleum-derived pollutants.

## 1. INTRODUCTION

The growing energy demand and the increase in the exploration, transportation, and use of oil have intensified the occurrence of environmental incidents, resulting in oil spills.[1] These events pose significant ecological risks, affecting biodiversity, water quality, and human health.[2] In this scenario, biodegradation by microorganisms appears to be a promising option for the remediation of areas polluted by fossil fuels.[3]

Biodegradation uses the natural ability of microorganisms, such as bacteria and fungi, to metabolize complex organic compounds found in petroleum, converting them into less harmful or toxic compounds. This procedure is considered an environmentally friendly and economically viable strategy for decontaminating oil and water affected by oil spills.[4] Thus, the use of local microorganisms in a polluted environment can enhance the effectiveness of bioremediation, reducing ecological damage and preventing the introduction of unusual species.[2,5]

Several microorganisms have been identified with the ability to decompose hydrocarbons. For example, bacterial toxins such as *Rhodococcus rhodochrous, Pseudomonas alcaligenes, Rhodococcus erythropolis*, and particular species of Acinetobacter degrade petroleum, primarily based on the source of carbon and ambient temperature.[6−8] Additionally, species such as *Aeromonas*, *Alcaligenes*, *Bacillus*, *Corynebacterium*, *Flavobacterium*, *Micrococcus*, *Mycobacterium*, *Pseudomonas*, and *Rhodococcus* have demonstrated the ability to biodegrade aromatic hydrocarbons with a biodegradation efficiency ranging from 60 to 70%.[9−11]

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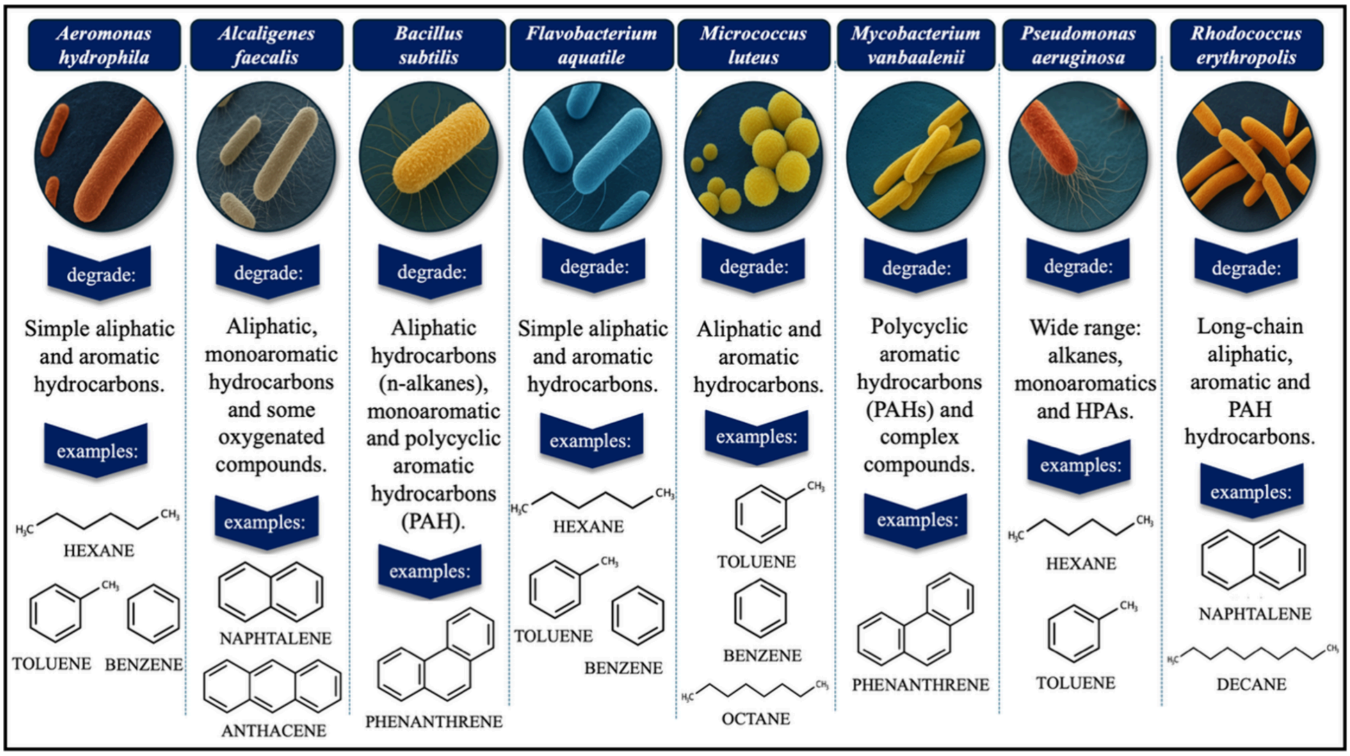


**Figure 1.** Representative species of some bacteria with biodegradation capabilities for some specific groups of hydrocarbons. Each species can act in the degradation of more than one organic compound and at different stages of the biotransformation of these substrates.

Figure 1 illustrates some of the listed bacteria and the primary groups of hydrocarbons that they degrade. These species are representative, but there are others within these genera with similar capabilities. Selection depends on the environment and type of contamination. These bacteria are particularly effective when used in microbial consortia, as each one acts on different classes of compounds, promoting a more complete degradation of the oily fraction.

The advantages of microbial biodegradation include reduced costs associated with the recovery of polluted environments, reduced environmental impacts, and the option of in situ application, thereby avoiding the removal and transportation of large quantities of contaminated soil or water.[12] Furthermore, the use of microorganisms present in polluted environments can enhance the effectiveness of bioremediation, thereby reducing ecological damage.[13] However, biodegradation by microorganisms also presents challenges. Several factors, including the composition of the oil, environmental conditions (such as temperature, pH, and nutrient availability), and the presence of competing microorganisms, can impact the effectiveness of the process.[14] Thus, the degradation of certain petroleum elements, such as polycyclic aromatic hydrocarbons (PAHs), occurs more slowly and requires specific microbial associations.[15] An additional challenge is to translate the results achieved in the laboratory to real field conditions, considering the complexity of environmental systems.[3]

Microbial biodegradation is an environmentally sustainable strategy, as it reduces the demand for more aggressive physical or chemical methods, which can cause additional damage to the ecosystem.[16] However, it is crucial to carefully analyze the dangers associated with the use of microorganisms in natural environments, ensuring that there are no ecological disruptions or harmful effects on local biodiversity.[17]

The importance of microbial biodegradation in the remediation of areas polluted by oil is undeniable; however, there are still scientific gaps to be filled.[18] It is essential to expand the understanding of the molecular and enzymatic processes involved in the degradation of various petroleum components, as well as to identify and characterize new microorganisms with degradation capabilities.[19,20] Furthermore, the incorporation of bioinformatics tools, such as omics analysis and computational modeling, can aid in understanding the interactions between microorganisms and in improving bioremediation processes.[21]

This study integrates a scientometric analysis and a literature review to offer a comprehensive overview of the biodegradation of petroleum-derived hydrocarbons. The scientometric analysis evaluated the scientific output over the past 20 years, identifying the most impactful studies, prominent authors, leading institutions, relevant journals, frequently used keywords, and evolution of research themes in the field. This enabled the identification of knowledge gaps and emerging trends, which guided the selection of key topics addressed in the literature review.

The literature review began by exploring the chemical and physicochemical properties of petroleum hydrocarbons and their environmental implications. It then examined the main microorganisms involved in biodegradation with an emphasis on the enzymes they produce, their degradation efficiencies, the classes of hydrocarbons they target, and typical degradation times. Mechanistic and thermodynamic aspects of enzymatic biodegradation were discussed in detail to deepen the understanding of microbial action on these compounds and to highlight potential biotechnological targets.

Furthermore, the review encompasses current bioremediation strategies, case studies, and practical challenges associated with implementing microbial degradation technologies. Finally, it outlines future perspectives for the field, emphasizing the


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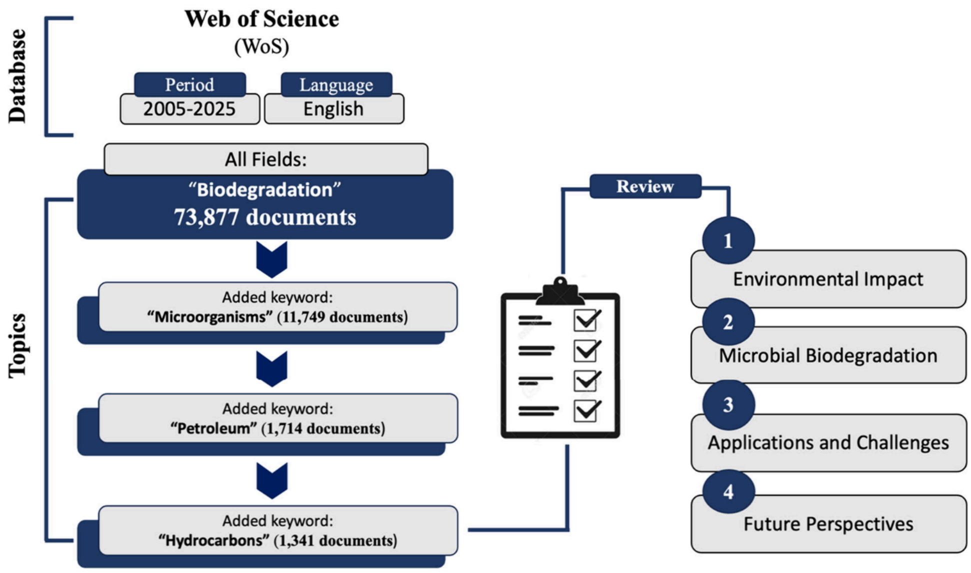


**Figure 2.** Flowchart of the methodology applied to research on the microbial biodegradation of petroleum and derivatives from 2005 to 2025. Refinements included document type and keywords: "Microorganisms", "Petroleum", and "Hydrocarbons". The review was structured around four main topics: Environmental Impact, Microbial Biodegradation, Applications and Challenges, and Future Perspectives.

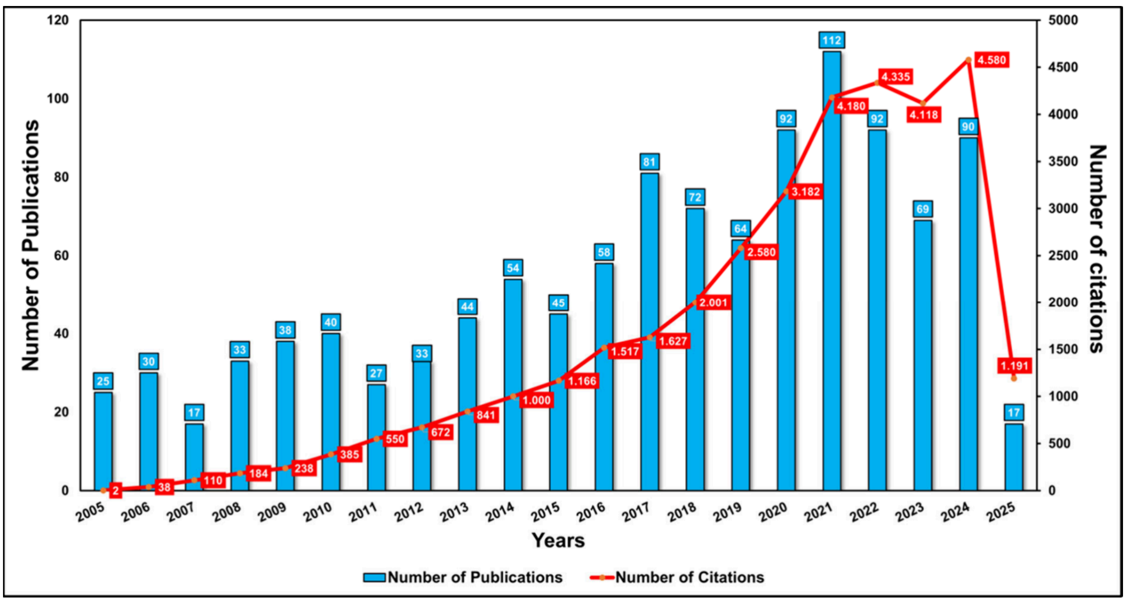


**Figure 3.** Annual distribution of publications (blue bars) and citations (red line) related to the microbial biodegradation of petroleum and derivatives in the period from 2005 to 2025.

integration of bioinformatics, molecular modeling, and other computational tools as well as opportunities for innovation and investment in sustainable remediation approaches.

## 2. SCIENTOMETRIC ANALYSIS OF SCIENTIFIC PRODUCTION

**2.1. Data Collection.** This study builds on previous studies.[22−25] The database was exported from the Web of Science (WoS) (https://www-webofscience-com.ez373.periodicos.capes.gov.br, accessed in April 2025) to carry out the scientometric analysis, as it is a platform widely recognized for its reliability and quality in indexing scientific publications and generating citations.[26,27]

The initial search in "all fields" used the keyword "Biodegradation" within the time range of 2005 to 2025, yielding a substantial number of 73,877 records for articles. To ensure the relevance of the selected documents, only original and review articles written in English were considered. Three thematic filters were then applied to refine the results and direct the search focus to the microbial biodegradation of petroleum and its derivatives. The first filter, with the term "microorganisms", reduced the number of publications to 11,749 articles. The application of the second term, "petroleum", restricted the results to 1,714 articles. Finally, the inclusion of the term "hydrocarbons" further refined the sample, resulting in 1,341 articles that make up the final database analyzed. The rigor applied in the selection and refinement stages allowed the consideration of only studies closely aligned with the investigative scope.[28−31] Figure 2 illustrates, schematically, the methodological steps employed in constructing the database


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**Table 1. Top Ten Scientific Journals with the Most Publications in the Area of Microbial Biodegradation of Petroleum**[a]

| Rank | Journal | W | IF | NP | NC | AC | P |
|---|---|---|---|---|---|---|---|
| 1 | *Chemosphere* | EN | 8.1 | 44 | 2429 | 55.20 | 3.86 |
| 2 | *Journal of Hazardous Materials* | NL | 12.2 | 43 | 2444 | 56.83 | 3.77 |
| 3 | *International Biodeterioration and Biodegradation* | EN | 4.1 | 37 | 1760 | 47.56 | 3.25 |
| 4 | *Science of the Total Environment* | NL | 8.2 | 33 | 1098 | 33.27 | 2.89 |
| 5 | *Environmental Science and Pollution Research* | GER | 5.8 | 29 | 1099 | 42.26 | 2.54 |
| 6 | *Microorganisms* | CH | 4.1 | 26 | 328 | 12.61 | 2.28 |
| 7 | *Frontiers in Microbiology* | CH | 4.0 | 25 | 1406 | 56.24 | 2.19 |
| 8 | *Bioresource Technology* | NL | 9.7 | 20 | 2415 | 120.75 | 1.75 |
| 9 | *Marine Pollution Bulletin* | EN | 5.3 | 20 | 767 | 38.35 | 1.75 |
| 10 | *Environmental Management* | USA | 2.7 | 18 | 878 | 48.77 | 1.58 |

[a]C = Country; IF = Impact Factor in 2023; NP = Number of Publications; NC = Number of Citations; AC = Average Citations; P = Percentage concerning the Total Number of Papers. USA = United States of America; NL = Netherlands; EN = England; CH = Switzerland; GER = Germany.

