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Review

Microbial and Enzymatic Biodegradation of Plastic Waste for a Circular Economy

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Abstract: Plastics play a crucial role in modern life, but their accumulation poses a serious threat to both the environment and human health. Due to their effects on the terrestrial and aquatic environment, it is essential to develop sustainable approaches to dispose of waste plastics. Traditional methods of plastic disposal, such as burning and landfilling, are problematic since they produce hazardous byproducts. Biodegradation is a potentially effective, eco-friendly approach which uses microbial consortia or isolated enzymes to break down plastic waste. Enzymes interact with plastic surfaces and hydrolyse the large polymer chains into smaller units. These byproducts can then be utilised as carbon sources by microbes, which are eventually converted into CO_2 and water. This review explores the principal approaches to plastic degradation, with a focus on existing and emerging polymers made to be readily biodegradable. In addition, sustainable valorisation methods for converting plastic waste into valuable byproducts are considered. The implementation of a circular plastic economy is expected to lead to further development, including scaling up of efficient plastic bio-upcycling processes, which can serve to stimulate environmental waste removal and value-added use of post-consumer plastic streams.

Keywords: plastic waste; microbial digestion; enzymatic biodegradation; circular economy

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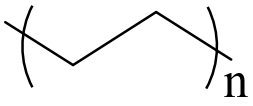
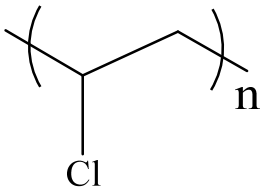
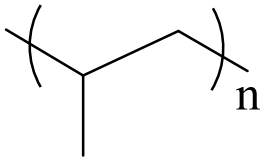
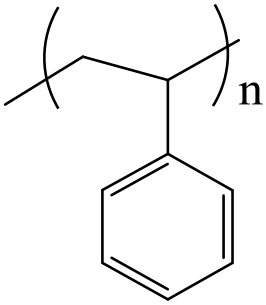
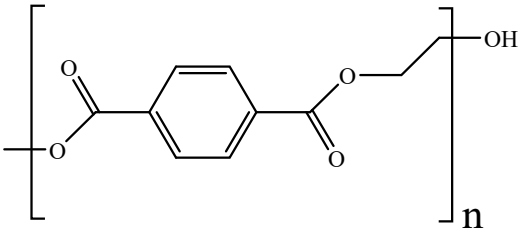
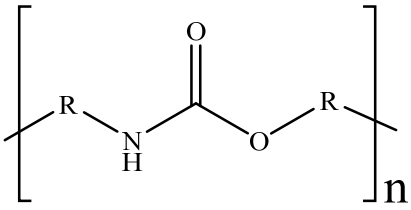
1. Introduction

Plastics have become an integral part of modern life due to their beneficial characteristics, including their versatility, light weight, durability, transparency, and chemical resistance. However, it is because of these characteristics that they have become inexpensive, disposable, and significant contributors to environmental damage [1]. The global production of plastics reached 460 million tons in 2022, with China and the European Union accounting for 32% and 17% of the world's synthetic plastic use, ranking first and second, respectively [2]. Synthetic plastics are polymers derived from chains of repeating monomers usually obtained from petrochemicals. Polyethylene (PE), polypropylene (PP), polyvinyl chloride (PVC), polystyrene (PS), polyethylene terephthalate (PET), and polyurethane (PU) are examples of common synthetic polymers [3]. Each type of plastic has unique qualities which make it useful in a wide variety of applications, including packaging, home goods, and automobile parts. Table 1 shows different types of synthetic plastics, their structures and their applications.

Table 1. The most common types of synthetic plastic and their structures and common uses.

Name	Structure	Uses	Reference
Polyethylene (PE)		Shopping bags, drinks bottles, food packaging material, plastic pipes.	[4]
Polyvinyl chloride (PVC)		Raincoats, shower curtains, window frames, indoor plumbing.	[4]
Polypropylene (PP)		Manufacturing chemical derivatives, packaging, automotive industries.	[5,6]
Polystyrene (PS)		Disposable cups, packaging materials, laboratory consumables, electronic instruments.	[7]
Polyethylene terephthalate (PET)		Food and beverage packaging, photographic film, insulated clothing.	[8]
Polyurethane (PU)		Plastic foams, cushions, rubber goods, synthetic leathers, adhesives, paints, fibres.	[9]

Plastics are widely used because of their versatility and efficiency, yet they have become one of the most pressing environmental concerns. The paradox lies in the fact that while plastics are useful and efficient materials, they have a durability that is misaligned with a material that is often designed for a single use, with its disposal becoming a significant threat to ecosystems, including land, marine, air, and water [2]. Studies have concluded that plastics and microplastics (plastic fragments less than 5 mm in size) can enter the human body through different means such as inhalation, ingestion, and dermal contact [10]. Long-term exposure can cause negative effects on human DNA and increase the risk of infertility and cancer [11,12].

