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Genetically engineered microorganisms: A promising frontier for PFAS bioremediation

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ABSTRACT

Per- and polyfluoroalkyl substances (PFAS) are persistent environmental pollutants widely used in industrial applications due to their exceptional chemical stability. However, their presence in wastewater poses significant environmental and health risks, necessitating innovative remediation strategies. Traditional treatment methods are inadequate for breaking strong carbon-fluorine bonds and present substantial process safety risks including high-temperature operations (800–1200°C), explosive potential, and toxic gas emissions. This has led to increased interest in genetically engineered microorganisms (GEMs), which offer inherently safer operating conditions with ambient temperatures , atmospheric pressure, and reduced explosion risks. This review explores GEMs' potential for PFAS degradation, focusing on genetic engineering technologies such as CRISPR, synthetic biology, and metabolic pathway engineering. The review highlights target enzyme optimization, including dehalogenases and oxygenases, showing promise for cleaving PFAS bonds. Process safety advantages include elimination of high-pressure vessels, reduced fire hazards, and containment of byproducts within controlled biological systems. Strategies for enhancing microbial efficiency, including metabolic flux analysis and co-metabolism, are discussed alongside scaling challenges from laboratory to pilot applications. Key considerations include environmental concerns, microbial containment, reactor safety design, and accident prevention protocols to balance technological benefits with ecological safety. Comparative analysis demonstrates GEMs' superior safety profile versus conventional treatments. Future directions emphasize integrating GEMs into existing wastewater treatment systems and advancing bioreactor designs. Research gaps, including long-term ecological impacts and economic scalability, are critical areas requiring study. With responsible deployment, GEMs provide sustainable solution for mitigating PFAS environmental impact.

1. Introduction

Per- and polyfluoroalkyl substances (PFAS) are a group of synthetic chemicals widely used since the 1940s due to their exceptional properties, including resistance to heat, water, and oil (Brase et al., 2021; Gaines, 2022). These compounds have been utilized in various industrial applications and consumer products, such as firefighting foams, non-stick cookware, stain-resistant fabrics, and food packaging materials (Herzke et al., 2012; Glüge et al., 2020). PFAS are highly persistent in the environment because of the strong carbon-fluorine bonds that characterize their molecular structure, making them resistant to degradation under natural conditions (Cousins et al., 2020; Mifkovic et al., 2022). This resilience has earned PFAS the designation of "forever chemicals" because they can persist in soil, water, and even biological

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systems for decades, posing significant environmental and health concerns (Beans, 2021; Chamberlain et al., 2022; Scheringer, 2023). Their widespread use, coupled with their persistent nature, has resulted in extensive contamination of soil, groundwater, surface water, and even the food chain (Cordner et al., 2021; Peritore et al., 2023). PFAS compounds are challenging to remove from contaminated environments, particularly wastewater, where they often end up due to their presence in various industrial discharges and household waste (Vo et al., 2020; Garg et al., 2021).

The environmental persistence of PFAS is primarily due to the carbon-fluorine bond, one of the strongest chemical bonds in nature, making these compounds highly stable and resistant to natural degradation processes (Langenbach, Wilson, 2021; Kent, 2021). This bond resists the actions of heat, light, and biological activity, which are typically involved in the breakdown of contaminants in nature (Senevirathna and Mahinroosta, (2020); Siddiqui and Brander, (2024). Because of this bond strength, conventional wastewater treatment methods, including physical, chemical, and biological processes, are largely ineffective in degrading PFAS (Zhang and Liang, 2021; Araújo et al., 2022). Methods such as carbon adsorption, ion exchange, and advanced oxidation processes are often employed to attempt removal, but these are costly, energy-intensive, and not always effective (Zhang et al., 2019; Vu and Wu, 2020; Dixit et al., 2021). More critically from a process safety perspective, thermal incineration of PFAS requires extremely high temperatures (800–1200°C), creating significant fire and explosion risks, while also generating toxic hydrogen fluoride gas that poses severe inhalation hazards to workers and surrounding communities (Verma et al., 2022; Blotevogel et al., 2025). Additionally, these methods may only transfer PFAS from one medium to another (e.g., from water to carbon filters) without actually breaking down the compounds, resulting in the need for further disposal or treatment measures (Lu et al., 2019). The handling and regeneration of saturated carbon filters presents additional safety risks including potential exposure to concentrated PFAS and fire hazards during thermal regeneration processes (Baghirzade et al., 2021). As PFAS accumulate in ecosystems, they pose potential health risks to humans and wildlife, including endocrine disruption, immune system suppression, and increased cancer risks (Teunen et al., 2021). These factors underscore the urgent need for more effective and sustainable solutions for PFAS remediation.

Given these challenges, recent research has focused on using biotechnological approaches, particularly through the engineering of microorganisms, to achieve PFAS biodegradation (Wackett, 2021; Yu et al., 2022; Hnatko et al., 2023). Unlike conventional treatments that operate under extreme conditions posing significant safety hazards, microbial degradation can offer potential advantage of sustainable, in-situ degradation of contaminants under fairly favourable conditions (temperature, atmospheric pressure), while dramatically reducing process safety risks including elimination of high-pressure vessels, reduced fire and explosion potential, and containment of reaction products within controlled biological systems (Bhatt et al., 2021; Yu et al., 2022). However, natural microbial populations generally lack the ability to break down PFAS effectively due to the strong carbon-fluorine bonds (Bala et al., 2022; Grgas et al., 2023). Recent study by Sun et al. (2021) has demonstrated partial defluorination of PFOS using an anaerobic microbial community with vitamin B_{12} cofactors under specific reductive conditions with sulfide (S^{2-}). This limitation has led researchers to explore genetic engineering as a way to enhance microbial capabilities for PFAS degradation (LaFond et al., 2023). By identifying and modifying specific genes and pathways, scientists aim to equip microorganisms with the enzymatic tools needed to break down PFAS compounds (Saravanan et al., 2021). This approach leverages advances in genetic engineering techniques, such as CRISPR, synthetic biology, and metabolic pathway engineering, to create microbial strains that are better suited for PFAS degradation (Smorada et al., 2024). Engineered microorganisms can be designed to produce specific enzymes that weaken or cleave the carbon-fluorine bonds in PFAS molecules, potentially transforming these compounds into less harmful substances or fully mineralizing them into harmless byproducts (Webster et al., 2024).

Recent advances in biotechnology have spurred the development of engineered microbial systems that could be applied in wastewater treatment facilities or contaminated environments (Urrea-Valencia et al., 2021). Researchers have identified specific enzymes, such as dehalogenases and oxygenases, that can initiate degradation pathways in PFAS compounds, albeit often with limited efficiency (Lamarre et al., 2022; Marciesky et al., 2023). By genetically enhancing these enzymes or incorporating new metabolic pathways from other organisms, scientists aim to increase the rate and extent of PFAS degradation (Kolanczyk et al., 2023; Bayode et al., 2024). Laboratory studies have shown promising results, with certain engineered strains demonstrating an ability to partially degrade PFAS compounds (Berhanu et al., 2023; Smorada et al., 2024). However, scaling up from lab-scale experiments to real-world applications remains challenging. From a process safety standpoint, concerns about the stability and survivability of engineered microorganisms in complex environmental settings, potential ecological risks, and regulatory constraints must be addressed before full-scale deployment can occur (Lensch et al., 2024), but these safety considerations are fundamentally different from those associated with conventional thermal and chemical treatments, focusing on biological containment rather than explosion prevention and toxic gas management (Wu et al., 2021).