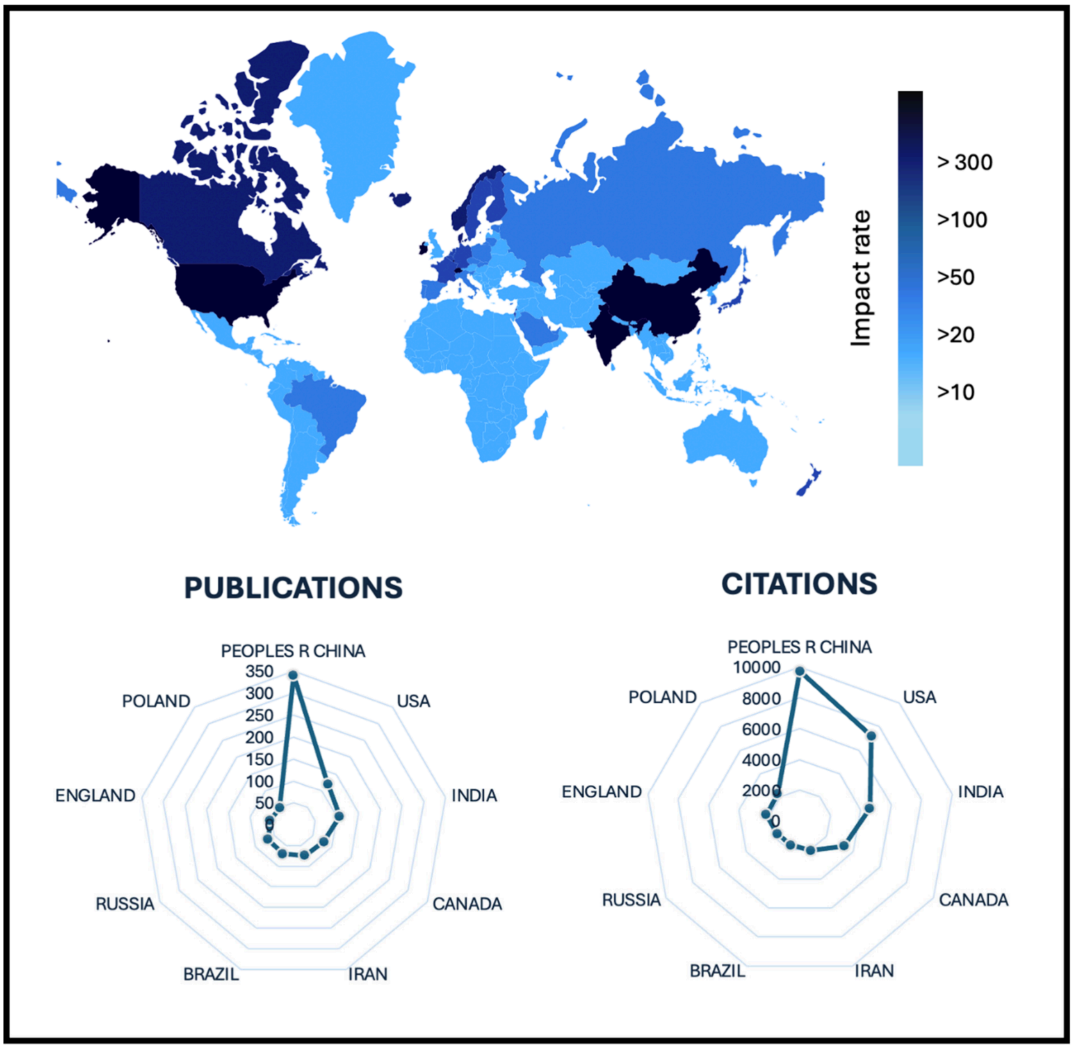


**Figure 4.** Global distribution of scientific impact in the field of microbial petroleum biodegradation. The world map displays the impact rate by country, represented by a gradient scale based on the number of publications (ranging from 10 to 300). The radar charts below display the top contributing countries in terms of (left) the number of publications and (right) the number of citations. China leads in both metrics, followed by the USA and India, indicating significant research output and influence in this field.

related to the microbial biodegradation of hydrocarbons from petroleum.

**2.2. Data Analysis.** *2.2.1. Temporal Evolution of Publications.* The WoS search found 1,341 articles published between 2005 and 2025. Figure 3 illustrates the distribution of publications over the last 20 years, revealing an increase in the scientific community's interest in the microbial biodegradation of petroleum and its derivatives. The analysis began in 2005, with a record of 25 published articles and a modest number of two citations. Moving forward to 2010, a gradual increase in both the number of publications and citations was observed, which can be attributed to the emerging global concern for the


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remediation of environmental contaminants in both marine and onshore environments. It is worth noting that at that time, an accidental oil spill on the Deepwater Horizon platform in the Gulf of Mexico caused the discharge of 3.19 million barrels of oil into the waters of the Gulf, becoming one of the most significant marine disasters in history, surpassed only by the Exxon Valdez spill in 1989.[32]

From 2019 onward, there was a significant increase in scientific production, reaching its peak in 2021, with 112 publications. The growth in citations was also crucial during this period, reaching a level of 4,150 citations in 2021, and this can be explained by the impacts and emerging threat of plastic derivatives to marine and terrestrial ecosystems, especially microplastic contaminants in the marine environment, drawing global attention to their fate, the consequences of toxicity, and remediation strategies.[33] Microplastics, originating from various sources, including textiles and industrial processes, cause physiological and neurological damage to fish, compromising their growth and overall health. When consumed, they pose risks to the food chain and can also impact human health.[34]

Over the last three years, as analyzed in the scientometric study, we found that although the number of publications decreased slightly, the volume of citations remained high, indicating that the published works continued to have a substantial academic impact. The drop in the number of publications observed in 2025 (31 publications and 1,191 citations) can be attributed to the fact that the data for this year is still in progress and not finalized.

*2.2.2. Distribution of Scientific Journals.* The analysis of scientific journals revealed that scientific publications on petroleum biodegradation by microbiological agents are distributed in 276 journals, and the ten most prolific journals are listed in Table 1. Most of the scientific articles were published in a small group of high-impact journals with broad international visibility, with emphasis on the English journals *Chemosphere* with an Impact Factor (IF) of 8.1 (in 2023) and *International Biodeterioration & Biodegradation* (IF = 4.1), and the Dutch *Journal of Hazardous Materials* (IF = 12.2). Chemosphere leads in the number of publications (44). At the same time, the *Journal of Hazardous Materials* has the highest total number of citations (2,444) and the highest average per article (56.83), evidencing its strong influence on the dissemination of research in the area under analysis. The journals *Science of the Total Environment*, *Environmental Science and Pollution Research*, and *Bioresource Technology* also stand out, the latter with an impressive average of 120.75 citations per article, despite the smaller number of scientific publications. European journals hold the majority of scientific publications and are consolidating research on the remediation of environmental liabilities.

*2.2.3. Distribution by Country and Institution.* Eighty-six countries were identified based on the declared origin of the corresponding authors, and Figure 4 shows the most productive countries. China leads with 247 publications and 8,387 citations, followed by the United States, with 101 publications and 6,252 citations, with the highest average of 61.90 citations per scientific publication. India ranks third with 82 publications and 4,307 citations. Brazil, with 54 publications and 1,911 citations, ranks sixth, averaging 35.38 citations per publication.

China leads in the absolute number of publications, reflecting a substantial national investment in environmental biotechnology and the remediation of petroleum waste. However, when analyzing research impact through average citations per article in Table 2, the United States stands out, suggesting that American studies tend to receive greater recognition and influence in the global scientific community, possibly due to higher visibility, international collaboration, or publication in high-impact journals.

**Table 2. 10 Most Prolific Countries in the Biodegradation of Petroleum and Its Derivative Products Using Microorganisms[a]**

| Rank | Country | NP | NC | AC | Total link strength |
|---|---|---|---|---|---|
| 1 | China | 247 | 8387 | 33.95 | 1347 |
| 2 | United States of America | 101 | 6252 | 61.90 | 834 |
| 3 | India | 82 | 4307 | 52.52 | 680 |
| 4 | Canada | 54 | 2801 | 51.87 | 407 |
| 5 | Australia | 35 | 1543 | 44.08 | 397 |
| 6 | Brazil | 54 | 1911 | 35.38 | 380 |
| 7 | Italy | 42 | 1205 | 28.69 | 304 |
| 8 | England | 43 | 1875 | 36.62 | 289 |
| 9 | Germany | 41 | 2010 | 49.02 | 283 |
| 10 | Iran | 57 | 1426 | 25.01 | 281 |

[a]NP = Number of Publications; NC = Number of citations; AC = Average citations (NC/NP).

Brazil, meanwhile, has been consolidating itself as a significant player in this area of research, likely due to its rich biodiversity, oil industry activity, and increasing academic output in environmental sciences. Despite producing a moderate number of publications, Brazil's total citation count remains lower compared to that of leading countries, indicating that while the research volume is growing, there may be a need to increase the international dissemination and visibility of Brazilian studies to enhance their global impact.

The network map in Figure 5 shows the grouping of countries that publish the most scientific articles and have obtained at least five citations, with the countries being represented by "circles" of different sizes and the degree of collaboration between them given by the thickness of the connecting "lines".[35] Five networks of clusters (or groupings) are formed on the map and are identified by the colored clusters. Again, China leads in terms of both scientific publications and cooperation with other countries within its cluster (blue-green clusters), especially with India, Australia, and Nigeria, as well as with clusters of neighboring countries with the orange cluster (USA, Canada, and Iran), green cluster (Brazil, Italy, Russia, Spain and Mexico), and purple cluster containing the countries Germany, England, and Egypt.

A total of 1,317 institutions were found based on the affiliation of the corresponding authors. Figure 6 illustrates the institutions with the most recent publications and the highest citation counts, represented by the "circle" with layers in warm and cool tones, where the warmest tones represent the concentration of recently published articles.[36] Chinese institutions, notably the Chinese Academy of Sciences, China University of Geosciences, and East China University of Science and Technology, contribute a significant number of publications and maintain strong connections with other global institutions. Brazilian institutions, such as the Federal University of Rio Grande do Norte and the Federal University of Rio Grande do Sul, also hold significant positions in the network, reinforcing the prominence of Latin America. More recent publications (2021−2023), represented in warm tones (red and orange), are concentrated in


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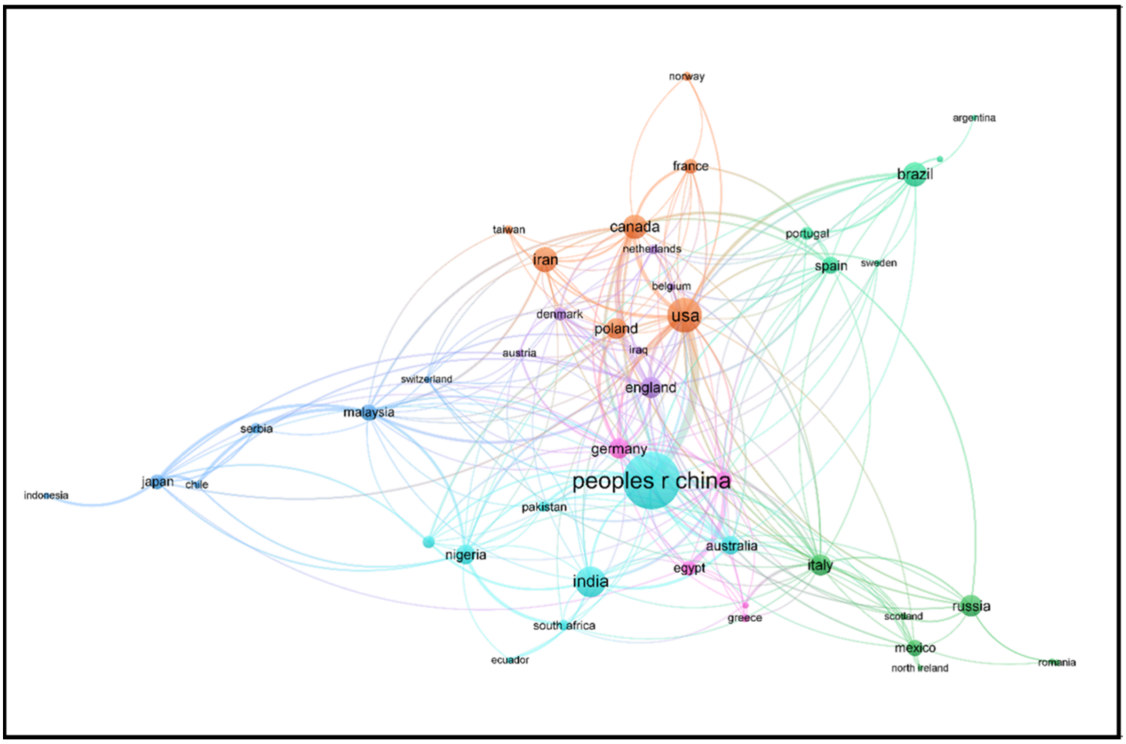


**Figure 5.** Scientometric analysis of the biodegradation of petroleum and its byproducts by microorganisms. Network visualization map showing collaboration among countries with at least five published articles. The thickness of the lines connecting two countries indicates the accumulation of coauthorships (thicker lines mean more published articles), and the colored clusters illustrate the groups of countries with a high level of collaboration.

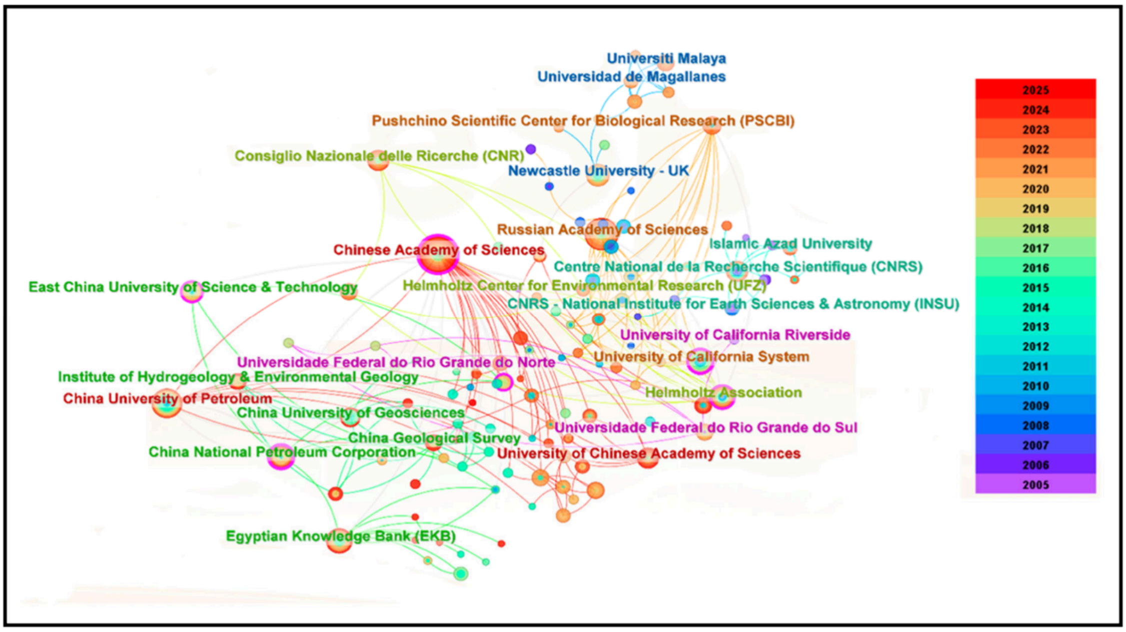


**Figure 6.** Scientometric analysis of the biodegradation of petroleum and its byproducts by microorganisms. Cluster network showing collaboration between organizations with at least five publications and 250 accumulated citations in CiteSpace.

institutions such as Universiti Malaya (Malaysia), Universidad de Magallanes (Chile), and Pushchino Scientific Center for Biological Research (PSCBR) (Russia), signaling a geographic decentralization of scientific research.