Approximately 460 million tons of plastic waste were generated globally in 2022 [13]. This includes various types of plastics, with PE, PP, and PET being the most concerning ones. These plastics are commonly used in household items such as bottles, containers, shopping bags, and wrappers. They are often found in the environment, contributing significantly to pollution [14]. For example, low-density polyethylene (LDPE) and bioplastics such as PLAs and PHAs are commonly used in plastic bags, while synthetic plastics like PET are widely used in textiles and as food containers [15]. Single use plastic waste for items such as food and drink products accumulates more quickly than waste from durable and expensive materials like laptops, televisions, and automotive parts [16,17]. Furthermore, such plastics are challenging to recycle due to their mixed nature. Only by using cleaned, non-mixed plastic can high-quality recycled products be produced [18].

Figure 1 shows how plastic management varies in the major world economies, with significant disparities in recycling, incineration, and mismanagement rates globally. Of the plastic waste generated worldwide, 49% is accumulated in landfills, 22% is classified as mismanaged (which ultimately ends up in landfills), 19% is incinerated, and only 9% is recycled. These figures vary among the top economies, with the United States having the highest landfilling rate (73%) while mismanagement rates range between 4% in the US and 46% in India.

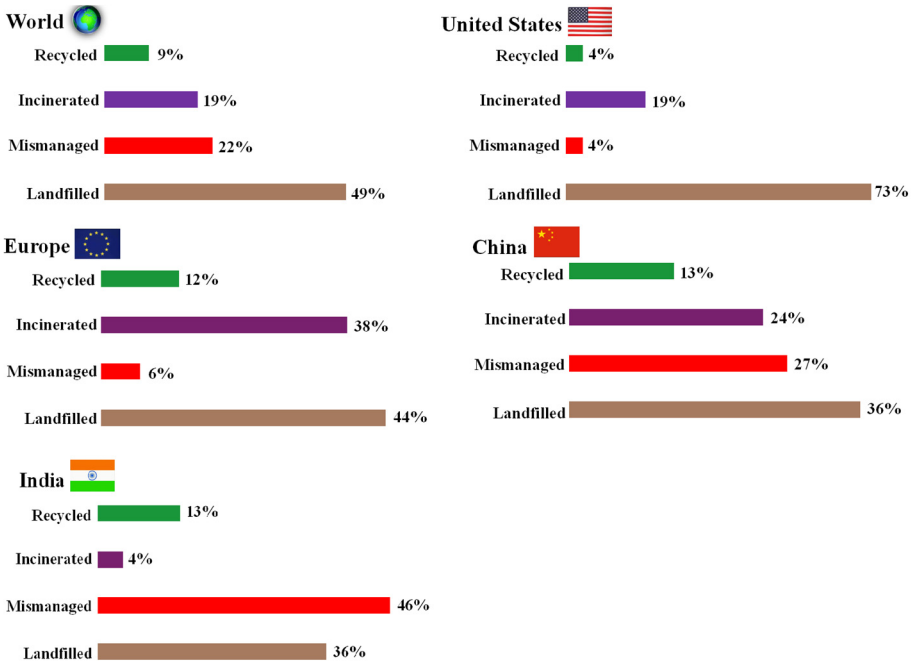


Figure 1. Plastic waste disposal management by region, globally, and in major economies. This image was reproduced from OECD (2023) [13] and processed by Our World in Data. Mismanagement refers to accumulation in landfill.