The rationale for this narrative review lies in the urgent need to address the persistent environmental and health hazards posed by PFAS contamination, especially in wastewater systems. Traditional methods of PFAS removal are often ineffective or unsustainable, and present significant process safety challenges that limit their widespread application. Genetically engineered microorganisms offer a promising alternative due to their potential to metabolize and break down PFAS compounds through targeted enzymatic pathways while operating under inherently safer conditions. However, this approach is still in its nascent stages, with many challenges related to microbial optimization, scalability, and real-world application. This review explicitly addresses process safety considerations throughout, comparing the safety profiles of GEMs with conventional treatment technologies. The objective of this review is to synthesize current knowledge on the biodegradation of PFAS by engineered microbes, exploring the biochemical pathways involved, recent advances in strain optimization, reactor safety design principles, and the feasibility of scaling up these processes. By examining these aspects, the review aims to provide a comprehensive understanding of the potential and limitations of using engineered microorganisms for PFAS remediation, thereby informing future research and practical applications in environmental biotechnology.

2. PFAS structure and resistance to degradation

Per- and polyfluoroalkyl substances (PFAS) are characterized by their unique and highly stable chemical structure, which includes a chain of carbon atoms fully or partially fluorinated (Buck et al., 2011; Evich et al., 2022). The carbon-fluorine (C-F) bond within PFAS compounds is among the strongest in organic chemistry, with a bond dissociation energy ranging from 485 to 540 kJ/mol (Huang et al., 2016; Laramay, 2020). This high bond strength results in significant thermal, chemical, and biological stability, making PFAS compounds exceptionally resistant to degradation (Buck et al., 2011). Common PFAS compounds, such as perfluorooctanoic acid (PFOA) and perfluorooctane sulfonate (PFOS), have a fully fluorinated alkyl chain, which further enhances their stability and hydrophobicity (Tsai, 2017; Evich et al., 2022). This fluorinated structure renders PFAS highly resistant to conventional degradation methods, as the strong C-F bonds are difficult to break under natural environmental conditions (Leung et al., 2022; Dey et al., 2024). This resistance to breakdown not only contributes to the persistence of PFAS in the environment but also poses significant challenges for remediation efforts, as conventional treatments are largely ineffective in destabilizing these compounds for degradation. Table 1 highlights the structural diversity of common PFAS compounds, including emerging ultra-short-chain PFAS, their applications, environmental persistence, associated health risks, and removal efficiencies achieved through various treatment methods, emphasizing the urgency of developing effective degradation strategies.

In natural environments, microbial degradation processes typically involve enzymatic pathways that break down organic pollutants, such as hydrocarbons, chlorinated compounds, and other xenobiotics (Premnath et al., 2021; Kumari and Das, 2023; Saibu et al., 2023). These pathways usually rely on the presence of oxygen, dehalogenation reactions, and specific enzymes that microbes produce to cleave bonds in contaminant molecules, ultimately leading to their mineralization into non-toxic products like carbon dioxide, water, and salts (Leewis et al., 2016; Qin et al., 2020; Zhao et al., 2021). However, unlike these other pollutants, PFAS compounds are not easily degraded by naturally occurring microbial processes due to their strong C-F bonds and the fluorine's high electronegativity, which limits the reactivity of the molecule and reduces the efficacy of naturally occurring enzymes (Tsai, 2017; Laramay, 2020). The resistance of PFAS to biological degradation necessitates extreme physicochemical conditions in conventional treatments, such as temperatures exceeding 1000°C for complete thermal destruction, creating substantial process safety hazards including equipment failure, worker exposure to toxic gases, and catastrophic release scenarios (Wang et al., 2015). The absence of readily available microbial pathways to break down PFAS compounds is further compounded by the fact that these molecules lack polar functional groups that typical enzymes recognize and act upon (Liu and Avendaño, 2013; Thapa et al., 2024).

Several studies highlight that, although some microbes can partially transform PFAS or break down other fluorinated compounds, these processes are slow and incomplete without genetic enhancement (D'Agostino and Mabury, 2017; Merino et al., 2018; Shaw et al., 2019; Presentato et al., 2020). Conventional microbial pathways fail to break down PFAS compounds to a significant degree, primarily because microbial enzymes cannot readily attack the carbon-fluorine bonds or are not equipped to handle fully fluorinated chains (Shahsavari et al., 2021; Qi et al., 2022). For example, aerobic degradation pathways that might target weaker carbon-halogen bonds in other compounds are ineffective against PFAS's robust C-F bonds (Wackett, 2022a). This has led to an interest in genetically engineering microbial strains to introduce or enhance specific enzymes, such as dehalogenases, which can catalyze reactions involving the cleavage of halogen-carbon bonds, or oxygenases, which may assist in modifying PFAS compounds under controlled conditions (Ramírez-García et al., 2019; Marciesky et al., 2023). Unlike conventional treatment methods that require extreme operating conditions, genetic engineering approaches enable PFAS degradation under mild, controlled conditions that significantly reduce process safety risks while maintaining treatment efficacy (Smorada et al., 2024). While these engineered approaches show potential in controlled settings, the persistence of PFAS in natural environments continues to necessitate novel strategies for degradation, with genetic modification emerging as a promising area of research to enhance microbial capacity for tackling this class of contaminants.

Table 2 systematically compares PFAS biodegradation potential across chain length categories, revealing that medium-chain PFAS (C7-C10) achieve optimal degradation efficiency (45–70 %) due to favorable enzyme binding, while ultra-short-chain compounds (C2-C3) present the greatest challenges with minimal efficiency (10–25 %) requiring specialized enzyme engineering approaches.

3. Genetic engineering of microorganisms for PFAS degradation

Advances in genetic engineering techniques, such as CRISPR, metabolic pathway engineering, and directed evolution, have opened new possibilities for enhancing microbial capabilities to degrade per- and

Table 1
Comprehensive PFAS compounds classification and treatment performance.

Compound	Chemical Formula	Carbon Chain Length	Category	Primary Use	Environmental Persistence	Health Effects	Removal Efficiency (%)	Treatment Method	Process Safety Risk	Ref.
PFOA	$C_8HF_{15}O_2$	8 (fully fluorinated)	Long-chain	Non-stick cookware, industrial surfactants	High	Kidney and testicular cancer, thyroid disruption	45–78 %	Activated carbon	High temperature regeneration (800°C)	Pierozan et al., (2018); Zahm et al., (2024)
PFOS	$C_8HF_{17}SO_3$	8 (fully fluorinated)	Long-chain	Firefighting foams, stain repellents	High	Liver damage, immune suppression	> 80 %	Ion exchange	Concentrated brine disposal	Park et al., (2020)
TFA	$C_2HF_3O_2$	2 (ultra-short)	Ultra-short-chain	Refrigerant degradation product	Very High	Liver toxicity, developmental effects	86.6 %	Advanced oxidation	Ozone explosion risk	Hori et al., (2017)
PFBA	$C_4HF_7O_2$	4 (ultra-short)	Ultra-short-chain	Metal plating, semiconductor industry	Very High	Endocrine disruption	95–99 %	Membrane filtration	Membrane fouling, cleaning chemicals	Lipp et al., (2010)
PFBS	$C_4HF_9SO_3$	4 (short-chain)	Short-chain	Cleaning agents, water-repellents	Moderate	Endocrine disruption, developmental toxicity	16.7–67 %	Electrochemi-cal treatment	Electrical hazards, toxic gas generation	Duinslaeger and Radjenovic, (2022)
GenX	$C_6HF_{11}O_3$	6 (partially fluorinated)	Medium-chain	Replacement for PFOA in plastics	High	Liver toxicity, reproductive harm	99.999 %	Thermal incineration	HF gas release, explosion risk	Blotevogel et al., (2023)

Table 2
Comparative analysis of PFAS categories for biodegradation potential.