*2.2.4. Most Cited Articles.* Table 3 presents the data collected between 2014 and 2024, along with the ten most relevant research articles on the biodegradation of petroleum and its derivative products by microorganisms, with a focus on mitigating environmental contamination. These works accumulate a total of 34,498 citations. The most cited article (827 citations) was written by Varjani[37] and addressed biodegradation with oleophilic microorganisms as an effective alternative to mitigate hydrocarbon pollution, which poses a threat to human and environmental health.

Atlas and Hazen[32] published the second most cited study, which has accumulated 579 citations alone. It was based on two

Table 3. Most Cited Articles in the Web of Science on Microbial Biodegradation of Petroleum and Its Derived Byproducts in the Last 20 Years (2005 to 2025)

| Rank | Article title | Authors | Year published | Citations |
|---|---|---|---|---|
| 1 | Microbial Degradation of Petroleum Hydrocarbons[37] | Varjani, Sunita J. | 2017 | 827 |
| 2 | Oil Biodegradation and Bioremediation: A Tale of the Two Worst Spills in US History[32] | Atlas, Ronald M.; Hazen, Terry C. | 2011 | 579 |
| 3 | Remediation of Soil and Water Contaminated with Petroleum Hydrocarbon: A Review[38] | Ossai, Innocent Chukwunonso; Ahmed, Aziz; Hassan, Auwalu; Hamid, Fauziah Shahul | 2020 | 503 |
| 4 | A New Look at Factors Affecting Microbial Degradation of Petroleum Hydrocarbon Pollutants[39] | Varjani, Sunita J.; Upasani, Vivek N. | 2017 | 334 |
| 5 | Biodegradation of Plastics: Current Scenario and Prospects for Environmental Safety[40] | Ahmed, Temoor; Shahid, Muhammad; Azeem, Farrukh; Rasul, Ijaz; Shah, Asad Ali; Noman, Muhammad; Hameed, Amir; Manzoor, Natasha; Manzoor, Irfan; Muhammad, Sher | 2018 | 321 |
| 6 | Bioremediation of Petroleum Hydrocarbons in Contaminated Soils: Comparison of Biosolids Addition, Carbon Supplementation, and Monitored Natural Attenuation[41] | Sarkar, D; Ferguson, M; Datta, R; Birnbaum, S. | 2005 | 265 |
| 7 | Bioremediation of Petroleum Hydrocarbons: Catabolic Genes, Microbial Communities, and Applications[42] | Fuentes, Sebastian; Mendez, Valentina; Aguila, Patricia; Seeger, Michael | 2014 | 236 |
| 8 | Phytoremediation of Petroleum-Contaminated Soils by *Mirabilis Jalapa* L. in a Greenhouse Plot Experiment[43] | Peng, Shengwei; Zhou, Qixing; Cai, Zhang; Zhang, Zhineng | 2009 | 232 |
| 9 | Microbial Metabolism and Community Structure in Response to Bioelectrochemically Enhanced Remediation of Petroleum Hydrocarbon-Contaminated Soil[44] | Lu, Lu; Huggins, Tyler; Jin, Song; Zuo, Yi; Ren, Zhiyong Jason | 2014 | 228 |
| 10 | Recent Studies in Microbial Degradation of Petroleum Hydrocarbons in Hypersaline Environments[45] | Fathepure, Babu Z. | 2014 | 221 |

Table 4. Ranking of the 24 Most Prominent Keywords Mentioned in the Most Cited Articles on the Biodegradation of Petroleum and Its Derivative Products by Microorganisms

| Rank | Keyword | Frequency | TLS | Rank | Keyword | Frequency | TLS |
|---|---|---|---|---|---|---|---|
| 1 | Biodegradation | 709 | 4535 | 13 | Microbial degradation | 112 | 774 |
| 2 | Bioremediation | 500 | 3428 | 14 | Contaminated soil | 111 | 806 |
| 3 | Degradation | 386 | 2564 | 15 | Remediation | 111 | 783 |
| 4 | Crude oil | 282 | 1901 | 16 | Biostimulation | 108 | 876 |
| 5 | Polycyclic aromatic-hydrocarbons | 273 | 1835 | 17 | Oil | 108 | 708 |
| 6 | Microorganisms | 230 | 1595 | 18 | Microbial community | 97 | 692 |
| 7 | Petroleum-hydrocarbons | 193 | 1292 | 19 | Diversity | 90 | 620 |
| 8 | Hydrocarbons | 173 | 1116 | 20 | Phytoremediation | 80 | 552 |
| 9 | Soil | 141 | 948 | 21 | Petroleum hydrocarbons | 78 | 664 |
| 10 | Bacterium | 140 | 936 | 22 | Biosurfactant | 71 | 609 |
| 11 | Petroleum | 125 | 816 | 23 | Degrading bacteria | 63 | 574 |
| 12 | Bioaugmentation | 124 | 1002 | 24 | Natural attenuation | 58 | 525 |

of the most significant environmental disasters resulting from offshore oil spills recorded in the United States. The Exxon Valdez spill in 1989 is often compared to the Deepwater Horizon spill in 2010, despite the differences in the environments affected. Although oil spills cause damage to higher organisms, native microorganisms play a crucial role in biodegradation processes, as they utilize petroleum hydrocarbons as an energy source, converting them into non-hazardous compounds and thereby reducing the environmental impact of these disasters.

The third most cited study, by Ossai et al.,[38] has 503 citations and provides a comprehensive review of remediation strategies for soil and water contaminated by petroleum derivatives. Also among the most relevant are Varjani and Upasani,[39] with 334 citations, reinforcing the researcher's leading role in biodegradation, and Ahmed et al.,[40] whose focus on the biodegradation of plastic derivatives broadens the discussion on environmental safety, with 321 citations. With a similar scope, the works by Sarkar et al.,[41] Fuentes et al.,[42] Peng et al.,[43] Lu et al.,[44] and Fathepure[45] totaled between 221 and 265 citations and compared bioremediation strategies in contaminated soils to microbial action in hypersaline environments.

*2.2.5. Quantitative Analysis of Frequent Keywords.* Table 4 presents a ranking of the most recurrent keywords in studies on the microbial biodegradation of petroleum and its derivative products. "Biodegradation" and "Bioremediation" are the two most frequently ranked terms in the analyzed articles, followed by the terms "Crude-oil", "Polycyclic aromatic-hydrocarbons" and "Petroleum-hydrocarbons", which refer to the increased interest in the degradation of persistent fossil hydrocarbons that are used as raw material sources in microbial biodegradation processes. The main agents in these processes include "Microorganisms" and "Bacteria", mostly linked to strategies such as "Bioaugmentation" and "Biostimulation" for the improvement of biodegradative processes, in addition to a complementary interest in "Phytoremediation". In essence, the keywords emphasize the relevance of preserving natural biodiversity and advanced biological methods for environmental remediation, which is also reinforced by the terms "Contaminated soil", "Diversity", and "Natural attenuation".

*2.2.6. Research Areas.* The distribution of scientific publications across thematic areas underscores the inherently multidisciplinary character of research on the biodegradation of petroleum and its derivatives by microorganisms, as illustrated in

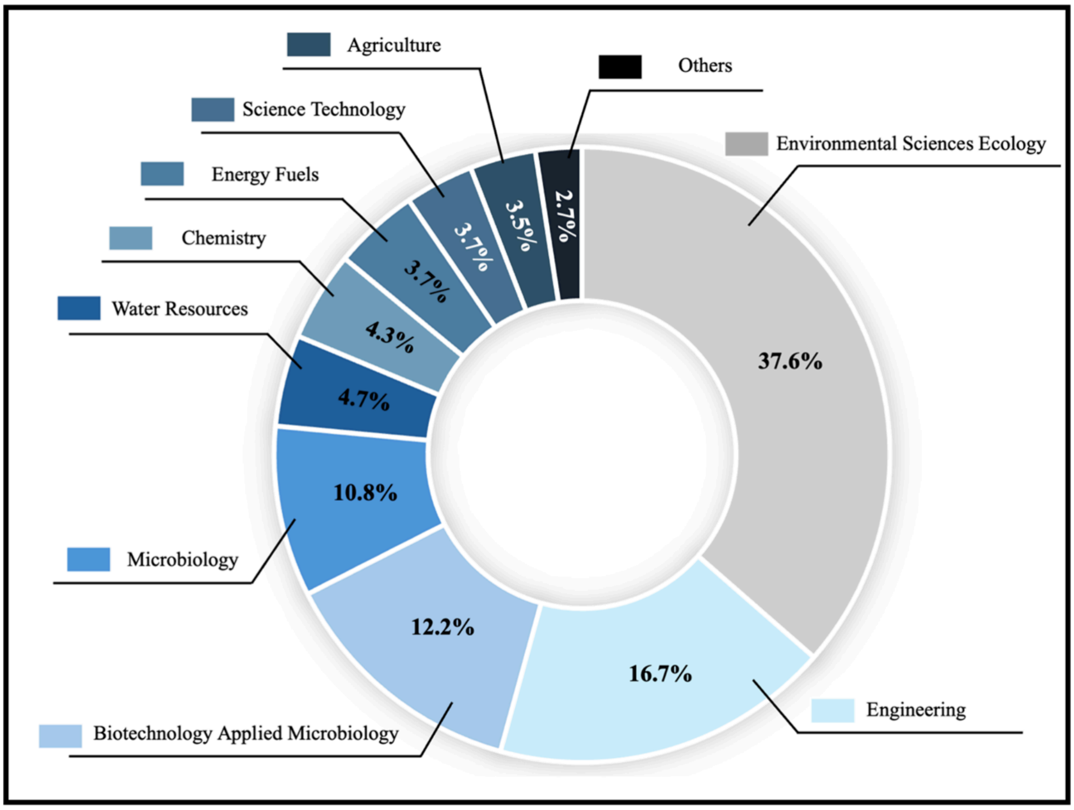


**Figure 7.** Percentage distribution of scientific publications by thematic areas related to the biodegradation of petroleum and its derivative products by using microorganisms.

Figure 7. The field is predominantly led by Environmental Sciences and Ecology (37.6%), reflecting a strong focus on remediating contaminated ecosystems and understanding the ecological impacts of petroleum pollutants. Engineering (16.7%) and Biotechnology & Applied Microbiology (12.2%) also contribute significantly, highlighting the development of bioreactors, process optimization, and microbial enhancement techniques aimed at improving bioremediation efficiency. The substantial share of Microbiology (10.8%) emphasizes the importance of isolating and characterizing oil-degrading strains and elucidating the metabolic pathways involved. Other notable fields include Water Resources (4.7%), which focuses on controlling aquatic pollution, and Chemistry (4.3%), which supports the analysis of contaminants and biodegradation intermediates. Areas such as Energy & Fuels, Agriculture, and broader Science and Technology topics, though less dominant, underscore the diversity of applications and the relevance of microbial biodegradation to energy recovery and environmental sustainability. Together, these thematic contributions highlight the crucial role of interdisciplinary approaches in developing microbial strategies for mitigating petroleum pollution.

*2.2.7. Emerging Trends.* The keyword cluster map generated by VOSviewer, presented in Figure 8, reveals three emerging clusters in research on the biodegradation of petroleum- and hydrocarbon-derived products. The blue and green clusters highlight, respectively, the advancement of technologies based on environmental microbiology through the use of microbial consortia in the degradation of hydrocarbons, and the adoption of sustainable strategies such as biostimulation and natural attenuation, aligned with Nature-Based Solutions (NbS). At the same time, the hybrid aspect emerges from combining hybrid methods that enable the integration of biological and physical-chemical processes in the remediation of contaminated subterranean environments with greater efficiency, as denoted in the red cluster. The remediation of petroleum hydrocarbons in marine and terrestrial environments,[46] the treatment of water contaminated with phenol,[47] and the consequent impacts caused by microplastic pollution in ecosystems[48] are relevant fronts within the scope of environmental remediation.