Landfill is the most common destination for waste plastic based on its simplicity and low-cost, as no capital cost is incurred except for the land (Figure 2). Landfills are chosen in many regions due to poor recycling infrastructure. Plastics which are landfilled pose a risk of leakage into rivers, lakes, and the ocean, creating water pollution [19]. Conversely, incineration is a thermal process used to treat plastic waste and concurrently reduce its volume. In some cases, the heat generated during incineration is utilised to produce electricity. However, incineration produces toxic byproducts, which contribute to air pollution. For example, Wu et al. reported that approximately 70.2 million tons (29% of the total) of plastic waste was burned without regulation worldwide in 2016, releasing almost a million tons of toxic aerosols into the atmosphere, with the majority occurring in developing regions [20,21]. Recycling is an alternative option which can be more environmentally friendly compared with landfilling or incineration. Mechanical

recycling involves segregation, cleaning, and reuse of the plastics. Whilst this approach reduces demand for virgin materials, the plastic created with this method can be of lower quality, whereas chemical recycling handles mixed plastics, creates new plastics, and offers a closed recycling loop. Chemical recycling processes release hazardous byproducts and require high amounts of energy [11].

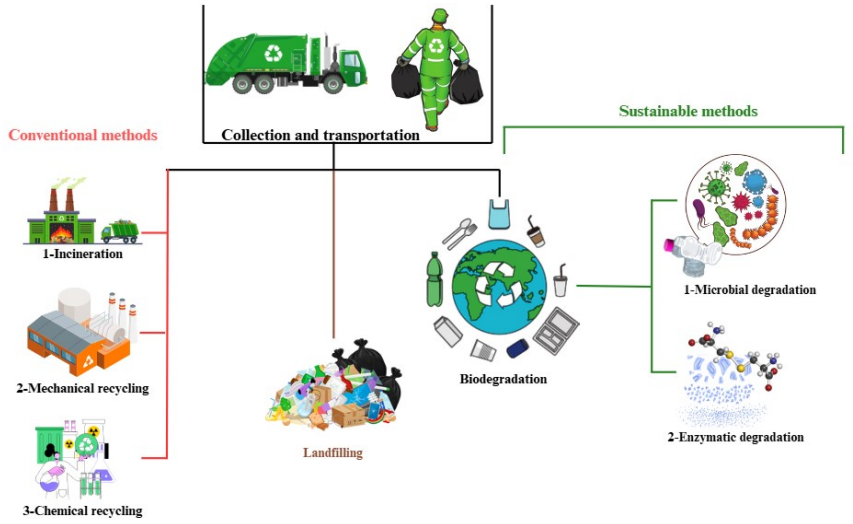


Figure 2. A schematic overview of the different approaches to plastic waste management, including conventional and sustainable approaches.

The development of biodegradable plastics and bioplastics has had a significant impact on the problem of increasing volumes of persistent plastics in the environment. Biodegradable plastics are defined as materials which are completely degraded to carbon dioxide and water by the action of naturally occurring microorganisms, such as bacteria, fungi, and algae, and as such are more easily broken down under natural conditions [22,23]. While the terms biodegradable plastics and bioplastics have been conflated and are used interchangeably, there is a notable difference between the two. As the name suggests, biodegradable plastics are degraded by bio-organisms, whereas bioplastics are produced or derived from biomaterials and are not necessarily biodegradable. For instance, some fossil fuel-derived plastics are biodegradable, like polybutylene adipate terephthalate (PBAT) and polybutylene succinate (PBS) [24]. However, polylactic acid (PLA), a common type of bioplastic (derived from fermented products), is degradable only in industrial composting sites and is not rapidly degraded under natural conditions [23]. Conversely, an example of non-biodegradable bioplastics are PETs derived from renewable resources, which are targeted to replace PETs from non-renewable resources [25]. Figure 3 shows the production rate of biodegradable plastics in 2023 [2]. Among various types, polylactic acid (PLA) and polybutylene adipate terephthalate (PBAT) together make up almost 60% of the bioplastics produced, while polyhydroxyl alkanoate (PHA) and polybutylene succinate (PBS) production is less than 10%. Starch-based polymers and blended plastics are beginning to emerge with strategically improved mechanical properties. These types of plastic offer a promising alternative due to their enhanced biodegradability and potential for lower environmental impacts than conventional plastics [26,27].