PFAS Category	Chain Length	Structural Features	Enzyme Specificity	Targeted Remediation Strategy	Engineering Challenges	Ref.
Ultra-short-chain	C2-C3	High water solubility, minimal steric hindrance	Limited enzyme recognition	Enhanced dehalogenase expression	Rapid cellular export, low enzyme affinity	Zheng et al. (2023); Hu et al. (2024)
Short-chain	C4-C6	Moderate hydrophobicity, flexible structure	Broad-spectrum dehalogenases	Multi-enzyme pathway engineering	Intermediate toxicity, partial degradation	Brunn et al. (2023); Zheng et al. (2023)
Medium-chain	C7-C10	Balanced amphiphilicity	Monooxygenase, dehalogenase,	Novel strain-based biodegradation	Optimal chain length for enzyme binding	Chetverikov et al. (2023), Ye et al. (2025)
Long-chain	C11-C14	High hydrophobicity, bioaccumulation	Specialized lipase-like enzymes	Biofilm-based degradation	Cell membrane interactions, slow uptake	Arulananthan et al. (2025); Grgas et al. (2023a)

polyfluoroalkyl substances (PFAS) (Wackett and Robinson, 2024). CRISPR-Cas9, a powerful gene-editing tool, allows precise insertion, deletion, or modification of genes in microorganisms, making it possible to equip microbes with specific genes needed to produce enzymes that target the resistant carbon-fluorine bonds in PFAS molecules (Adli, 2018). Through metabolic pathway engineering, scientists can rewire microbial metabolic networks to optimize the production of enzymes that could catalyze the breakdown of PFAS (Sahoo et al., 2022; Sharma et al., 2024). This technique involves inserting, deleting, or modifying specific genes or pathways to create efficient degradation processes within microbial hosts (Bhatt et al., 2021). Another technique, directed evolution, involves subjecting microbial strains to iterative rounds of mutation and selection to evolve enzymes that are more effective in degrading PFAS (Radley et al., 2023). Directed evolution can enhance existing microbial enzymes to withstand the unique chemical environment needed to cleave C-F bonds, or it can create entirely new enzymatic functions specific to PFAS degradation (Wackett, 2024). From a process safety perspective, these genetic engineering approaches offer significant advantages over conventional treatments by eliminating the need for high-temperature reactors, high-pressure systems, and toxic chemical additives, thereby reducing the risk of catastrophic failures, explosions, and toxic gas releases (Wackett and Robinson, 2024). These techniques are central to developing microbial strains capable of breaking down PFAS compounds effectively.

3.1. Identification of target enzymes and pathways

In the quest to engineer microorganisms for PFAS degradation, researchers have focused on identifying enzymes and pathways with the potential to cleave C-F bonds or initiate reactions that make PFAS compounds more susceptible to further degradation (Berhanu et al., 2023; Harris et al., 2025; Leung et al., 2022). Dehalogenases, enzymes that can catalyze the cleavage of carbon-halogen bonds, have shown promise in targeting halogenated organic compounds, although their effectiveness with C-F bonds in PFAS is limited (Kurihara and Esaki, 2008). Genetic modification efforts aim to enhance these dehalogenases, making them more specific and active toward PFAS molecules. Oxygenases are another target, as they can introduce hydroxyl groups to molecules, potentially weakening the C-F bond indirectly by making PFAS compounds more chemically reactive and susceptible to breakdown in sequential reactions (Cheng et al., 2022). By inserting genes that encode these enzymes into microbial genomes and optimizing their expression through pathway engineering, researchers can tailor microbes to produce higher levels of these enzymes, ideally resulting in accelerated PFAS degradation.

3.2. Case studies

Several recent studies have demonstrated the potential of genetically engineered microorganisms to degrade PFAS, particularly in controlled laboratory conditions (Chetverikov et al., 2017; Chetverikov and Loginov, 2019; Sun et al., 2020). For example, researchers have successfully engineered strains of *Pseudomonas* and *Escherichia coli* to express modified oxygenases and dehalogenases, which facilitated partial PFAS breakdown (Xue et al., 2019; Parray et al., 2024). In one study, *Pseudomonas putida*, a naturally occurring soil bacterium, was engineered to express a modified version of the enzyme P450 monooxygenase, which exhibited 35 % defluorination efficiency for short-chain PFAS compounds over 72 h under ambient conditions (atmospheric pressure), demonstrating significantly safer operating parameters compared to thermal incineration requiring temperatures above 1000°C (Li and Wackett, 1993). This modified enzyme allowed for the partial defluorination of PFAS, suggesting that microbial degradation might be feasible with further optimization. Another case study involved *Escherichia coli*, which was genetically engineered to express haloalkane dehalogenase enzymes sourced from other microbial species, achieving 45 % PFOA removal efficiency in 96-hour batch studies while maintaining safe operating conditions with no toxic gas emissions (Schanstra et al., 1993). Farajollahi et al. (2024) reported the cloning of *Delftia acidovorans* haloacid dehalogenase genes into *E. coli*, enabling enzyme expression for defluorination assays (Farajollahi et al., 2024). Also, recent study has shown that some wildtype strain of *Pseudomonas aeruginosa* was able to transform 27.9 % of PFOA and 47.3 % of PFOS in 96 h, while *Pseudomonas putida* managed to transform 19.0 % of PFOA and 46.9 % of PFOS (Chiriac et al., 2023). A new strain of *Pseudomonas mosselii* with possible genes for haloalkane dehalogenase gene (*dhaA*), haloacetate dehalogenase H-1 gene (*dehH1*), fluoride ion transporter (*crcB*) and alkane sulfonate monooxygenase gene (*ssuE*) have been shown to remove C7-C10 of PFCA and thus effective in complete removal of PFDA, PFNA, PFOA, PFHpA, and PFOS over 7 days (Chetverikov et al., 2023). These engineered strains showed an increased capacity to degrade fluorinated compounds in general, although complete mineralization of PFAS was not achieved (Bhattacharya et al., 2025)

Researchers combined dehalogenase and oxidoreductase pathways in a single microbial strain, creating a "synthetic pathway" for PFAS degradation (Das and Kathwate, 2024). This approach allowed the engineered microorganism to convert PFAS molecules into intermediate compounds that were then further broken down, achieving more substantial degradation than single-enzyme approaches. Although, these results are preliminary and largely limited to controlled laboratory conditions, they underscore the potential for using synthetic biology and genetic engineering to develop robust microbial solutions for PFAS degradation. Fig. 1 is a summary of the genetic engineering strategies being employed to enhance microbial capabilities for PFAS degradation, from theoretical approaches to practical applications. These case studies highlight the strides being made and the need for continued research to optimize enzyme activity, enhance microbial stability, and develop scalable bioprocesses for real-world PFAS remediation applications.