Microplastics are persistent contaminants that originate from fossil hydrocarbons and are mainly the result of the accumulation of plastic waste in the environment.[49] This accumulation occurs due to the long durability of plastics, improper disposal, and the release of toxic additives during their decomposition, which contributes to the ongoing contamination of soil, water, and ecosystems.[48] If current trends continue, it is estimated that by 2050, around 500 million tons of plastic waste will be produced, with the potential for there to be more plastic than fish in the oceans.[50]

## 3. ADVANCED ANALYSIS

### 3.1. Environmental Impact of Spills.

*3.1.1. Chemical Nature and Ecological Impact of Oil-Derived Hydrocarbons.* Petroleum is a complex mixture predominantly composed of hydrocarbons (82–87%), which may also contain heteroatoms such as oxygen, sulfur, and nitrogen, along with trace amounts of metals.[51] The four primary classes of chemical compounds in petroleum are alkanes (paraffins), cycloalkanes (naphthenes), aromatics, and asphaltenes.[51] However, the chemical composition of petroleum can vary depending on its geological origin, leading to notable changes in its physical characteristics and properties,[52] which can significantly affect its economic value.[53] This variability allows petroleum to occur naturally in liquid, gaseous, or solid states. Nonetheless, its primary utilization is as

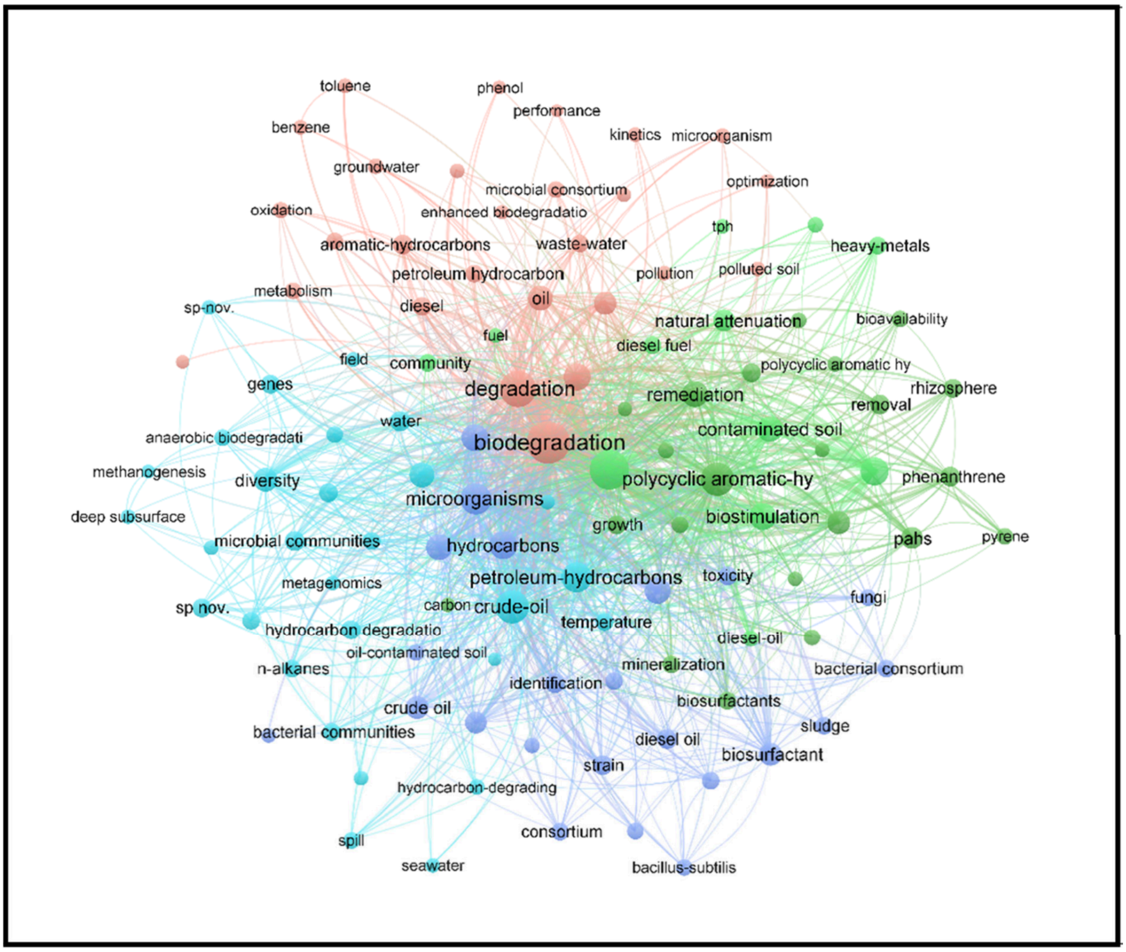


**Figure 8.** Visualization network of keywords with the highest occurrences in searches of microbial biodegradation of petroleum and its derivative products.

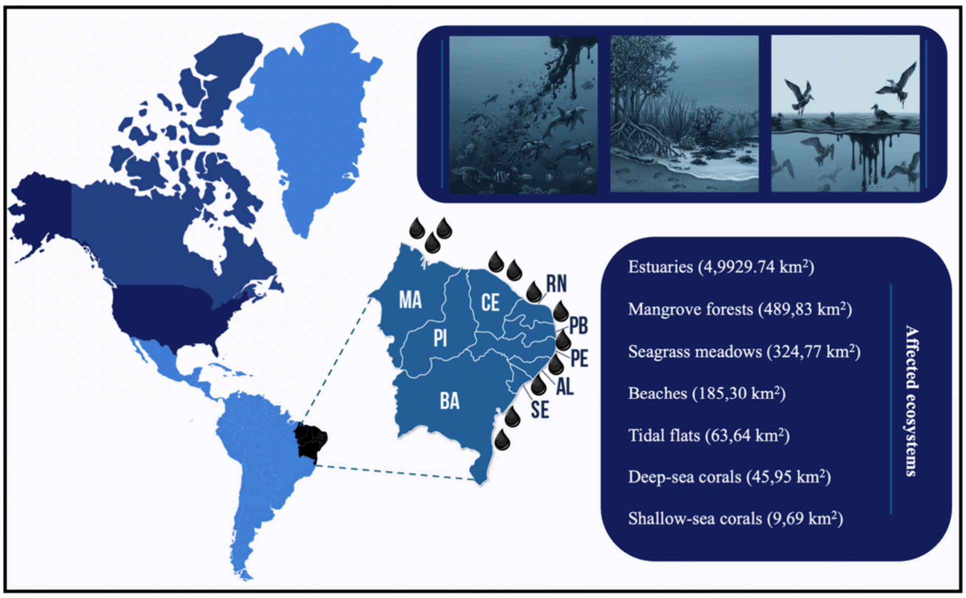


**Figure 9.** Geographic distribution and environmental impact of the oil spill that occurred along the northeastern coast of Brazil. The map highlights the affected states and indicates the extent of the impacted ecosystems, including estuaries, mangrove forests, seagrass meadows, beaches, tidal flats, and coral reefs. On-site images of the spill show oil residues on the shore and marine vegetation.

natural gas and crude oil, serving as raw materials for fuel production.[53]

According to Palmgren and Ivarsson,[54] a significant portion of environmental pollutants and toxins consists of hydrocarbon



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mixtures that, when released into the environment, cause various ecological issues, altering the climate and affecting the health of organisms within ecosystems. Due to the presence of inert components in their structure, these pollutants can accumulate in nature for extended periods, prolonging their effects.[54] As an example, in recent years, the Brazilian northeastern coast experienced one of the most severe oil spill incidents in its history, originating from a Venezuelan-flagged vessel, whose crude oil leaked and drifted across the Atlantic Ocean before reaching the shore. This environmental disaster had a direct and devastating impact on sensitive coastal and marine ecosystems, including estuaries, mangrove forests, seagrass meadows, tidal flats, and coral reefs.[55] The oil contamination not only affected biodiversity but also compromised ecosystem services essential to local communities. As illustrated in Figure 9, the states most impacted by the spill included Maranhão, Piauí, Ceará, Rio Grande do Norte, Paraba, Pernambuco, Alagoas, Sergipe, and Bahia. The figure highlights the extent of the spill, revealing the physical presence of oil on beaches and marine vegetation. The total area of affected ecosystems reached alarming levels, with nearly 5,000 $km^2$ of estuaries and hundreds of square kilometers of mangroves and coral reefs contaminated.[56]

Alkanes are saturated hydrocarbons that do not contain functional groups and can be cyclic, aromatic, branched, or straight-chained.[54] The straight-chained alkanes, known as *n*-alkanes, are found in crude oil, comprising chains of up to 40 carbon atoms, and are primarily used as fuels, such as methane, butane, and propane.[54] In living organisms, exposure to *n*-alkanes can cause various issues, including disruption of cell membrane structures; physical contamination, such as hydrophobic liquids adhering to animal fur and feathers; and harm to aerobic species by affecting oxygen availability in contaminated environments.[54]

Cycloalkanes are saturated cyclic hydrocarbons, with or without alkyl substituents, commonly found in the chemical structure of petroleum.[57] Consequently, the introduction of these compounds into terrestrial ecosystems is significant, given the high annual production of petroleum.[58] Cyclohexane, a typical representative of cycloalkanes, can enter the environment through petroleum and fuel spills.[57] Due to its structure and other physicochemical properties, such as low water solubility, it exhibits high resistance to degradation.[58]

Aromatic compounds are hydrocarbons that contain at least one ring with conjugated bonds and delocalized electrons, which confer significant stability.[59] Polycyclic aromatic hydrocarbons (PAHs) are toxic pollutants commonly found in nature and produced during the incomplete combustion of organic matter,[60] originating from natural sources, such as volcanic eruptions, or anthropogenic sources, such as petroleum refining. PAHs are standard components in petroleum and pose serious risks to human health due to their carcinogenic, mutagenic, and genotoxic potential. These compounds are highly resistant to biodegradation and can easily accumulate in the environment due to their structural angularity, low water solubility, and low volatility.[61]

According to Ahmadi et al.,[62] asphaltenes are defined as complex organic compounds with structures formed by polyaromatic rings to which heteroatoms and aliphatic side chains are attached, resulting in high molecular weight.[62] These compounds constitute the most polar and dense fraction of petroleum and are frequently found in significant concentrations in soils contaminated by exploration, transportation, and refining activities, as well as by unconventional petroleum exploitation, which exacerbates the problem.[63] When deposited in soil, asphaltenes can negatively impact soil properties, evidenced by increased toxicity, reduced pore availability, and changes in electrical conductivity, texture, bulk density, and pH.[63] Furthermore, due to their low volatility, limited solubility in water and organic solvents, and inherent structural complexity, asphaltenes exhibit high resistance to environmental degradation processes, granting them a notable capacity to persist in the environment for extended periods[63]

To reduce the environmental impacts resulting from ecosystem contamination by toxic compounds present in petroleum residues, the scientific community has focused efforts on developing and optimizing biological degradation techniques. These methods stand out as effective and sustainable approaches for treating persistent organic pollutants.[61] According to Palmgren and Ivarsson,[54] bioremediation is a method in which the natural properties of organisms are utilized to remove or convert toxic pollutants into less harmful substances. This technique has been applied since the 1970s,[54] highlighting its potential and relevance in mitigating the adverse effects resulting from petroleum residue contamination.

*3.1.2. Conventional Remediation Methods.* Currently, petroleum is one of the world's primary energy sources and is used as a raw material for various petrochemical products, such as transportation fuels, lubricants, asphalt, paints, and even plastics.[64] Despite the advantages of its broad application, the high annual production of petroleum has also become an environmental concern,[58,64] since, as previously noted, the chemical components of petroleum can pose various risks to human health and the environment and are considerably resistant to remediation.[54,58,61,63]

Remediation of a contaminated site is a process aimed at restoring an area affected by contaminants, through techniques that promote reduction, containment, or removal of the contamination source.[65] According to Santos et al.,[64] the selection of a remediation technique for areas contaminated by hydrocarbons derived from petroleum residues depends on factors such as the source and extent of contamination, the type of contaminated matrix, and the parameters of the technique itself, which must be chosen considering application costs, time, and available resources. Furthermore, the relationship between the efficiency of each method and the contaminant concentration must be considered, since techniques that show positive effects in remediating high concentrations of a contaminant may not be efficient at lower concentrations of the same.[65] Other factors to consider are the environmental impacts resulting from the application of the technique, its effects on the health of organisms inhabiting the affected area, especially humans, and compliance with legislation and regulations.[64]

According to Hansen,[65] remediation can be classified according to the mode of application at the contaminated site as *in situ* treatment or *ex situ* treatment, which are the most cited in the literature, and treatment within or near the contaminated area, which will not be relevant for the present study.

(a) *Ex situ* treatment: In this method, the contents of the affected area are removed by excavation or pumping and transported to a unit specialized in the chosen treatment technique, where the material is treated and eventually returned to the original site for replacement, in the case of soil treatment. The primary advantages of this method are its shorter treatment time and the consistency of the technique. However, it incurs higher costs compared to *in*


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*situ* techniques, as it involves additional processing steps and carries risks of secondary contamination due to the removal and transport of contaminated material.[66]

(b) *In situ* treatment: In this method, the treatment system is installed and operated directly at the affected site, eliminating the need for removal of contaminated material. Therefore, these techniques have lower costs compared to *ex situ* techniques and present a low risk of secondary contamination, as the material does not need to be removed or transported. However, there are numerous cases in which *ex situ* techniques are more suitable, such as when technical constraints exist, in highly heterogeneous soils, or when contaminants are located in areas of low accessibility or are completely inaccessible, among other factors that prevent the application of *in situ* techniques.[66] Furthermore, according to Pérez and Aguiar,[67] remediation can also be categorized based on treatment principles into chemical, thermal, and biological treatments, which will be discussed in more detail later.

(c) Chemical treatment: These techniques utilize controlled chemical reactions to convert a toxic contaminant into a less active or inert compound, thereby reducing its environmental impact. This type of treatment, also known as chemical oxidation, employs oxidizing agents as remediation mediators in the affected area.[67] Some oxidants widely applied in this treatment include ozone, hydrogen peroxide, Fenton reagent, and persulfate.[68] Despite their high efficiency and rapid kinetics, this method presents several limitations and risks that must be carefully considered. First, chemical treatment techniques have various limitations related to the physicochemical properties of the material to be treated, being directly dependent on pH, temperature, and impurity levels, among other characteristics that can significantly affect the technique's efficiency.[66] Additionally, in some cases, a large quantity of oxidant may be required, which, besides significantly increasing the treatment cost, reduces its effectiveness, for example, in soils rich in organic matter or with high concentrations of reducing agents. Another factor to consider is the risk of altering the geochemistry of the treated area, which may compromise the life and well-being of species inhabiting that environment.

(d) Thermal treatment: In this process, a heat source is applied to the contaminated area to intensify the volatilization of compounds and promote contaminant separation. When performed *in situ*, this treatment allows relatively rapid decontamination of the affected area. However, it may be disadvantageous due to the high costs associated with the required energy and equipment. Conversely, *ex situ* thermal treatment can achieve high efficiency. Nevertheless, its environmental impacts must be strictly controlled and monitored.[67] Moreover, it is necessary to monitor and control the volatile byproducts generated during treatment, especially when there is a risk of toxicity. After the primary remediation stage, the retained hydrocarbons must be sent to a secondary treatment system, such as catalytic oxidation chambers or condensers, before being released into the atmosphere. The requirement for these additional stages constitutes an operational limitation of the method.[66]

Furthermore, remediation can be carried out through physical treatment, which involves the application of physical barriers that prevent the passage of contaminated material, thereby avoiding its contact with the treated area. This type of treatment is primarily used in marine environments to control oil spills. In this process, containment equipment such as booms and skimmers is commonly employed to prevent contact between the contaminated and clean areas. Physical control of aquatic contaminants can also be performed using lipophilic and hydrophobic adsorbent materials that retain oil in water bodies.[69] Although widely applied, physical methods present significant operational and environmental limitations. For example, booms may be inefficient in rough marine conditions, require anchoring and recurrent maintenance, and can degrade and disperse the contaminant. Similarly, skimmers are less effective in turbulent waters and are susceptible to clogging. The efficiency of adsorbents, in turn, depends on factors such as the density and viscosity of the contaminant oil.

Considering the limitations presented by physical, thermal, and chemical remediation methods, bioremediation emerges as a promising alternative as it combines efficacy, low operational cost, and reduced environmental impact.