Increasingly, researchers are exploring the possibility of biotechnological approaches to plastic degradation involving the use of microbes or enzyme preparations. Considerable research has focused on the biodegradation of synthetic plastics [28–30]. Ideally, biodegradable plastics are those which can be completely decomposed from complex polymeric structures into simpler chemicals and biomass when exposed to natural environmental conditions and microbial enzymatic action [22,23] (see Table 2). Concurrently, newly synthesised biodegradable plastics are an active research area. However, it is important to note that not all bioplastics are inherently biodegradable under typical en-

vironmental conditions; many require specific conditions such as industrial composting to facilitate effective degradation [31]. It is also worth noting that many biodegradable plastics can persist for long periods in landfills due to a lack of bioplastic-degrading organisms. Although plastic biodegradation is considered a green, safe, and low-energy input process, it is worth noting that these benefits have primarily been proven on laboratory scales [32,33]. The scalability and effectiveness of this process on an industrial scale has not yet been fully demonstrated.

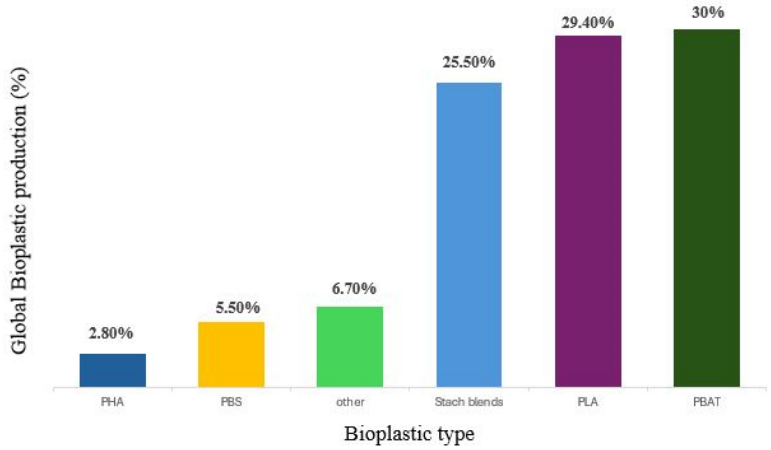


Figure 3. Production of biodegradable plastics in 2023 (based on data derived from [22–24]), where PHA is polyhydroxyalkanoate, PLA is polylactic acid, PBS is polybutylene succinate, and PBAT is polybutylene adipate terephthalate.

The concept of a circular economy is based on reducing waste, reusing materials, and recycling products to create a closed-loop system that minimises environmental impact. In this context, biodegradable plastics are crucial as they can be easily degraded and integrated back into the environment compared with synthetic plastics [34]. However, significant research is required to fully achieve a closed loop of minimised plastic use, coupled with re- or up-cycling, as positive steps towards a circular economy. Key biological strategies to achieve this goal are synthesising biodegradable bioplastics, bio-driven degradation and recycling of plastics, and upcycling of plastics for waste into valuable products. In the next section, the focus is on the methods of bio-driven degradation of plastics and bio-based plastic valorisation as a waste-to-resource approach, contributing to the goal of a sustainable circular economy. By enhancing waste management practices, improving the microbial and enzymatic degradation, and developing new biodegradable plastics, plastic pollution can be reduced and its reuse promoted, thereby supporting the principles of a circular economy.

Table 2. Common types of biodegradable plastic and their structures and their uses.

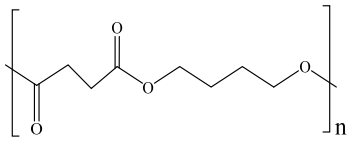
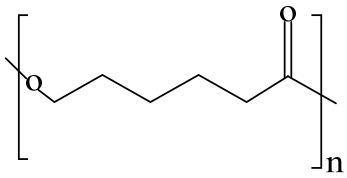
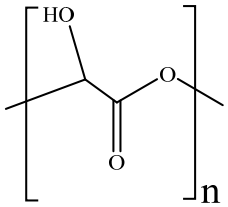
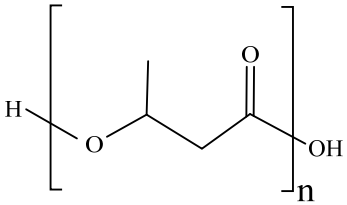
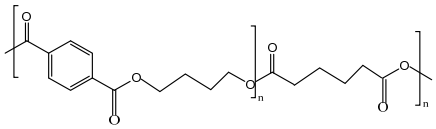
Types	Structure	Biodegradation in Soil	Biodegradation in Aqueous Environment	Uses	References
Poly butylene succinate (PBS)		85% after 150 days	2% after 117 days	Packaging material and coating films	[35,36]