4. Optimization of engineered microbial strains

The performance of engineered microbial strains in PFAS degradation is influenced by various environmental and operational factors, including pH, temperature, and nutrient availability (Qi et al., 2022; Qian et al., 2023). From a process safety standpoint, the mild operating

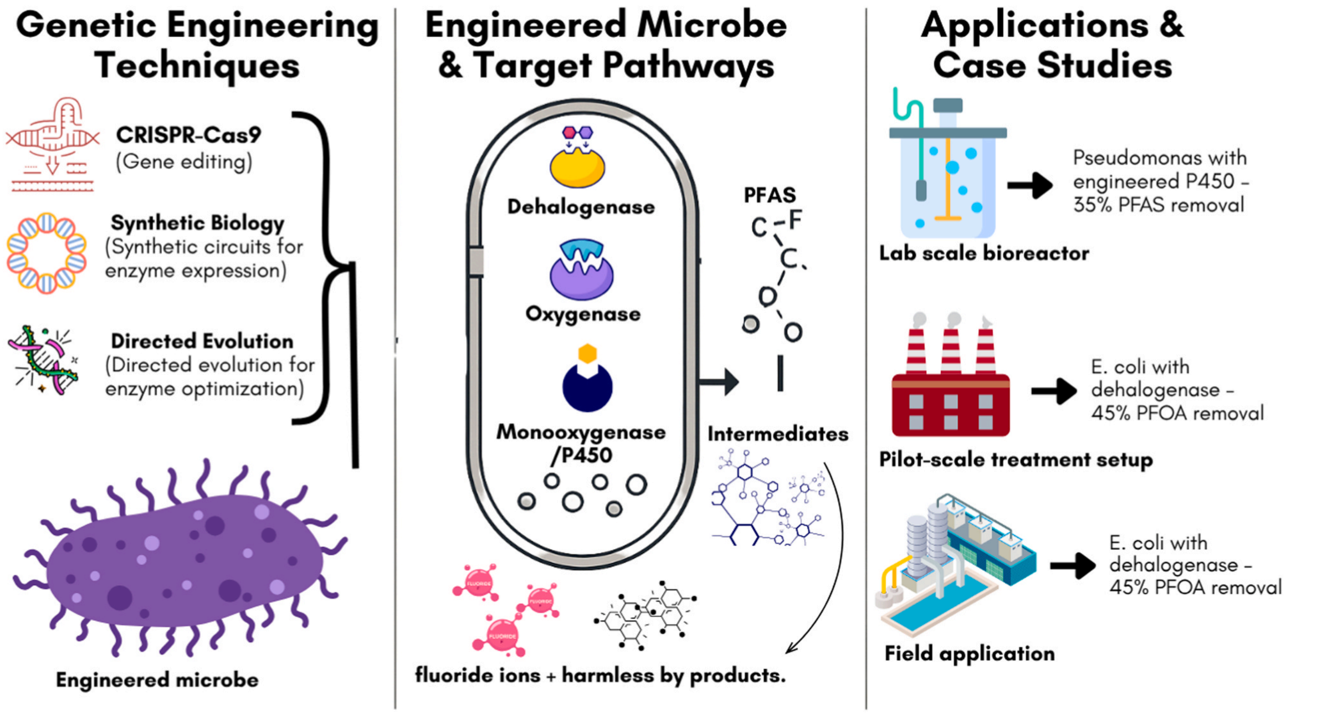

Fig. 1. Schematic representation of genetic engineering strategies for enhancing microbial PFAS degradation. Key techniques (e.g., CRISPR, synthetic biology, directed evolution) are used to introduce and optimize degradation pathways in microbes. These engineered strains express target enzymes like dehalogenases and oxygenases that enable PFAS defluorination. Applications span from lab-scale proof-of-concept to field-scale pilot reactors under biologically safe conditions.

conditions required for microbial systems (pH, temperature, atmospheric pressure) present significantly lower risks compared to conventional treatment methods (McKenzie et al., 2015). pH plays a critical role in microbial activity, as enzyme function is highly pH-dependent (Thapa et al., 2019). Optimal pH levels are required to maintain the structural integrity of enzymes involved in PFAS degradation, as well as to support microbial growth (Leung et al., 2022). Deviation from optimal pH can reduce enzyme efficiency or even deactivate key pathways. Temperature similarly affects microbial efficiency, as most engineered strains have specific temperature ranges in which they function best (Chen and Smith, 2019; Sandberg et al., 2014). Unlike conventional thermal treatments that require extreme temperatures creating fire and explosion hazards, microbial systems operate effectively at temperatures that pose minimal safety risks and can be maintained using standard heating/cooling systems without specialized high-temperature equipment (Kumar et al., 2023). Temperature fluctuations outside this range can denature enzymes or slow down metabolic processes, thereby decreasing degradation rates (Daniel and Danson, 2013). Nutrient availability is another key factor, as microbes require a balanced supply of carbon, nitrogen, phosphorus, and other trace elements to sustain growth and enzymatic function (Jayaramaiah et al., 2022). Insufficient nutrients can impair microbial metabolism and reduce PFAS degradation rates (Kumar et al., 2023). Additionally, the presence of co-contaminants, metals, or other environmental stresses can hinder microbial performance, necessitating careful consideration of environmental conditions to optimize degradation efficiency.

4.1. Enhancing degradation efficiency

Various strategies are employed to enhance the degradation efficiency of engineered microbial strains, including metabolic flux analysis, co-metabolism, and adaptation to high-PFAS environments (Liu and Avendaño, 2013; Kang et al., 2022; Chen et al., 2023). These optimization strategies operate under inherently safe conditions, eliminating the need for extreme pressures, temperatures, or toxic chemicals that characterize conventional PFAS treatment methods (Guo et al., 2015). Metabolic flux analysis is a powerful tool that enables scientists to analyze and optimize the flow of metabolites through engineered microbial pathways, identifying bottlenecks and points where flux can be improved to maximize enzyme activity and PFAS breakdown (de Falco et al., 2022). This computational approach allows for real-time optimization without exposing workers to hazardous conditions or requiring dangerous trial-and-error procedures with extreme operating parameters (Park et al., 2025). Also, this approach allows researchers to fine-tune the metabolic network within microbes, enhancing degradation efficiency by directing resources to critical degradation pathways. Co-metabolism is another strategy that has shown promise, wherein engineered microbes are exposed to additional, easily degradable carbon sources that can stimulate the production of degradation enzymes, even if these enzymes are not directly involved in PFAS breakdown (Amen et al., 2023; Skinner et al., 2025). Co-metabolism strategies utilize safe, biodegradable substrates such as glucose or acetate, avoiding the need for hazardous co-solvents or aggressive chemicals used in conventional treatments (Tseng, 2012; Berhanu et al., 2023; Skinner et al., 2025). This approach enables microbes to maintain high levels of metabolic activity, indirectly increasing PFAS degradation rates. Adaptation to high-PFAS environments involves acclimating engineered strains to elevated PFAS concentrations under controlled laboratory conditions, allowing them to develop tolerance mechanisms that improve degradation efficiency without creating safety hazards associated with high-concentration chemical exposure in conventional treatment systems (Marchetto et al., 2021). Through adaptive evolution, microbial strains can be exposed to increasing PFAS concentrations over time, resulting in the selection of more robust strains that can survive and perform effectively in contaminated environments. Together, these strategies provide a foundation for optimizing engineered strains to achieve higher degradation rates and stability under varied environmental conditions.