*3.1.3. Comparison between Conventional and Biological Methods.* Bioremediation is a set of remediation methods that utilize living organisms, such as plants and microorganisms, to degrade or reduce contaminants in soils or water bodies.[70] Some widely applied biological methods include bioaugmentation, biostimulation, vermicomposting, and phytoremediation, the latter being, according to the literature, one of the most used techniques.[70]

Bioremediation methods can be classified as either *in situ* or *ex situ* methods.[66] *In situ* treatment consists of employing native microorganisms from the affected area to remediate contaminants, and these methods are widely used due to their low cost and considerable effectiveness.[66] *Ex situ* bioremediation, in turn, involves removing the contaminated material from its original location and treating it in a separate treatment unit located elsewhere or in a distinct system.[66] These methods are highly versatile and can be applied to treat a wide variety of contaminants.[66]

A large body of research demonstrates the effectiveness of bioremediation in the treatment of petroleum-contaminated soils, without causing aggressive reactions or generating harmful byproducts to the environment, thus representing a sustainable alternative for the remediation of contaminated areas.[68] Furthermore, bioremediation is a relatively low-cost method and can eliminate specific contaminants.[68]

Although practical and sustainable, bioremediation methods may require a significant amount of time for effective treatment, and their efficiency depends on factors such as contaminant concentration in the affected region, the nature of the contaminants, pH, temperature, and salinity of the contaminated material, among others.[68] Nevertheless, proven methods already exist for selecting the most favorable microbial consortia for each type of area or contaminant, such as preliminary laboratory tests performed on samples of the contaminated material, which allow for the optimization of treatment application time.[68] Table 5 presents the main advantages and disadvantages of bioremediation compared to other previously discussed treatment methods.[66,70]

In summary, the comparison between conventional remediation approaches and bioremediation highlights the considerable potential of the latter in addressing petroleum-contaminated sites, offering superior cost-effectiveness, high long-term efficacy, and most critically minimal adverse environmental


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**Table 5. Comparative Table Outlining the Advantages and Disadvantages of Various Oil Remediation Methods, Highlighting the Differences between Conventional and Biological Processes**

| Method | Advantages | Disadvantages |
|---|---|---|
| Bioremediation | Cost-effective | Longer treatment time |
| | Does not cause adverse environmental impact | Limited predictability |
| | Easy to apply | Effectiveness conditioned by environmental factors |
| | Definitive treatment of contaminants, in some cases | May not be effective at high contaminant concentrations |
| | Allows for the treatment of specific contaminants | |
| Chemical Remediation | Rapid reactions | Complex application |
| | High efficiency | High reagent consumption, resulting in elevated costs |
| | Effective at high contaminant concentrations | Limited predictability |
| | Generally does not require post-treatment steps | Effectiveness conditioned by environmental factors |
| | | Not sustainable |
| | | May generate toxic byproducts |
| Thermal Treatment | Easy to apply | May emit volatile pollutants into the atmosphere |
| | Can be applied *in situ* or *ex situ* | High energy consumption |
| | High efficiency | Requires additional steps for the treatment of volatile byproducts |
| Physical Remediation | Rapid treatment | High equipment costs |
| | High effectiveness | Harmful to the environment |
| | Definitive contaminant removal | Risk of secondary contamination |
| | Applicable to high contaminant concentrations | Complex application |

impact, factors of growing importance in contemporary environmental management. While conventional methods, despite their immediate effectiveness, are often associated with significant ecological disturbances, the formation of toxic byproducts, and elevated operational costs, in addition to practical limitations regarding their applicability, bioremediation emerges as a sustainable and economically viable alternative. Consequently, the development and implementation of bioremediation strategies constitute substantial advancement in the pursuit of more efficient, sustainable, and ecologically sound solutions for the remediation of petroleum-impacted environments.

## 3.2. Microbial Biodegradation of Petroleum.

*3.2.1. Main Groups of Microorganisms.* The biodegradation of petroleum and its derivatives is a crucial biotechnological process for the environmental remediation of areas contaminated by hydrocarbons. Among the most employed microorganisms in this process are filamentous fungi, yeasts, and bacteria, each exhibiting specific degradation capabilities and adaptability to various environmental conditions.[71] Several criteria are considered when selecting microorganisms for biodegradation studies, including their metabolic capacity to degrade specific hydrocarbons, such as aliphatic chains, aromatic compounds, or polycyclic aromatic hydrocarbons, by using them as a carbon source. Another critical criterion is the ability of these microorganisms to produce oxidative and hydrolytic enzymes, as these enzymes are predominantly responsible for efficiently catalyzing the degradation reactions.[72] Resistance to contaminated environments characterized by high salinity, extreme pH levels, and toxicity is also a valuable trait in selecting microorganisms for the degradation of these pollutants.[73]

Bacteria are widely employed due to their rapid growth rates and remarkable adaptability to diverse environmental conditions. Among the most prominent species is *Pseudomonas aeruginosa*, which is capable of degrading alkanes and BTEX compounds through the action of mono- and dioxygenases. This species demonstrates a degradation efficiency of approximately 70–90% within 7–14 days.[74–76] *Alcanivorax borkumensis* is another key species, primarily involved in the degradation of long-chain linear alkanes (C10–C32), with the AlkB enzyme as a primary catalytic agent. It typically achieves an average degradation efficiency of up to 95% over 10–20 days.[77–79]

**Table 6. Main Microorganisms Used in the Biodegradation Process of Petroleum-Derived Hydrocarbons, Highlighting Each Group of Microorganisms, Taxonomic Group, Degraded Hydrocarbons, Enzymes Involved, Degradation Efficiency, Time, and Original Reference with Experimental Data**

| Microorganism | Taxonomic Group | Degraded Hydrocarbons | Involved Enzymes | Degradation Efficiency (%) | Time (days) | References |
|---|---|---|---|---|---|---|
| *Pseudomonas aeruginosa* | Proteobacteria | Alkanes, BTEX | Monooxygenases, dioxygenases | 70–90% | 7–14 | 92, 93 |
| *Alcanivorax borkumensis* | Proteobacteria | Linear alkanes (C10–C32) | Alkane monooxygenase (AlkB) | Up to 95% | 10–20 | 94, 95 |
| *Rhodococcus erythropolis* | Actinobacteria | Alkanes, PAHs | Monooxygenases, dehydrogenases | 60–85% | 15–30 | 96–98 |
| *Bacillus subtilis* | Firmicutes | Alkanes, light aromatics | Lipases, peroxidases | 50–70% | 7–20 | 99, 100 |
| *Aspergillus niger* | Ascomycota | PAHs, BTEX | Laccases, peroxidases, cytochrome P450 | 65–85% | 10–25 | 101, 102 |
| *Penicillium chrysogenum* | Ascomycota | Alkanes, simple aromatics | Monooxygenases, laccases | 60–80% | 15–30 | 103–105 |
| *Fusarium solani* | Ascomycota | PAHs | Peroxidases, phenoloxidases | 50–75% | 15–28 | 106, 107 |
| *Trametes versicolor* | Basidiomycota | PAHs, asphaltenes | Laccases, Mn-peroxidase | Up to 90% | 20–30 | 108, 109 |
| *Candida tropicalis* | Ascomycota | Alkanes, light aromatics | Cytochrome P450, alkane hydroxylase | 60–80% | 10–20 | 110–112 |
| *Yarrowia lipolytica* | Ascomycota | Alkanes (C10–C20), PAHs | Monooxygenases, lipases | 70–90% | 7–14 | 113, 114 |
| *Rhodotorula mucilaginosa* | Basidiomycota | BTEX, simple aromatics | Oxidases, peroxidases | 50–75% | 10–20 | 115–117 |
| *Saccharomyces cerevisiae* | Ascomycota | Short-chain aromatics | Dehydrogenases, monooxygenases | ~50% | 10–15 | 118, 119 |


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*Rhodococcus erythropolis* is also frequently utilized in hydrocarbon biodegradation studies, capable of degrading both polycyclic aromatic hydrocarbons (PAHs) and alkanes through the use of monooxygenases and dehydrogenases, with reported efficiencies ranging from 60 to 85% over 15−30 days.[80−82]

Filamentous fungi exhibit a high capacity for extracellular secretion of oxidative enzymes, which are particularly useful in the degradation of complex and poorly soluble compounds.[83,84] *Aspergillus niger* acts on PAHs and BTEX compounds by producing laccases, peroxidases, and cytochrome P450 enzymes, all of which play critical roles in biodegradation processes. This microorganism demonstrates degradation efficiencies ranging from 65 to 85% within 10−25 days.[85,86] Another highly promising fungus is *Trametes versicolor*, which is effective in the degradation of PAHs and asphaltenes. It secretes laccases and manganese peroxidase (Mn-peroxidase) and can achieve degradation efficiencies of up to 90% within 30 days.[87]

Yeasts exhibit good tolerance to hydrocarbons and are effective in the degradation of both aliphatic and aromatic compounds. Two species are particularly prominent in the literature: *Yarrowia lipolytica*, known for degrading alkanes (C10−C20) and PAHs through the activity of monooxygenases and lipases, with degradation efficiencies ranging from 70 to 90% within 7−14 days; and *Candida tropicalis*, which is capable of degrading aromatic hydrocarbons and alkanes. This yeast produces enzymes such as cytochrome P450 and alkane hydroxylase, which are involved in its biodegradation processes, achieving efficiencies between 60% and 80% over up to 20 days.[88−91]

Table 6 presents a compilation of experimental data related to biodegradation reactions carried out by microorganisms. It highlights key microbial species from each group discussed as well as the specific hydrocarbons evaluated in the respective studies. The enzymes responsible for the degradation are also emphasized, as they play a fundamental role in directly catalyzing these biotransformations. Additionally, Table 6 outlines the average efficiency of the biodegradation process and the time required for its completion. The efficiency of biodegradation depends on several factors, including the concentration and type of hydrocarbon, nutrient availability, presence of oxygen, and environmental conditions. Both laboratory and field studies consider a biodegradation range of 50% to 90% of the total hydrocarbon mass to be acceptable. The average time required to achieve this level of efficiency typically ranges from 7 to 30 days depending on the microorganism involved, the type of contaminant, and the characteristics of the surrounding environment.

*3.2.2. Factors Affecting Degradation.* The efficiency of hydrocarbon biodegradation by microorganisms is highly dependent on environmental factors that influence enzymatic activity, microbial growth, and bioavailability of the compounds. Key parameters include the temperature, pH, nutrient availability, salinity, oxygen presence, and substrate type. Temperature directly affects microbial metabolism and the solubility of the hydrocarbons. Moderate temperatures (25−35 °C) enhance enzymatic activity and support the growth of most hydrocarbon-degrading microorganisms.[120−122] Very low temperatures (<15 °C) reduce the degradation rate; however, psychrotrophic species, such as Pseudomonas spp., may still function, albeit at a slower pace. High temperatures (>40 °C) can denature enzymes or inhibit the growth of nonthermotolerant strains.[123]

pH influences both enzymatic stability and cell membrane permeability. The optimal pH range for biodegradation typically lies between 6.5 and 8.5, although this range can vary depending on the specific microorganism..[124] Fungi such as *Trametes versicolor* can tolerate broader pH fluctuations, whereas bacteria generally require conditions closer to neutral pH.[125]

Nutrient availability is another crucial factor that must be taken into consideration. Nitrogen and phosphorus are essential for the synthesis of proteins and nucleic acids, thereby regulating microbial growth.[126] The ideal C/N/P ratio for effective biodegradation is approximately 100:10:1. Environments with excess carbon (in the form of hydrocarbons) and limited nitrogen and phosphorus availability tend to exhibit a reduced degradation efficiency. Biostimulation through the addition of these nutrients can enhance the degradation rate by up to 2-fold.[127]

High salinity can inhibit the activity of most nonhalotolerant bacteria; however, some species exhibit resistance, such as *Alcanivorax borkumensis*, which is halophilic and functions efficiently in marine environments with salinity levels up to 3.5%. Marine fungi and specific yeasts also demonstrate a good tolerance to moderate salinity. Nevertheless, increasing salinity levels can significantly reduce the efficiency of biotransformation processes.[128]

Oxygen availability is a key factor that directly influences the biodegradation rate, as most hydrocarbon degradation reactions are aerobic and require molecular oxygen for monooxygenases and dioxygenases to function.[129] Proper aeration of soil and water is essential to sustain oxidative metabolism. In anaerobic environments, degradation is still possible but occurs at a much slower rate, relying on alternative electron acceptors such as nitrate, sulfate, or $CO_2$.[130]

Substrate type and bioavailability are also determining factors in the biodegradation process. Short-chain hydrocarbons (such as light alkanes) are more readily bioavailable and easier to degrade.[131] In contrast, compounds such as high-molecular-weight polycyclic aromatic hydrocarbons (PAHs) and asphaltenes exhibit low solubility and limited accessibility, often requiring pretreatment or the use of specialized microbial consortia.[132] Biosynthetic surfactants (biosurfactants), produced by microorganisms such as *Bacillus subtilis*, enhance emulsification and facilitate enzymatic access to hydrophobic substrates.[133]

*3.2.3. Biochemical Mechanisms. 3.2.3.1. Stages of the Metabolic Process.* The biodegradation of hydrocarbons generally proceeds through three main stages, each involving specific biochemical and enzymatic processes.[134] The first step is activation of the hydrocarbon, which typically involves an initial oxidation or cleavage of the hydrocarbon chain to increase its reactivity and solubility. This process is often catalyzed by oxygenases, such as monooxygenases and dioxygenases, which introduce hydroxyl groups into the hydrocarbon structure, thereby converting it to more polar compounds, like alcohols. In the second stage, these activated compounds undergo intermediate metabolic transformations, including sequential oxidation steps that convert alcohols to aldehydes and subsequently to carboxylic acids. These intermediates are progressively shortened through $\beta$-oxidation or other catabolic pathways. Finally, in the third stage, the resulting smaller molecules, often acetyl-CoA or similar intermediates, enter central metabolic pathways such as the tricarboxylic acid (TCA) cycle or specific fermentation routes.[135−137] Within these pathways, the compounds are fully oxidized, enabling the


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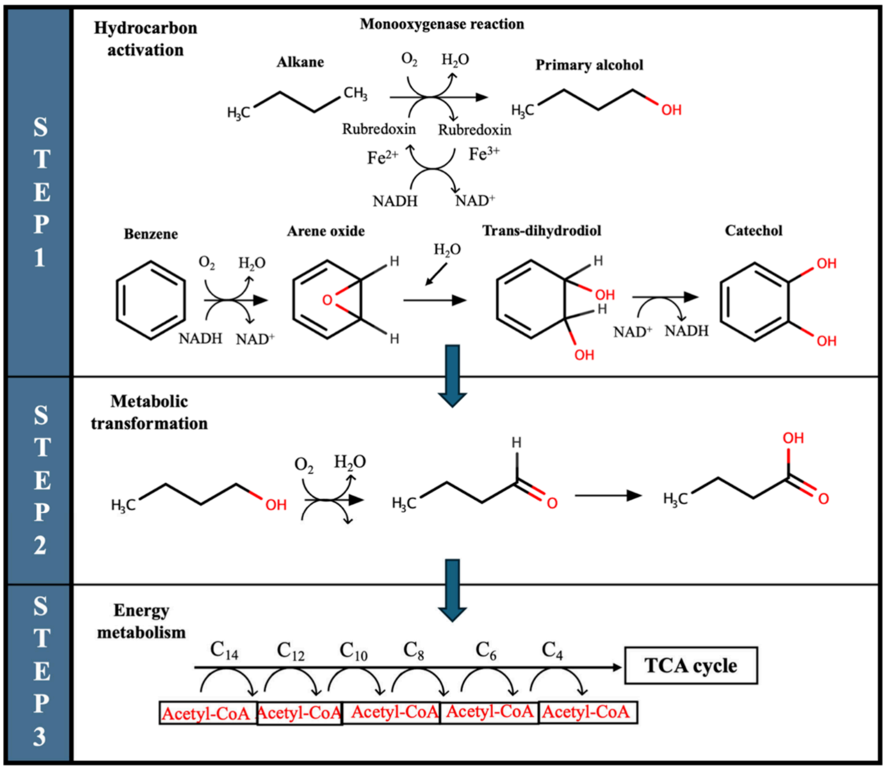


**Figure 10.** Simplified stages of the metabolic process involved in the biotransformation of hydrocarbons by microorganisms. The first stage illustrates a simplified oxidation mechanism catalyzed by a monooxygenase; the second stage depicts possible products of partial and complete oxidation; and the final stage presents a simplified view of the incorporation of these compounds into the microorganism's energy metabolism.

microorganism to extract energy and generate biomass, completing the biodegradation process.[138] Figure 10 illustrates these steps in a general and simplified manner, highlighting the initial activation phase, subsequent partial or complete oxidation stages, and the incorporation of the resulting molecules into the microorganism's central energy metabolism.