Table 2. *Cont.*

Types	Structure	Biodegradation in Soil	Biodegradation in Aqueous Environment	Uses	References
Poly caprolactone (PCL)		99% after 136 days	78% after 117 days	Agriculture mulching films, long-term item	[35,37,38]
Polylactic acid (PLA)		16% after 180 days	2% after 117 days	Food containers and shopping bags	[35,39,40]
Polyhydroxy butyrate (PHB)		99% after 136 days	83% after 117 days	Bottles, wrapping material, shopping bags	[35,37,40]
Poly(butylene adipate-co-terephthalate) (PBAT)		21% after 180 days	2% after 117 days	Bags, mulching film	[35,39,41]

2. Microbial and Enzyme-Based Degradation of Plastic

2.1. Microbial Degradation of Plastics

Both synthetic and bio-plastics can be degraded by the action of microbes, including bacteria, fungi, and actinomycetes [42,43]. Biodegradation of polymers in the environment starts with the process of biodeterioration, where the mechanical, chemical, and physical properties of plastic surfaces change due to thermal and photo-oxidation. These structural changes occur under the influence of environmental conditions (i.e., temperature, moisture, and sunlight). Microorganisms augment this biodeterioration through the formation of biofilms on plastic surfaces [44,45]. After biofilm formation, the constituent monomers are broken down [46,47], and these smaller monomers are taken up into the microbial cell, where they are broken down to produce energy [48].

2.1.1. Bacterial Biodegradation

Bacteria produce enzymes which are involved in plastic biodegradation [49]. Many bacterial communities isolated from landfills and oceans in recent years have demonstrated capabilities in plastic decomposition and utilisation [50]. The capabilities of certain microorganisms, particularly *Pseudomonas* sp., in accelerating the degradation and metabolism of synthetic plastics, including polystyrenes and polyethylene, are of special interest [51,52]. For example, a *Pseudomonas* strain isolated from a landfill site showed 8.7% PE degradation following 60 days of incubation [53]. In another *Pseudomonas* study, *Pseudoxanthomonas* sp. NyZ600, isolated from activated sludge, was found to depolymerise polycaprolactone (PC) films into two degradation products—bisphenol A and 4-cumylphenol—which are monomers of PC [54]. A PET-degrading enzyme from *Ideonella sakaiensis* PETase is capable of completely breaking down PET in six weeks. This plastic was previously considered non-

biodegradable. *Ideonella sakaiensis* secretes PETase enzymes, which causes the breakdown of PET at 30 °C. This enzyme produces an intermediate, mono (hydroxyethyl) terephthalate (MHET), which is absorbed by the cell and processed by the enzyme MHET hydrolase. The end-product of these two enzymatic processes is terephthalic acid and ethylene glycol, both of which are monomers that the organism uses for its growth [55].

2.1.2. Fungal Biodegradation

Fungi play a significant role in biodegradation due to their ability to produce extracellular enzymes [56]. These enzymes include cellulases, ligninases, and cutinases which are effective in degrading various polymers [57]. The biological degradation of polyurethane, polystyrene, and polyethylene samples by filamentous fungi isolated from Antarctica was also reported. Here, plastic films were incubated with different fungal isolates at 18 °C for 90 days. Among them, *Penicillium* sp. demonstrated the highest degradation efficiency, achieving 28.3% degradation of polyurethane, 8.39% degradation of polystyrene, and 3.53% degradation of low-density polyethylene. This finding highlights that cold-adapted fungi can potentially degrade a range of plastics under low-temperature conditions, which could be beneficial for biodegradation in extreme environments [58]. Furthermore, out of 18 screened fungal strains—based on their ability to degrade polyurethane polyethylene, and tyre rubber—*Fusarium, Penicillium, Botryotina cnerea* EN41, and *Trichoderma* showed the highest potential to degrade these plastics without any pretreatment [59]. Another ascomycete, *Penicillium*, which is involved in PU degradation, was found to be particularly effective when compared with other ascomycete such as *Aspergillus* and *Alterniaia*, as reported by Magnin at el. These fungal strains can use the polyester PU as their sole carbon source [60].