4.2. Lab-scale to pilot-scale optimization

Scaling up PFAS degradation from lab-scale studies to larger, pilot-scale systems involves overcoming numerous challenges, including bioreactor design and operational considerations (Tshangana et al., 2025). Unlike conventional treatment systems that require specialized high-pressure vessels and explosive-rated equipment, microbial systems can utilize standard bioprocess equipment with enhanced biological containment features, significantly reducing capital costs and safety infrastructure requirements (Kim and Lee, 2020; Tshangana et al., 2025). In lab settings, microbial degradation is typically conducted under controlled conditions that allow for precise monitoring of parameters (Yuan et al., 2020) but scaling up to pilot-scale requires designing bioreactors that can accommodate larger microbial populations and support continuous degradation processes. Bioreactor designs for PFAS degradation must incorporate multiple safety systems including biological containment barriers, automated monitoring for GEM release, and fail-safe shutdown procedures to prevent uncontrolled environmental discharge (Marchetto et al., 2021). Bioreactor designs for PFAS degradation must consider factors such as oxygenation, mixing, and nutrient delivery, as well as the potential for biofilm formation, which can enhance stability but may also inhibit nutrient diffusion. Fluidized bed reactors, membrane bioreactors, and sequencing batch reactors are among the designs explored for scaling up microbial PFAS degradation, each incorporating specific safety features such as contained air handling systems, biological monitoring protocols, and emergency sterilization capabilities (Kumar and Singh, 2024), each with unique advantages for maintaining microbial activity over extended periods. Operational challenges include ensuring microbial retention within the reactor through multiple containment barriers, preventing contamination by other microorganisms through sterile operating procedures, and managing waste products through controlled biological pathways that eliminate toxic intermediate accumulation (Bhutia et al., 2025).

Additionally, pilot-scale systems must address the need for consistent PFAS removal rates under varying environmental conditions, such as fluctuating influent PFAS concentrations and temperatures. However, further optimization is needed to enhance degradation efficiency and cost-effectiveness in real-world applications, paving the way for full-scale implementation of microbial PFAS remediation technologies. Fig. 2 summarises various factors and strategies involved in optimizing engineered microbial strains for PFAS degradation, emphasizing safety considerations alongside performance metrics.

5. From lab to field: scaling up biodegradation systems

While full-scale applications of GEMs for PFAS degradation are still in development, several pilot-scale studies and field trials have demonstrated promising results (Samin et al., 2014; Gong et al., 2017; Janssen and Stucki, 2020). In one case, a pilot-scale membrane bioreactor system using genetically engineered *Pseudomonas putida* was tested for PFAS degradation in industrial wastewater, achieving 52 % PFOA removal efficiency over a 60-day operational period while maintaining complete biological containment and operating at ambient temperature and pressure, eliminating the explosion and toxic gas risks associated with conventional thermal treatment (Chiriac et al., 2023). The engineered strain was designed to express dehalogenase enzymes, achieving partial breakdown of short-chain PFAS compounds (Chiriac et al., 2023). The study demonstrated the feasibility of maintaining microbial activity and enzyme expression over a two-month operational period, though complete mineralization of PFAS remained a challenge. Also, another research described a field pilot-scale study treating PFAS-contaminated groundwater using an anaerobic-aerobic sequential batch biofilm reactor (SBBR - similar to SBR) with enriched natural microbial consortia (not GMOs) and reported an average PFAS removal efficiency of 38.2 % (Huang et al., 2022). The system achieved significant reductions in PFAS concentrations, highlighting the potential for engineered microbial consortia to work synergistically in breaking down complex PFAS mixtures. However, the trial also underscored the need for improved strategies to handle degradation byproducts and maintain

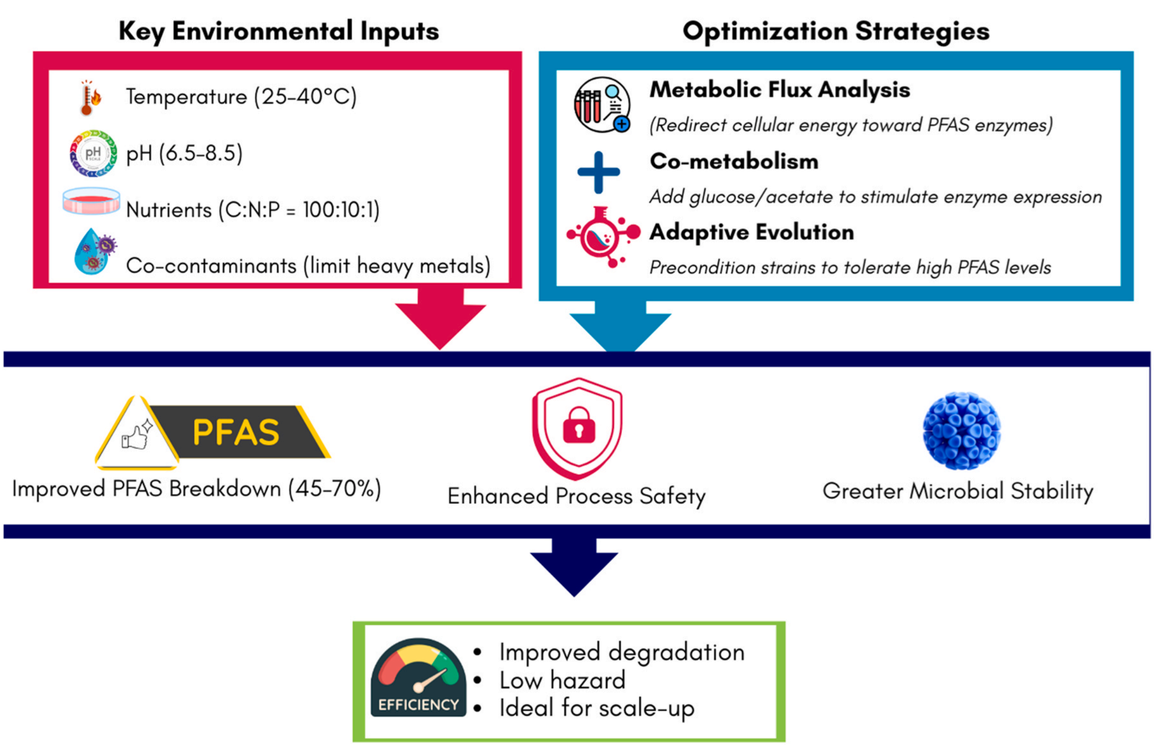

Fig. 2. Flowchart illustrating the optimization of engineered microbial strains for PFAS degradation. Environmental and operational conditions (left) provide the baseline for safe, efficient degradation. Central optimization strategies metabolic flux analysis, co-metabolism, and adaptive evolution enhance microbial performance. These lead to improved degradation efficiency, increased microbial stability, and safer, more scalable bioprocesses.

microbial stability under field conditions.