Table 7 provides an overview of the reactions involved in the enzymatic biodegradation of hydrocarbons as well as their roles in the final metabolic process of utilizing this carbon source. Understanding the specific pathways and reactions, as well as identifying the key genes and enzymes involved, has been fundamental for the application of these strategies by research groups and their researchers.

**Table 7. Main Types of Biochemical Reactions Involved in Microbial Degradation of Petroleum Hydrocarbons, Including Examples and Their Respective Roles in Transforming Hydrocarbon Structures into Intermediates for Metabolic Assimilation**

| Reaction Type | Example | Function | References |
|---|---|---|---|
| Oxidation | R-$CH_3$ → R-$CH_2OH$ | Introduces functional groups | 139, 140 |
| Hydroxylation | R-H → R–OH | Increases solubility and reactivity | 141, 142 |
| Aromatic ring oxidative cleavage | Aromatic → Dicarboxylic acid | Breaks down the polycyclic hydrocarbon structure | 143, 144 |
| $\beta$-Oxidation | Fatty acid → Acetyl-CoA | Generates energy via the Krebs cycle | 145, 146 |
| Carboxylation | R-H → R-COOH | Enables entry into central metabolic pathways | 147, 148 |

*3.2.3.2. Role of Enzymes.* The efficient degradation of hydrocarbons depends on the presence of microorganisms that possess enzymatic repertoires adapted to the type of compound and the environmental conditions. These enzymes are typically produced as a part of their adaptive metabolic response to the presence of hydrocarbons in the environment, which serve as alternative carbon and energy sources under nutrient-limited or contaminated conditions.[149] The enzymes are often secreted extracellularly or associated with the cell membrane, facilitating the initial activation of otherwise inert hydrocarbon molecules. For example, mono- and dioxygenases are commonly expressed by bacteria, such as Pseudomonas and Rhodococcus, in response to aromatic and aliphatic hydrocarbons. In contrast, fungi such as Trametes versicolor upregulate oxidative enzymes, including peroxidases, under ligninolytic or hydrocarbon-rich conditions. These enzymatic systems allow microbes to survive and proliferate in polluted environments by enabling them to utilize hydrocarbons as substrates for growth and energy production. Table 8 outlines the major enzyme classes involved in these processes, their biochemical functions, and the representative microbial genera known to produce them.

*3.2.3.3. Metabolic Pathways Involved.* The microbial degradation of petroleum involves specific metabolic routes depending on the type of hydrocarbon present. These routes are catalyzed by oxygenases and other oxidoreductases and lead to the incorporation of hydrocarbons into central metabolic pathways.[162]

Alkanes are typically degraded through the terminal oxidation pathway, where the terminal methyl group is oxidized step by step until it is converted into a carboxylic acid. This acid enters the $\beta$-oxidation cycle and is eventually funneled into the citric acid cycle (TCA).[163] Figure 11 shows the general reaction


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**Table 8. Major Classes of Enzymes Involved in the Microbial Biodegradation of Petroleum-Derived Hydrocarbons, Their Biochemical Functions, and Representative Producing Microorganisms[a]**

| Enzyme Class | Function | Representative Microorganisms | References |
|---|---|---|---|
| Monooxygenases | Insert one atom of oxygen into the hydrocarbon molecule | *Pseudomonas, Yarrowia, Candida* | 150, 151 |
| Dioxygenases | Incorporate two oxygen atoms, primarily into aromatic rings | *Pseudomonas, Rhodococcus* | 152, 153 |
| Peroxidases (MnP, LiP) | Degrade PAHs and other recalcitrant compounds | *Trametes versicolor, Phanerochaete* | 154, 155 |
| Cytochrome P450 | Hydroxylation of complex hydrocarbons | *Candida tropicalis, Aspergillus* | 156, 157 |
| Alkane hydroxylases | Oxidize alkanes into primary alcohols | *Alcanivorax, Pseudomonas* | 158, 159 |
| Dehydrogenases | Oxidize alcohols and aldehydes into carboxylic acids | *Pseudomonas putida, Rhodococcus erythropolis, Acinetobacter calcoaceticus* | 160, 161 |

[a]The listed enzymes act in the initial and intermediate stages of hydrocarbon biotransformation, enabling activation, oxidation, and subsequent assimilation of these compounds.

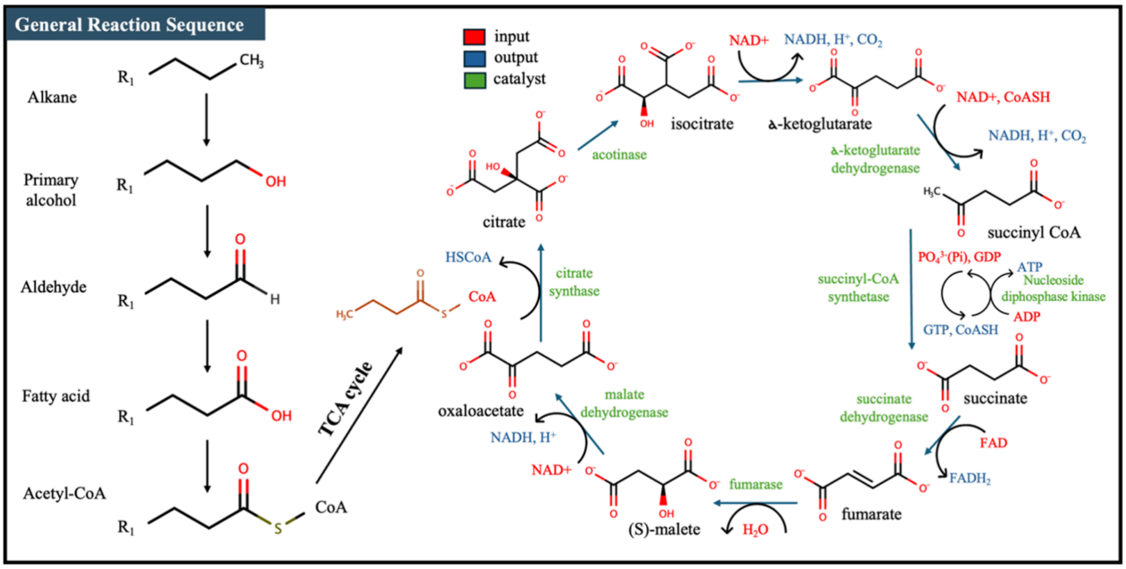


**Figure 11.** General scheme of the biodegradation reaction of alkane hydrocarbons and description of the stages of the TCA cycle for the final degradation process in the metabolism of the microorganism.

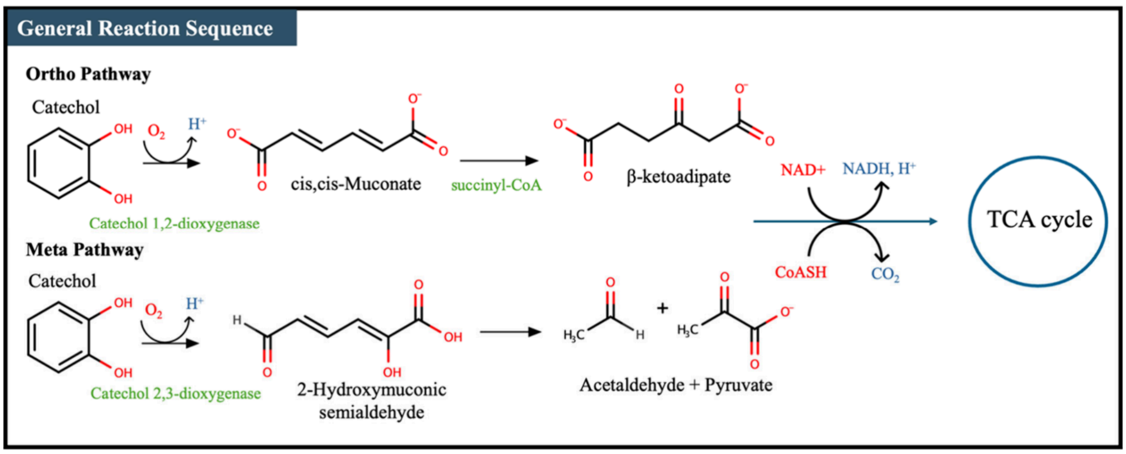


**Figure 12.** General scheme of the biodegradation reaction of aromatic hydrocarbons by the ortho and meta pathways, leading to the formation of products for the TCA cycle.

sequence of the process. The TCA cycle is the final metabolic pathway in the microbial degradation of hydrocarbons, where intermediate compounds, such as acetyl-CoA, derived from earlier oxidation steps, are fully oxidized to carbon dioxide ($CO_2$). This cycle takes place in the cytoplasm of prokaryotes or the mitochondria of eukaryotic microorganisms and serves as a central hub for energy production. In this pathway, acetyl-CoA, produced from the breakdown of alkanes, PAHs, or other hydrocarbon derivatives, enters the TCA cycle and combines with oxaloacetate to form citrate. Through a series of enzymatic steps, citrate is progressively oxidized, releasing $CO_2$, generating NADH and $FADH_2$, and regenerating oxaloacetate to continue



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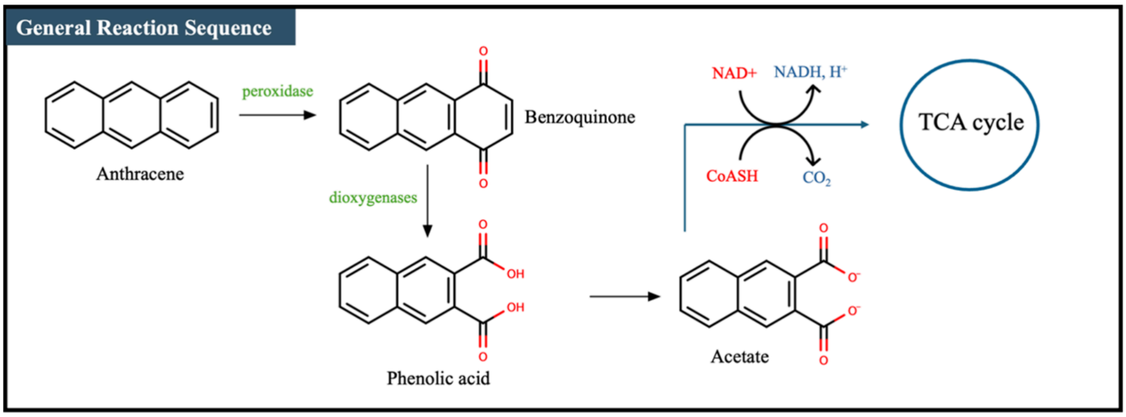


**Figure 13.** General scheme of the biodegradation reaction of polycyclic aromatic hydrocarbons (PAHs), such as anthracene, requires more complex enzymatic systems due to their low solubility and structural rigidity.

the cycle. The reducing equivalents (NADH and $FADH_2$) are then used in the electron transport chain to produce ATP, which fuels cellular processes.[164]

The microbial degradation of aromatic hydrocarbons, such as benzene, toluene, ethylbenzene, and xylene, collectively known as BTEX compounds, involves a series of biochemical steps that convert these persistent and hydrophobic molecules into assimilable metabolic intermediates. The process begins with the activation of the aromatic ring through the action of dioxygenase enzymes, which incorporate two oxygen atoms into the compound.[165] This initial oxidation increases the reactivity and solubility of the molecule, resulting in the formation of dihydroxylated intermediates, such as catechol or protocatechuate, key substrates for subsequent ring-cleavage reactions.[166] These intermediates are further processed via two main enzymatic pathways: the ortho-cleavage and meta-cleavage routes. In the ortho-cleavage pathway, catalyzed by catechol 1,2-dioxygenase, the aromatic ring is cleaved between the two hydroxyl groups, resulting in the production of cis,cis-muconic acid. This compound is metabolized into $\beta$-ketoadipate and subsequently converted into acetyl-CoA and succinyl-CoA, which enter the tricarboxylic acid (TCA) cycle. In contrast, the meta-cleavage pathway, mediated by catechol 2,3-dioxygenase, cleaves the ring adjacent to the hydroxyl groups, yielding 2-hydroxymuconic semialdehyde. This intermediate is further converted into pyruvate and acetaldehyde, which are also assimilated into the central metabolic routes. Ultimately, these pathways enable microorganisms to transform toxic and recalcitrant aromatic hydrocarbons into energy-rich compounds, which are fully oxidized through the TCA cycle, thereby supporting microbial growth and energy production.[167] Figure 12 highlights both processes.