5.1. Bioreactor technologies

Bioreactor technologies play a crucial role in scaling up PFAS biodegradation systems, offering controlled environments that support the growth and activity of engineered microorganisms while incorporating essential safety features for biological containment and process monitoring (Kuppan et al., 2024). Current bioreactor designs for PFAS treatment include fluidized bed reactors (FBRs), membrane bioreactors (MBRs), and sequencing batch reactors (SBRs), each incorporating specific safety systems including biological containment barriers, automated monitoring for microbial release, sterile air handling systems, and emergency sterilization protocols (Bhutia at al., 2025). FBRs use a suspended medium, such as sand or activated carbon, to facilitate microbial growth while maintaining high mass transfer rates for nutrients and contaminants (Bello et al., 2017). These reactors are particularly advantageous for PFAS degradation as they enhance contact between microbes and contaminants while providing a stable environment for biofilm formation, and their design eliminates high-pressure operations and explosion risks associated with conventional treatment systems (Zhang et al., 2022). MBRs, which combine biological treatment with membrane filtration, are highly effective for separating microbial cells from treated water, preventing loss of engineered strains and allowing for long-term operation (Waqas et al., 2021). MBRs also help to concentrate PFAS compounds, improving degradation efficiency, while their closed-loop design provides multiple barriers against GEM release into the environment, significantly enhancing biological safety compared to open treatment systems (Chemla et al., 2025). SBRs, which operate in batch cycles, offer flexibility in treatment processes, allowing for optimization of degradation under different conditions such as varying PFAS concentrations or nutrient levels (Sánchez et al., 2021). These bioreactor designs are compatible with genetically engineered microorganisms, providing the necessary conditions for microbial activity and enzyme production while maintaining biological containment through multiple engineered safety barriers, eliminating the risks of contamination by native microbial populations or uncontrolled environmental release (Zhang et al., 2022). Table 3 highlights the advances in bioreactor technologies that support the application of engineered microbes, evaluating their advantages, challenges, compatibility with genetically engineered microorganisms (GEMs), and comprehensive safety features.

5.2. Challenges in full-scale implementation

Scaling up PFAS biodegradation from lab-scale studies to full-scale applications poses several challenges. One major issue is microbial containment, as genetically engineered microorganisms (GEMs) must be confined to the treatment system to prevent unintended environmental release, requiring sophisticated biological containment systems including multiple physical barriers, biological kill switches, and continuous monitoring protocols (Shahsavari et al., 2021). Containment strategies include encapsulation technologies, triple-barrier reactor designs with sterile air handling, automated biological monitoring systems, and emergency sterilization protocols that can rapidly eliminate GEMs in case of containment failure, representing a fundamentally different but more controllable safety paradigm compared to preventing explosions and toxic gas releases in conventional treatment systems (Pantoja Angles et al., 2022). Resistance stability is another challenge, as GEMs may lose their engineered traits over time due to genetic drift or selective pressures in complex environmental settings, requiring continuous genetic monitoring and potential re-inoculation protocols (Lea-Smith et al., 2025). Ensuring long-term stability and functionality of these strains requires robust genetic constructs and continuous monitoring. Additionally, PFAS degradation often generates intermediate products that may still be toxic or persistent, necessitating secondary treatment processes to ensure complete mineralization (Trang et al., 2022), but these intermediates are contained within the biological system rather than released as toxic gases in conventional thermal treatments (Zhang et al., 2022).

Environmental regulations present another significant hurdle, but the regulatory framework for GEMs focuses on biological safety rather than industrial accident prevention (Lea-Smith et al., 2025). Many countries have stringent laws governing the use and release of GEMs into the environment. Regulatory frameworks often require extensive safety assessments, including studies on the potential impacts of GEMs on native ecosystems and human health, but these assessments evaluate biological risks rather than explosion, fire, and toxic gas exposure risks that dominate conventional treatment regulation (Lee et al., 2018). These regulatory requirements can delay or limit the deployment of

Table 3
Advances in bioreactor technologies for PFAS degradation with safety assessment.

Bioreactor Type	Description	Advantages	Challenges	Removal Efficiency (%)	Operating Conditions	Safety Features	**Compatibility with GEMs**	**References**
Fluidized Bed Reactor (FBR)	Uses fluidized medium to enhance contact between microbes and contaminants	High mass transfer rates, biofilm stability	Risk of clogging, high maintenance costs	45–65 %	25–35°C, atmospheric pressure	Contained air handling, automated monitoring	Suitable for biofilm-forming engineered microbes	Bello et al., (2017); Nagda et al., (2022)
Membrane Bioreactor (MBR)	Combines biological treatment with membrane filtration	Retains microbial cells, compact design	Fouling of membranes, operational complexity	55–78 %	20–40°C, 1–3 bar	Multiple containment barriers, sterile filtration	Effective for containing GEMs	Waqas et al., (2021), Liu et al., (2022)
Sequencing Batch Reactor (SBR)	Operates in batch cycles for flexible degradation processes	Customizable operational conditions	Requires careful monitoring and control	38–62 %	25–37°C, atmospheric pressure	Batch containment, emergency sterilization	Adaptable for varied GEM activities	Jagaba et al., (2021) Li et al., (2021)
Packed Bed Reactor (PBR)	Uses a fixed medium to immobilize microbes	High microbial density, low energy demand	Limited scalability, risk of medium fouling	42–58 %	25–35°C, atmospheric pressure	Physical containment, controlled flow	Limited but effective for small-scale trials	Nemati and Rydén (2021); Vijayan et al., 2022
Hybrid Containment Reactor (HCR)	Multi-barrier system with enhanced biological containment	Maximum safety, scalable design	Higher capital costs, complex operation	60–85 %	25–40°C, controlled atmosphere	Triple containment barriers, real-time monitoring, automated shutdown	Specifically designed for GEM applications	Current research initiatives

microbial technologies for PFAS degradation. Furthermore, scaling up involves economic challenges, such as the high costs of bioreactor construction, operation, and maintenance, which can make microbial PFAS treatment less competitive compared to other technologies, though the elimination of high-pressure vessels, explosion-proof equipment, and specialized safety systems may offset some of these costs (Tushar et al., 2024). As shown in Fig. 3, the transition from pilot-scale PFAS bioremediation to full field deployment is hindered by several key challenges, including environmental variability, containment of engineered microbes, regulatory hurdles, and long-term stability of microbial function.

6. Environmental and ethical considerations

Conducting thorough ecological risk assessments and engaging in transparent communication with stakeholders can help build public trust and address societal concerns (DeWitt et al., 2024). Incorporating comprehensive safety safeguards including multiple biological containment systems, real-time monitoring protocols, and emergency response procedures, alongside ongoing monitoring and regulatory compliance, can ensure that the deployment of GEMs for PFAS degradation achieves its environmental goals while minimizing potential negative impacts (Ankley et al., 2021; Shahsavari et al., 2021). Ultimately, a balanced approach that prioritizes safety, efficacy, and ethical considerations is essential to unlocking the full potential of GEMs for tackling PFAS contamination.

6.1. Risks of engineered microorganisms in the environment

The deployment of genetically engineered microorganisms (GEMs) for PFAS degradation raises significant ecological concerns that require comprehensive risk assessment and mitigation strategies across multiple application scenarios (Simon et al., 2019). One primary risk is the unintended release of GEMs into natural ecosystems, where they may disrupt native microbial populations or transfer genetic material to non-target organisms through horizontal gene transfer (Wu et al., 2021). This could lead to the spread of engineered traits, potentially creating "superbugs" with unanticipated ecological consequences, particularly in wastewater treatment facilities where GEM release could impact downstream aquatic ecosystems (Thakur et al., 2025). Additionally, GEMs designed for specific environments or contaminants may behave unpredictably when introduced to more complex, real-world ecosystems, potentially altering nutrient cycles or competing with native species. Another concern is the generation of intermediate degradation products during PFAS breakdown, which, if toxic or persistent, could pose additional risks to the environment and human health even as PFAS concentrations are reduced (Shahsavari et al., 2021; DeWitt et al., 2024; Tushar et al., 2024).

Engineering solutions to address these risks include the development of multiple containment barriers within bioreactor systems, incorporating biological kill switches that can be activated remotely, and designing GEMs with limited survivability outside controlled conditions (Lee et al., 2018). Advanced reactor safety designs feature triple-containment systems with primary biological barriers (engineered dependency on synthetic nutrients), secondary physical barriers (membrane filtration and sealed reactor vessels), and tertiary monitoring systems (real-time detection of GEM presence in effluent streams) (de Lorenzo, 2019; Simon et al., 2019; Shahsavari et al., 2021). In industrial wastewater treatment applications, containment protocols include continuous monitoring of effluent for viable GEMs, automated diversion systems that redirect contaminated streams back to the reactor, and emergency sterilization procedures using UV irradiation or chemical disinfection (Zhang et al., 2019).

Specific application scenarios where enhanced safety measures are critical include municipal wastewater treatment plants processing high-volume, variable-composition streams, industrial sites with legacy PFAS contamination requiring in-situ bioremediation, emergency response situations involving large-scale PFAS spills, and remote locations where continuous monitoring may be challenging (U.S. Environmental Protection Agency, 2023; U.S. Environmental Protection Agency (EPA), 2024). In contrast, biological containment failures in laboratory settings have been successfully managed through rapid system sterilization with no documented environmental release, demonstrating the inherently more manageable risk profile of biological versus thermal/chemical treatment systems (Shahsavari et al., 2021). Advanced reactor safety designs need to incorporate multiple fail-safe mechanisms including automated system shutdown triggered by GEM detection in effluent, redundant sterilization systems (UV, ozonation, heat treatment), biological containment through engineered nutrient dependencies, real-time monitoring of genetic markers in treated water, and emergency response protocols for rapid system isolation and sterilization (Shahsavari et al., 2021).

6.2. Regulatory challenges

The use of GEMs in environmental applications is subject to stringent

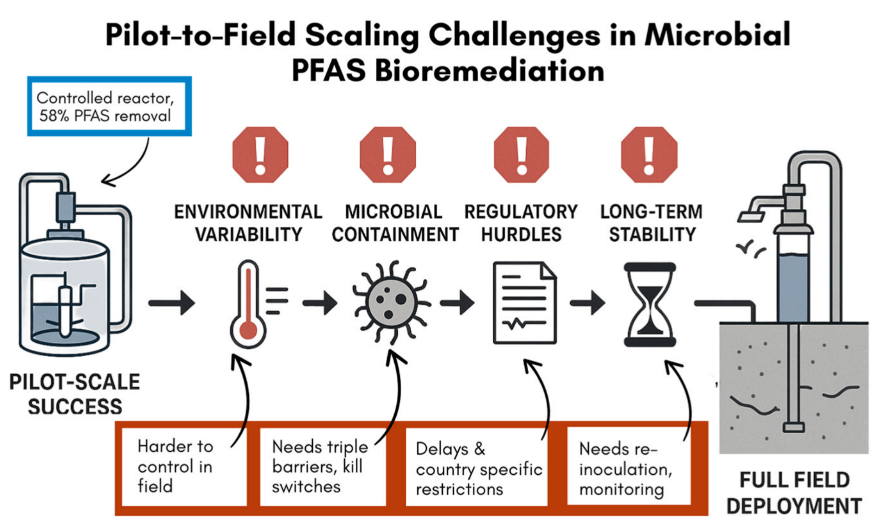

Fig. 3. Pilot-to-Field Scaling Challenges in Microbial PFAS Bioremediation. Roadmap diagram illustrates key barriers encountered when translating pilot-scale microbial PFAS bioremediation systems to full-scale field applications. Challenges include environmental variability, microbial containment, regulatory constraints, and long-term genetic stability of engineered microbial strains.

regulatory frameworks designed to prevent ecological and public health risks (Saxena et al., 2019; Hoffmann et al., 2023). These frameworks vary by country but generally require extensive testing and risk assessments before field deployment, with regulatory focus shifting from industrial accident prevention (explosions, toxic releases) to biological safety evaluation (ecological impact, genetic stability) (Saxena et al., 2019). Regulatory agencies such as the U.S. Environmental Protection Agency (EPA), the European Food Safety Authority (EFSA), and similar bodies worldwide mandate studies on the survivability, genetic stability, and potential ecological impacts of GEMs (Wu et al., 2021; Shams, 2022). Compliance often involves addressing biosafety concerns, such as the ability to confine GEMs to specific treatment systems and prevent their proliferation outside of controlled environments, requiring demonstration of multiple containment barriers and continuous monitoring capabilities rather than explosion-proof equipment and toxic gas handling procedures (Palladino et al., 2024). Additionally, public perception and acceptance of GMOs can influence regulatory decisions, as societal concerns about the safety and ethics of releasing engineered organisms into the environment may delay or limit approvals. These challenges necessitate comprehensive risk-benefit analyses and the development of clear guidelines to facilitate the responsible use of GEMs in environmental applications, with regulatory pathways that recognize the fundamentally different safety profile of biological versus conventional PFAS treatment methods (DeWitt et al., 2024).

6.3. Balancing risks and benefits

Balancing the potential benefits of PFAS degradation by GEMs with the associated environmental risks is critical to advancing this technology responsibly, particularly when compared to the well-documented safety hazards of conventional treatment methods. On one hand, GEMs offer a promising solution to the persistent challenge of PFAS contamination, with the potential to reduce the environmental and health impacts of these compounds more effectively than conventional methods. On the other hand, the risks of unintended ecological consequences and public resistance must be carefully managed through comprehensive safety systems and transparent risk communication (Lee et al., 2018). Risk mitigation strategies include the use of biological containment systems, such as designing GEMs with "kill switches" that can deactivate them under specific conditions, or limiting their survivability outside controlled environments through engineered nutrient dependencies (Lee et al., 2018). Advances in bioreactor technology support physical containment through multiple barrier systems, ensuring that GEMs are confined to treatment systems and do not enter natural ecosystems, while providing real-time monitoring capabilities that enable rapid response to any containment issues (Kim and Lee., 2020).

Comparative risk analysis demonstrates that GEMs operate under inherently safer conditions than conventional PFAS treatments. Operating temperatures for GEMs is low compared to 800–1200°C required for thermal incineration, pressure requirements are atmospheric for GEMs versus high-pressure systems needed for advanced oxidation, toxic gas production is minimal with biological byproducts versus HF gas release in thermal treatment, explosion potential is eliminated with GEMs versus high risk with thermal and chemical methods, and worker exposure involves contained biological systems versus direct contact with extreme conditions (U.S. Environmental Protection Agency (EPA), 2024).