The microbial degradation of polycyclic aromatic hydrocarbons (PAHs), such as anthracene, phenanthrene, and pyrene, involves a more complex and specialized enzymatic machinery due to the compounds' low aqueous solubility, high molecular weight, and rigid multiring structures. These characteristics make PAHs particularly recalcitrant in the environment. The degradation process is often initiated by white-rot fungi and certain adapted bacteria that possess the ability to secrete potent extracellular oxidative enzymes, such as lignin peroxidase, manganese peroxidase, laccases, and cytochrome P450 monooxygenases.[168] Figure 13 shows this process and the steps in a simplified form, from the initial oxidation to the introduction of carboxylic groups into the Krebs cycle. These enzymes catalyze the initial transformation of PAHs into more reactive intermediates such as quinones and arene oxides (epoxides), increasing their solubility and susceptibility to further enzymatic attack. These intermediates are subsequently converted to phenolic acids and related compounds through a series of hydroxylation, dehydrogenation, and rearrangement reactions. The resulting phenolic structures undergo ring cleavage by dioxygenases, producing aliphatic acids, such as acetate and succinate. These smaller metabolites are then funneled into the tricarboxylic acid (TCA) cycle, where they are fully oxidized to $CO_2$ and water, providing energy and biosynthetic precursors for microbial growth. This multistep degradation process enables microorganisms to mineralize highly hydrophobic and toxic PAHs, contributing significantly to the bioremediation of contaminated environments.[169]

### 3.3. Applications and Challenges of Petroleum Biodegradation.

*3.3.1. Applied Techniques.* Some techniques have been studied for the degradation or removal of total petroleum in contaminated areas, whether chemical, physical, or biological techniques.[170] Bioremediation is a decontamination technique that uses raw materials such as plants, bacteria, and fungi in the process of decontaminating environments, to recover or reduce the contaminated area.[171] Bioremediation is a promising alternative to be used in several sectors, especially in the rehabilitation of environments contaminated by petroleum, which uses microbial activity to carry out the process of biochemical degradation of hydrocarbons into less toxic substances, most of which are present in soils contaminated by petroleum.[172,173]

There are a few bioremediation treatments that can be used. The first is *ex situ*, in which the contaminated soil is excavated; a higher cost is required for the process, because in addition to removing the soil for analysis in a controlled environment, some additions are made, such as biostimulation and bioaugmentation.[174,175] In biostimulation, nutrients, oxygen, or other compounds are added to the soil, stimulating the growth and activity of microorganisms already present.[176,177]

However, in bioaugmentation, a microbial inoculation process is carried out, in which so-called "beneficial microorganisms" or other specific organisms are added, increasing the existing microbial population or inserting nonexistent microorganisms, to improve the quality of the contaminated soil, in which the fixation process is carried out so that the environment absorbs the nutrients, accelerating the biodegradation process.[174] *Ex situ* treatment is generally the most commonly used


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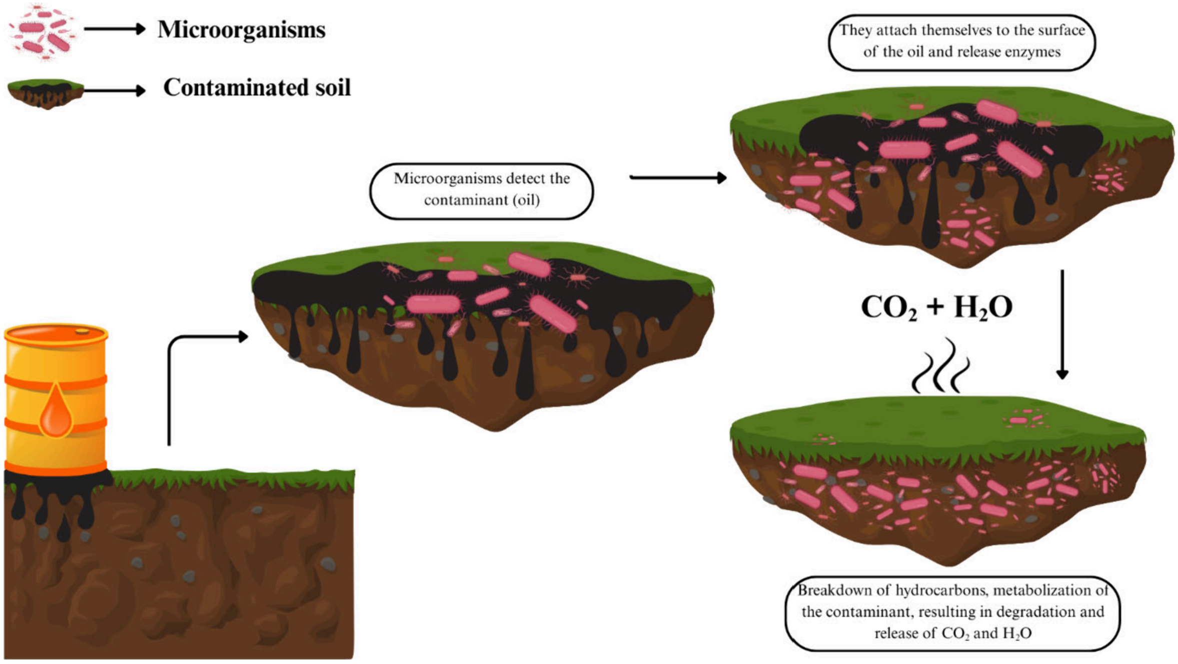


**Figure 14.** Diagram of the bioremediation process: action of microorganisms in contaminated soil.

method when dealing with more serious contaminations, but it is worth noting that the costs are high, requiring significant amounts of materials and labor.[178]

The second type of treatment is *in situ* bioremediation, which is used in studies directly at the contaminated site, allowing the use of natural microbial activity; this is the proposal with the least environmental impact and is the most attractive and economically viable, as it minimizes the disturbance of the ecosystem.[179,180] However, the effectiveness of the treatment is directly linked to the permeability of the soil, in addition to the levels of nutrients and the availability of oxygen present; the *in situ* treatment or technique is the most widely used in the world.[181]

Figure 14 presents the simplified scheme of the action of microorganisms in contaminated soil, in which the microorganisms detect the contaminant present, such as petroleum, attach themselves to the surface of the oil, release enzymes that break the hydrocarbon chains, and begin the process of adding oxygen; the large hydrocarbon molecules then are broken down into smaller molecules, which finally metabolize the identified contaminant, degrading and releasing $CO_2$ and $H_2O$.[182,183]

In addition to the treatments mentioned above, there are also the most popular ones, such as composting,[184] the use of bioreactors,[185−187] and natural attenuation, which becomes efficient when combined with other techniques; however, it is a natural process based on slow monitoring.[188,189]

Phytoremediation is a promising technique for use in the bioremediation process. Fungi and plants are used to decontaminate the water and soil. This method incorporates some other strategies that take advantage of all the properties of plants, such as phytoextraction, phytovolatilization, and phytostabilization, in which the effectiveness is directly related to the availability of pollutants and the plant species used.[190] Unlike chemical or physical remediation, phytoremediation requires fewer resources and, consequently, lower financial expenses, as it uses plants in the soil rehabilitation process, in addition to being a natural and sustainable process for combating toxic pollutants.[191,192]

There is also the land-farming technique for the bioremediation process. In this technique, oily residues containing organic carbon are applied to the soil, typically to enhance the microbial activity. This technique is used together with fertilizers.[193] The area where it is applied to treat biological degradation is termed the arable zone. This technique is used in places contaminated by sludge or oily contaminants. However, it is considered a high-cost technique, mainly when it refers to petroleum hydrocarbons as the primary contaminant principal.[194]

In general, the application of bioremediation promotes the metabolization of microorganisms into organic substances, which contain the nutrients and energy necessary for the process, requiring activation of these microorganisms to enable biodegradation. These organic compounds are metabolized through the processes of respiration, fermentation, or co-metabolism.[195,196]

Bioremediation offers sustainable solutions to soil contamination by petroleum. Still, its effectiveness depends on the strategies implemented, focusing on the challenges encountered at the site to be analyzed. In addition to the type of contaminant, the availability or lack of oxygen, the complexity of the hydrocarbons, and the microbial dynamics, these factors must also be studied. Hybrid approaches should be considered, especially when dealing with mixed contaminants, as the integration of different methods can yield promising results when combined with physical treatments.

*3.3.2. Case Studies.* Pollution caused by petroleum hydrocarbons is still a concern; therefore, analyses using different methods are employed with caution to avoid drastic contamination. Several techniques can be used in such studies, three of which are natural attenuation, bioaugmentation-assisted landfarming, and landfarming; all are applied to soils contaminated by petroleum hydrocarbons (TPH), with the bioaugmentation-assisted landfarming technique being the most promising, with an 86% reduction in total TPH.[197]

Several bioremediation techniques are used to recover contaminated environments, including the use of bioreactors, which are also a component of the bioremediation process. The


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work of Chikere et al. (2016)[186] highlights the use of stirred tank bioreactors, some containing fertilizers or manure, but the bioreactor that showed the highest percentage of reduction in petroleum hydrocarbons and increase in biomass was the one containing NPK fertilizer (97%), in addition to having found approximately 24 bacterial species, of the genera *Bacillus sp* and *Pseudomonas sp* and others, evidencing that the bacterial population found in contaminated soil can be used in the bioremediation process, degrading the hydrocarbons present.

The composting technique applied to the bioremediation process is one of the best-known techniques, because it is a low-cost and easy-to-operate technique.[198] Bioremediation by composting requires a diverse microbial community, which directly influences the success of the bioremediation process.[184] Physical-chemical parameters directly influence the biological composting process, and the optimization of these parameters is the main factor for a successful bioremediation process, such as in conjunction with other bioremediation techniques, as in the study on the degradation of hydrocarbons in soil contaminated by lead and motor oil, being treated by composting and phytoremediation techniques.[199]

In the study by Lin et al. (2012)[200] diesel oil was incorporated into food waste; the resulting mixture was subjected to the composting process, and several parameters were analyzed, including moisture content, temperature, and variation in total petroleum hydrocarbon (TPH) levels. The results demonstrated the effectiveness of the composting process in the decomposition of diesel oil in 10 days, due to the reduction of TPH, in addition to finding 11 species of *Oleiphilus*, proving that the composting of food waste contained a variety of microorganisms that provide a wide capacity for decomposition of oils. It was concluded that it is an effective method for the bioremediation process of soils contaminated by oils, without requiring bioaugmentation or biostimulation.[200]

Bioaugmentation is an emerging strategy to accelerate the bioremediation process. In the study by Gao et al. (2022),[201] bioaugmentation was employed in a marine environment, specifically in the waters of the South China Sea, which were contaminated by crude petroleum. The bacterium *Pseudomonas aeruginosa* ZS1 was used in the bioremediation process of oil degradation in the absence and presence of the bacterium ZS1. The analyzed results showed that the presence of microbial communities decreased at the site due to contamination; however, they obtained a crude petroleum degradation rate, upon adding the ZS1 bacteria, of 50% in just 50 days, in addition to the efficient degradation of alkanes present, such as C13 alkanes and solid *n*-alkanes, proving the effectiveness of the process.[201]

In the work of Bidja Abena et al. (2019),[188] a study of the biodegradation of total petroleum hydrocarbons (TPH) was conducted in five soils considered highly contaminated, with microbiological, physical, and chemical analyses performed on all collected soils. Bioaugmentation and natural attenuation techniques with nutrient insertion were used, as a result of which the effectiveness of bioaugmentation was verified, when compared to natural attenuation, with a result of 48% TPH degradation; the bioaugmented strains were able to resist high TPH rates, in addition to not having interfered with the survival capacity of native microorganisms, with a good influence on the five different types of soils.

In the study by Al-Dhabaan et al. (2021),[202] the technique called microremediation was used, also one of the bioremediation techniques, in which fungi are used to treat contaminated soils. The study was carried out in soil contaminated with crude petroleum, and the fungal strains to be analyzed were isolated, totaling 22 fungal isolates, of which only three showed significant potential for degradation of crude oil, namely, *Aspergillus niger*, *Aspergillus polyporicola*, and *Aspergillus spelaeus*, with emphasis on *Aspergillus niger*, which showed a biodegradation capacity of 58%, in addition to having emitted a high percentage of $CO_2$ (28%), when compared to the others, proving the effective biodegradation of petroleum.

Figure 15 indicates the most commonly used techniques in the bioremediation process, variations of *in situ* and *ex situ*,

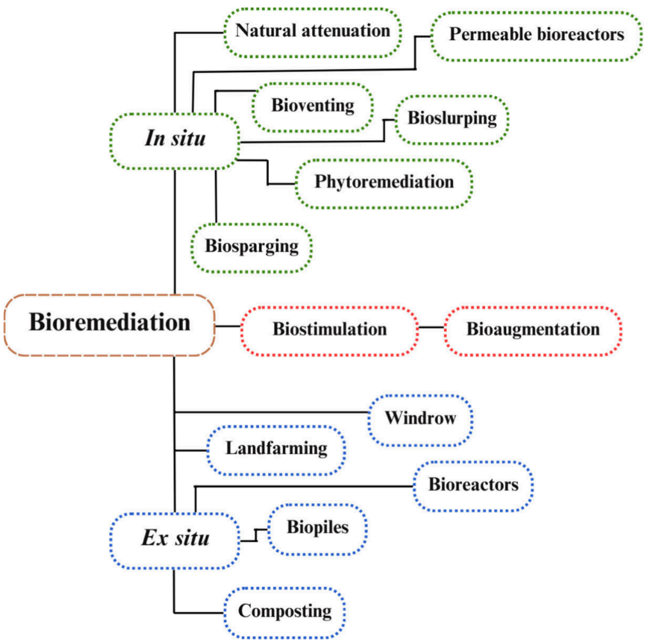


**Figure 15.** Main bioremediation techniques, classified as *in situ* and *ex situ*, with an indication of possible applications and strategies for biostimulation and bioaugmentation.

which can be used as complementary strategies to biostimulation and bioaugmentation, being applied as needed to accelerate or contribute to the efficiency of the bioremediation process, either together or individually, applied at the sites of origin of the contamination (*in situ*) or in a controlled environment outside the contamination site (*ex situ*).[203,204] Biostimulation or bioaugmentation may not be necessary in specific techniques, such as natural attenuation, in which minimal intervention is employed. However, in some cases, they can be applied together, if required. *Ex situ* techniques often allow the simultaneous combination of biostimulation and bioaugmentation, especially the bioreactor technique.[187,205]

Phytoremediation has been widely discussed when it comes to soils contaminated by toxic agents, which harm the development of microbial communities in these soils, becoming popular because it presents an excellent cost-benefit when compared to other bioremediation techniques, in addition to being ecologically acceptable, as it uses plant species to restore contaminated sites, as well as not impacting soil structures, as it still promotes a fertile environment.[190,206]

Phytoremediation, although a slow technique, results in the recovery of contaminated environments in a more ecological way, especially when combined with other methods, such as plant–microbe interaction, which can increase its effectiveness,[207] as in the recent study by Wechtler and collaborators


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(2023), who carried out tests to analyze contaminated soil from the coculture of the plant species *Miscanthus x giganteus* (MxG) and *Trifolium repens L.* They evaluated microbial activity, density, and biomass and identified that the MxG species caused an increase in microbial activity in the soil, stimulating the increase in degradation bacterial communities, in addition to the rise in fungal density and microbial biomass.[208]

In the study by Verâne et al. (2020),[209] a phytoremediation system was developed to remove polycyclic aromatic hydrocarbons (PAHs) present in mangrove sediments contaminated by crude petroleum, utilizing the species *Rhizophora mangle*. A comparative study between phytoremediation and natural attenuation was conducted, which yielded promising results. The pH of the water used in the experiments ranged from 4.9 to 8.4 over 90 days. After a detailed analysis, it was found that phytoremediation was more efficient in degrading 16 PAHs (60.76%) in mangrove sediments.

Scientific studies demonstrate that when the technique is applied correctly to a contaminated environment, it is possible to achieve significant results in the bioremediation process, with the potential to restore and recover ecosystems in an ecologically sound and environmentally sustainable manner.

*3.3.3. Limitations and Obstacles.* The bioremediation process presents several challenges to be overcome, despite being a promising technology. The challenges range from laboratory to field scale, due to operational logistics, microbial dynamics present, and existing environmental variabilities.[210] Among the environmental factors, the type of soil stands out, which determines microbial activity, oxygen levels, pH, and temperature, such as soils with minimum permeability rates.[211]

The complexity of hydrocarbons is also an essential factor to be considered, because when they have a high molecular weight they tend to degrade more slowly. One measure to be taken would be photooxidation in the pretreatment of hydrocarbons. In this chemical process, the oxidation is carried out catalyzed by light, whether natural or artificial, and the hydrocarbons are transformed into oxygenated compounds, increasing their bioavailability.[212]

The application of techniques such as bioaugmentation can also cause some disturbances in microbial dynamics, disturbing native microbial communities, which affects the effectiveness of the process,[176] in addition to the high costs and long periods necessary to achieve success. The work of Escobar-Alvarado and collaborators (2018)[199] reported that 66% of TPH degradation was achieved using a combination of composting and phytoremediation methods. However, it is evident that despite the sustainable and low-cost technology analyzed, more time is required to achieve higher percentages of degradation in soils contaminated with oils.

At the laboratory scale, experimental conditions are also essential for achieving positive results in bioremediation research, as homogeneous contaminated soil samples make replication and study in heterogeneous samples difficult.[198] The search for bioaugmentation strains also faces a microbial limitation, as some cultivable microorganisms may have a low percentage available, and the possibility of introduced strains presents inferior performance due to competition with native soil species.[213] In other words, microbial survival is also an essential factor to consider, as some bioaugmented strains fail to thrive in the inserted environment due to toxicity or insufficient population density.[214]

Environmental variability remains a limiting factor in the application of bioremediation. Fluctuations in groundwater and soil permeability can disrupt microbial activity, as can cold climates that reduce contaminant degradation rates.[215] A study applying bioremediation in Greenland was conducted on diesel-polluted soil. The land-farming technique was used in soil conditions found in an Arctic region. Fertilizers were added to optimize the biodegradation. The degradation of total petroleum hydrocarbons (TPH) was evaluated. As a result, the presence of petroleum-degrading microorganisms was detected in the Arctic soil. Although 64% of the diesel was removed, the study demonstrated that, due to conditions such as temperature, some other analyses were complex to conduct during the process.[216]

Transportation and excavation costs in the bioremediation process are pretty high, especially when it comes to implementing *ex situ* methods, which are pretty expensive, followed by bioreactors, as they require specialized infrastructure and energy for mixing/aeration.[217] Slow degradation is also one of the risks, usually over months or years, and can lead to the migration of pollutants, especially during heavy rains and in porous soils, in addition to untreated sites that can attract animals, increasing ecological risks during long remediation periods.[218]

The limited applicability of contaminants is considered, since the bioremediation process is quite effective for organic pollutants; however, in the presence of heavy metals or radioactive materials, it becomes less effective, requiring specific and extensive techniques and studies to be applied during the process.[182,219] Bioremediation in contaminated soils faces the persistent challenges of accessibility and the bioavailability of pollutants. However, it is still an effective and low-cost process, depending on the technique to be implemented, due to greater efficiency and the ability to deal with a variety of pollutants.[220]

Bioremediation is a sustainable, environmentally friendly, and low-impact process with up-and-coming techniques for remediating contaminated environments. It has several advantages over traditional methods, which typically employ toxic products that are detrimental to the environment and human health. However, all progress and positive responses from bioremediation depend on several factors, such as those mentioned above, which require further studies and analyses, as well as investment in research in the area and greater incentives and social awareness about the methods applied.[221]

## 4. FUTURE TRENDS AND PERSPECTIVES

**4.1. New Technologies.** Bioremediation is considered an excellent technique for the recovery of contaminated environments, enabling environmental remediation and the restoration of social spaces.[222] Several methods are used in the process, among which the combination of nanobioremediation and microbial consortia stands out, since nanoparticles are used to remove contaminants, whether inorganic or organic pollutants, in contaminated environments, such as wastewater, groundwater, and soil.[221] Nanobioremediation has enormous potential in nanotechnology, with several applications, especially for the removal of toxic pollutants, with a reduction in poisonous consequences.[223,224]

A recent study was conducted using nanotechnology to improve microbial proliferation in an environment contaminated by oil spills, in which graphene oxide quantum dots (GOQDs) were used to increase the proliferation of the native strain of *Bacillus cereus* that degrades polycyclic aromatic hydrocarbons (PAHs), commonly found in oil spill-contaminated sites, obtaining a degradation result of 53% after 3.5


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days.[225] Another study utilized $Fe_2O_3$ nanoparticles in combination with bacterial species and ZnO nanoparticles to accelerate the bacterial biodegradation process in water and soil samples contaminated with crude petroleum. $Fe_2O_3$ nanoparticles combined with the species *Psychrobacter faecalis* S3 achieved 97.89% biodegradation of oil in just 3 days, proving the effectiveness and applicability in the *in situ* bioremediation process.[226,227]

Genetic engineering and microbial consortia have been prominent in the bioremediation process in recent years. Genetic engineering involves specific studies related to modifications of microbial genomes, which allows the advancement of pollutant degradation;[228] microbial consortia are synthetic communities of microorganisms, developed to degrade complex contaminants by metabolic division.[229]

Genetic engineering stands out as an innovative approach. With the use of CRISPR/Cas9 technology, it edits the genome, altering or inserting the expression of genes that encode enzymes, such as the hydrolase and oxygenase groups, present in the degradation process, enabling the creation of improved microorganisms capable of degrading resistant pollutants in addition to greater resistance to stresses, such as salinity and heat, enhancing microbial resistance in hostile places.[230] Editing in specific regions of the receptor genome has already been highlighted as an essential technology applied in the metabolism of xenobiotics in fungi[231] and has allowed the modification of toxic intermediates into harmless byproducts. In addition, CRISPR/Cas9 has a relevant impact on the phytoremediation technique, as it enables greater plant stability and efficient removal, improving the application capacity of the technique.[232]

Microbial consortia can degrade more complex compounds such as oil, sewage pollutants, and plastics. By combining the community of selected and manipulated microorganisms, it is possible to obtain promising bioremediation results.[229] The increase in enzymatic diversity provides high rates of contaminant degradation. Fungi, bacteria, and others act together to offer better degradation of pollutants, such as the use of the synthetic microbial consortium, containing *Nitratireductor*, *Rhizobium*, *Rhodococcus*, *Paenarthrobacter*, and *Delftia*, in hypersaline wastewater; efficient biodegradation of acetoacetanilide, with reduced salinity, being resistant to hypersaline stress, and obtaining an ideal microbiome for the degradation of acetoacetanilide from organic compounds.[233]

Biodegradation studies of compounds associated with the primary contaminants used in the bioremediation process have been widely discussed, presenting innovative proposals to be included in bioremediation.[234] The possibility of degrading poly(ethylene terephthalate) (PET) using artificial microbial consortia was evaluated. The consortium consisted of the species *Bacillus subtilis*, *Rhodococcus jostii*, and *Pseudomonas putida*, all of which were genetically modified and capable of secreting PET monohydroxyethyl terephthalate hydrolase (MHETase) and hydrolase (PETase), as well as monohydroxyethyl terephthalate hydrolase (MHETase). The weight reduction rate of PET films was 31% in just 3 days, in addition to degrading 23.2% of PET films at room temperature, demonstrating great potential for degradation of complex compounds found in contaminants when artificial bacterial consortia were applied.[235]

An *ex situ* biodegradation study using bioaugmentation was applied in conjunction with the bacterial consortium for crude petroleum degradation. Using six bacterial isolates, the species *P. aeruginosa*, *Ochrobactrum sp*., and *Stenotrophomonas maltophilia*, which were analyzed gravimetrically and chromatographically, showed 83% degradation of paraffin present in crude petroleum, demonstrating the potential to biodegrade hydrocarbon pollutants such as wax.[236]

Advances have been occurring rapidly. Biodegradation responses have obtained highly satisfactory results, with promising responses employed; analyses in different environments and using various methodologies have been studied more clearly to inform advances in studies related to bioremediation.[204] Soils from subarctic Canada were evaluated for the biostimulation response of hydrocarbon degradation (TPH) and in oil-contaminated soils, obtaining high biodegradation rates of 85% in 50 days, when compared to systems amended by analyzed nutrients, concluding that the addition of nutrients in the contaminated subarctic site influenced the native microbial community. Some hydrocarbon-degrading genera were also identified, such as *Pseudomonas*, *Nocardioides*, *Polaromonas*, and others.[237]

Given so many technological and scientific advances, it is notable that the way contaminated environments are treated has changed, with precise and effective interventions.[238,239] The use of nanotechnology, genetic engineering tools, microbial consortia, and advances in phytoremediation techniques[182,190] are just some of the many expansions developed in biological processes, which allow for greater efficiency in the degradation of contaminants with reduced environmental impacts. These present even more sustainable solutions that will enable adaptations according to current environmental demands in more complex or sensitive environments.

**4.2. Integration with Other Fields.** Nanotechnology has emerged as a promising resource for increasing the effectiveness of the microbial biodegradation of hydrocarbons. Nanomaterials, such as zerovalent iron (nZVI) nanoparticles and metal oxides, have enhanced the bioavailability of pollutants by adsorbing or emulsifying hydrophobic compounds, thereby facilitating their absorption by bacteria.[240] Furthermore, these nanomaterials can serve as support for the immobilization of microorganisms and enzymes, favoring greater stability and catalytic efficiency.[241]

Recent research highlights the harmonious interaction between microorganisms and nanomaterials, showing that the interaction between both can accelerate the degradation of hydrocarbons.[242,243] For example, the use of biochemically produced iron oxide nanoparticles is effective in eliminating pollutants in aquatic environments.[242]

The use of bioinformatics tools, such as molecular docking and molecular dynamics simulations, has played a crucial role in understanding the interactions between microbial enzymes and hydrocarbon substrates.[244] These strategies enable the prediction of affinity between enzymes and pollutants, the identification of essential catalytic residues, and the proposal of reaction processes.[245] By integrating omics data with microbial metabolic network modeling, we can identify the metabolic pathways responsible for degrading various categories of hydrocarbons.[246] This combination of theoretical and experimental information facilitates the creation of more efficient microbial consortia for bioremediation.[247]

Biocatalysis, which uses enzymes or whole microorganisms as catalysts for chemical reactions, plays a crucial role in the biodegradation of hydrocarbons.[248] Enzymes such as monooxygenases, dioxygenases, and peroxidases are responsible for converting complex compounds into less toxic intermediates.[249] The modification of catalytic properties, based on structural and


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functional information obtained through bioinformatics, has enabled the alteration of catalytic characteristics, thereby increasing the specificity and effectiveness in pollutant degradation.[250] Furthermore, the incorporation of enzymes into nanomaterials has been investigated to improve their stability and reuse in bioremediation processes.[251]

The combination of nanotechnology, bioinformatics, and biocatalysis constitutes a promising multidisciplinary strategy for the recovery of areas affected by oil and its derivatives.[252] This technological integration enables the creation of more effective, targeted, and sustainable strategies, enhancing the degradation capacity of microorganisms and enzymes, while also having a significant impact on reducing environmental liabilities.[253]

**4.3. Research Directions.** Although there has been remarkable progress in understanding the processes of microbial biodegradation of hydrocarbons, several questions remain unanswered. The complexity of the microbial assemblages responsible for hydrocarbon degradation represents one of the most significant obstacles.[254] The interaction between different species of microorganisms in polluted environments is complicated and still poorly understood. More studies are needed to understand how these interactions affect the effectiveness of biodegradation.[255]

The scalability of biodegradation techniques is also a significant obstacle. Several efficient laboratory processes face obstacles when moving to large-scale applications due to factors such as environmental variability and operating costs.[256] Therefore, ecological interferences, such as the introduction of exogenous microorganisms or supplementary materials, can have a detrimental effect on local ecosystems. It is crucial to conduct risk assessments and implement mitigation strategies to ensure the viability of interventions.[240,257]

Several recent studies have investigated innovative methods to improve the biodegradation of petroleum and its derivatives.[258] The use of local microorganisms has proven to be a promising tactic. Researchers from the Federal University of Rio Grande do Norte (UFRN) conducted genomic studies of microorganisms that degrade hydrocarbons from petroleum, highlighting their potential in the bioremediation of polluted areas.[259] In the search for innovative biocatalysts, the National Center for Research in Energy and Materials (CNPEM) discovered a new enzyme known as "OleTPRN", which can transform fatty acids into alkenes (olefins), crucial chemical intermediates in the manufacture of sustainable fuels and other industrial products.[260]

The union of several areas, such as microbiology, nanotechnology, and bioinformatics, has the potential to accelerate the development of more efficient solutions for the biodegradation of hydrocarbons. Cooperation among research entities, the industrial sector, and the government will be crucial to overcoming current obstacles and driving the widespread application of sustainable technologies.

## 5. CONCLUSION

The comprehensive review of microbial biodegradation of petroleum and its derivatives presents a thorough analysis of the current state of research, highlighting significant advancements and ongoing challenges in this field. The study highlights the significance of microbial biodegradation as a sustainable and effective approach for mitigating the environmental consequences of petroleum contamination. The work provides an in-depth review of the microbial biodegradation of petroleum, covering key microorganisms, enzymatic mechanisms, and factors influencing the degradation process and offering a solid foundation for understanding the complexities of biodegradation. The inclusion of a scientometric analysis reveals the growing interest and significant increase in scientific publications on microbial biodegradation from 2005 to 2025, highlighting the leading countries and journals in this research area and providing valuable insights into the global research landscape. The study examines the environmental impact of petroleum spills. It compares conventional and biological remediation methods, highlighting the advantages of microbial biodegradation, including reduced costs and environmental effects, which reinforce its potential as a preferred remediation strategy. The review also highlights emerging technologies, such as nanobioremediation and genetic engineering, as promising future directions to enhance the efficiency of microbial biodegradation, which is crucial for advancing research and developing innovative solutions. The importance of this work lies in its comprehensive approach to addressing environmental challenges posed by petroleum contamination. By integrating scientific literature, data analysis, and future perspectives, the study offers a comprehensive view of the field, highlighting the crucial role of microbial biodegradation in achieving sustainable environmental remediation.

The insights gained from this review can guide future research, policy-making, and practical applications in the field of bioremediation. The study identifies key microorganisms, such as *Pseudomonas aeruginosa* and *Alcanivorax borkumensis*, as practical degraders of hydrocarbons. The scientometric analysis shows a significant increase in publications on microbial biodegradation, with China leading in the number of publications (247) and citations (8,387), followed by the United States. High-impact journals like *Chemosphere* and *Journal of Hazardous Materials* are prominent in this field, indicating the quality and relevance of the research. The integration of bioinformatics tools and emerging technologies, such as nanobioremediation and genetic engineering, is highlighted as a future direction to enhance the efficiency of microbial biodegradation. In conclusion, this paper presents a comprehensive and insightful analysis of microbial biodegradation of petroleum, highlighting its significance, strengths, and future potential. The findings and recommendations presented in this study are invaluable for advancing research and practical applications in environmental remediation.

## ■ ASSOCIATED CONTENT

### Data Availability Statement

The data supporting this study are available from the corresponding author upon reasonable request.

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