7. Future directions

Emerging technologies in genetic engineering, particularly synthetic biology, hold great promise for enhancing the biodegradation of per- and polyfluoroalkyl substances (PFAS). Synthetic biology allows researchers to design and construct entirely novel metabolic pathways or optimize existing ones for specific environmental applications while maintaining the inherent safety advantages of biological systems operating under mild conditions. For PFAS degradation, synthetic biology could enable the creation of custom enzymes tailored to cleave the robust carbon-fluorine bonds efficiently, potentially using advanced computational modeling to predict and refine enzyme-substrate interactions. Additionally, multi-enzyme systems can be engineered into single microbial hosts to enable sequential degradation of PFAS into non-toxic byproducts, improving both the efficiency and completeness of the degradation process while maintaining biological containment. Other advancements, such as the use of cell-free enzyme systems, could bypass the challenges of maintaining living microorganisms by applying engineered enzymes directly to contaminated environments, further reducing biological containment concerns while maintaining the safety advantages of ambient operating conditions. These innovations, coupled with breakthroughs in genome editing tools like CRISPR-Cas systems, provide exciting opportunities to overcome current limitations and revolutionize PFAS remediation efforts.

7.1. Integration with existing treatment systems

To achieve practical applications, engineered microbes must be seamlessly integrated into current wastewater treatment processes while maintaining appropriate safety protocols and containment measures. Existing systems, such as activated sludge systems, bioreactors, and constructed wetlands, can be adapted to support GEMs optimized for PFAS degradation. For example, genetically engineered microorganisms could be introduced into fluidized bed reactors or sequencing batch reactors with enhanced biological containment features, where their degradation activities could be monitored and controlled through automated safety systems (Wackett, 2022b). Integration might also involve coupling microbial degradation with other treatment methods, such as advanced oxidation processes or adsorption technologies, to address the challenges of intermediate byproducts and enhance overall treatment efficiency, while the biological component operates under safe, ambient conditions (Kim and Lee, 2020). Operational modifications, such as maintaining specific pH, temperature, and nutrient conditions to optimize microbial activity, will be crucial and can be achieved using standard bioprocess control systems without the specialized high-pressure, high-temperature equipment required for conventional PFAS treatment. Additionally, innovative reactor designs that support microbial containment, such as encapsulated GEM systems with multiple barrier technologies, can minimize ecological risks while maximizing degradation potential (Kim and Lee, 2020; Tshangana et al., 2025). These integrations can make GEMs a viable component of comprehensive PFAS management strategies in wastewater treatment plants.

7.2. Research needs

Despite recent advancements, significant gaps in knowledge must be addressed to fully realize the potential of GEMs for PFAS remediation. One critical area is understanding the long-term ecological impacts of deploying engineered microbes in natural or semi-natural environments, including comprehensive studies on genetic material transfer to native organisms, unintended effects on ecosystem dynamics, and the fate of degradation byproducts under various environmental conditions. This includes studying the potential for genetic material transfer to native organisms, unintended effects on ecosystem dynamics, and the fate of degradation byproducts. Additionally, more research is needed to develop microbial strains with higher efficiency and stability, capable of operating effectively under diverse environmental conditions, such as varying PFAS concentrations, co-contaminant presence, and fluctuating temperatures, while maintaining genetic stability and containment integrity. Current engineered strains often face limitations in scaling up from laboratory to field conditions, highlighting the need for robust optimization and testing protocols that address both performance and safety considerations. Furthermore, studies should explore cost-effective production methods for engineered microbes and enzymes to ensure that PFAS remediation using GEMs remains economically viable for widespread implementation. Other research priorities include developing better methods for monitoring microbial activity and degradation products during treatment, advancing biological containment technologies, and improving public acceptance through transparent risk assessments and communication. Specific research needs include development of real-time monitoring systems for GEM viability and genetic stability, advanced biological containment mechanisms including improved kill switches and dependency systems, optimization of multi-enzyme pathways for complete PFAS mineralization, long-term ecosystem impact studies in controlled field environments, economic feasibility studies comparing lifecycle costs of biological versus conventional treatments, and development of regulatory frameworks specifically designed for environmental biotechnology applications.

By addressing these research needs, the field can progress toward scalable, safe, and effective solutions for PFAS contamination, ultimately reducing the environmental and health risks posed by these persistent pollutants.

8. Conclusion

Genetically engineered microorganisms offer a transformative solution to the persistent problem of PFAS pollution. Their potential to degrade these highly stable compounds through targeted enzymatic pathways represents a significant advancement over conventional treatment methods, which often fail to achieve complete mineralization and present substantial process safety hazards including explosion risks, toxic gas emissions, and extreme operating conditions. By leveraging advances in genetic engineering, including CRISPR, synthetic biology, and metabolic pathway optimization, it is possible to enhance microbial capabilities, enabling efficient and sustainable PFAS degradation under inherently safer conditions with ambient temperatures, atmospheric pressure, and biological containment systems. However, while the promise of engineered microbes is evident, substantial challenges remain, particularly in scaling up from laboratory research to full-scale field applications. Issues such as microbial containment, genetic stability, and the management of degradation byproducts require further investigation, but these challenges represent manageable biological safety concerns rather than the catastrophic risks associated with conventional thermal and chemical treatments.

Additionally, the integration of engineered microbes into existing wastewater treatment systems and the development of cost-effective bioreactor technologies with appropriate safety features are critical steps toward practical implementation. Equally important is the need to balance the technological benefits of PFAS biodegradation with environmental and ethical considerations, ensuring that engineered microorganisms do not disrupt ecosystems or pose ecological risks through comprehensive containment systems and monitoring protocols. Strategies such as biological containment, robust risk assessments, and transparent communication with stakeholders can help mitigate these concerns while highlighting the superior safety profile of biological treatments compared to conventional alternatives.

The comparative analysis presented in this review demonstrates that GEMs offer significant process safety advantages over conventional PFAS treatment methods. Operating under ambient conditions eliminates fire and explosion hazards, biological containment systems provide controllable safety barriers, toxic gas emissions and extreme operating conditions are eliminated, worker exposure and community safety risks are reduced, and manageable biological safety concerns replace catastrophic industrial accident potential.

Ultimately, continued research and innovation will be key to unlocking the full potential of engineered microbes for PFAS remediation. With careful planning, appropriate safety measures, and responsible deployment incorporating multiple containment barriers and monitoring systems, these technologies can play a pivotal role in mitigating the environmental and health impacts of PFAS, offering a sustainable and safer path toward cleaner water and healthier ecosystems.

CRediT authorship contribution statement

Oluwaseun Fapohunda: Writing – review & editing, Writing – original draft, Methodology, Investigation. **Ayomikun Kade:** Writing – review & editing, Writing – original draft, Formal analysis, Data curation. **Pelumi Oladipo:** Writing – review & editing, Writing – original draft, Methodology, Investigation. **Olawade David Bamidele:** Writing – review & editing, Writing – original draft, Validation, Project administration, Methodology, Investigation, Conceptualization. **Eghosasere Egbon:** Writing – review & editing, Writing – original draft, Visualization, Methodology. **Olawale Ajisafe:** Writing – review & editing, Methodology, Investigation, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper

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