2.1.3. Algal Biodegradation

Algae, particularly microalgae, are involved in biodegradation because of their ability to enhance the breakdown of plastic [61,62]. For example, studies have shown that microalgae can grow on the surface of PE, facilitating degradation. When isolated from waste plastic bags colonised by green algae, *Uronema africanum*, a microalga, was reported to initiate the breakdown of low-density polyethylene (LDPE) sheets in 30 days [60]. Only a few algae have been reported to break down plastics, specifically those that release ligninolytic and exopolysaccharide enzymes. While algae show the potential to degrade plastic, it is important to note that biodegradation in the natural environment is slower, which leads to concerns about accumulation of microplastics [63], and algae are difficult to grow as they require specific light conditions and appropriate nutrient levels [64]. Maintaining such conditions consistently can be more complex than for other microorganisms.

2.1.4. Microbial Consortia

Microbial consortia have shown significant potential in plastic biodegradation by leveraging the synergistic effect of various microbial communities, enhancing the degradation efficiency beyond what individual strains can achieve [65,66]. Plastics are often more susceptible to fungi and bacteria when applied in consortia [59]. For example, several PET-degrading strains such as *Sarcina aurantiaca* (TB3), *Bacillus subtilis* (TB8), *Aspergillus flavus* (STF1), and *Aspergillus niger* (STF2) were obtained from plastic waste disposal sites. The efficacy of these isolates in PET degradation was investigated on PET films for 60 days at 37 °C as individual organisms and as microbial consortia (TB3 + TB8 + STF1 + STF2). This study showed 28.78% (*w*/*w*) weight loss for the PET films through the microbial consortia (*S. aurantiaca* + *B. subtilis* + *A. flavus* + *A. niger*). Further investigations on the isolate's hydrophobicity, viability, and total protein concentration showed that there were no hazards to human health or the environment when using this microbial consortium to degrade PET-based waste [67]. Another microbial consortium of biodegradation was assessed in both mixed and individual forms. *Penicillium raperi, Aspergillus flavus, Penicillium glaucoroseum*, and other *Pseudomonas* sp. were tested for their biodegradation ability under

both unstimulated and H_2O_2-stimulated conditions. In the unstimulated conditions, the strains were tested under both mixed cultures over 270 days and as individual cultures over 100 days, while the H_2O_2-stimulated strains were tested only in the mixed culture for 30 days. Among these isolated strains, *Aspergillus* flavus showed the highest weight loss (of 5.5% (*w*/*w*)) of PE within 100 days in unstimulated culture conditions [68].

2.1.5. Biodegradation in Different Environments

In the marine environment, plastics undergo photodegradation and biodegradation, leading to weight loss and changes in their properties. Microorganisms form biofilms on the surfaces of these plastics, which facilitates degradation [69]. In a study conducted by Sarkhel et al. [70], the degradation potential of *Aspergillus* sp. (a fungal species) and *Vibrio* sp. (a bacterial species) isolated from the marine environment was investigated. Over a six-week period, the bacterial strain demonstrated 35% degradation of plastic bottle waste, while the fungal strain achieved 22% degradation. This study also evaluated various influencing factors, such as temperature, pH, and inoculum concentration, to optimise the degradation conditions. These findings suggest that bacteria, specifically *Vibrio* sp., are better than fungi at breaking down plastic waste under the conditions tested, making bacterial treatment a more efficient approach for plastic disintegration in marine environments [68].

In soil, the degradation of plastics varies significantly. Conventional plastics like PE and PVC can persist for decades [71,72]. However, some bacteria, such as *Lysinibacillus* sp. isolated from soil, have demonstrated the ability to degrade PE and PP [73]. On the other hand, biodegradable plastics can degrade much faster than conventional plastics. For example, PHB shows 99% degradation in soil after 136 days, while PCL also degrades by 99% in soil within 136 days. PBS degrades by 85% after 150 days in soil. The degradation rates of these plastics in aqueous environments are also noteworthy. After 117 days, PBS degraded by 2%, PCL degraded by 77.6%, and PHB degraded by 83.0%. These examples illustrate that the same type of plastic can degrade at significantly different rates in different environments [35,36,38].

Despite these studies, challenges and limitations exist in microbial plastic degradation. Reliable reports are mostly limited to specific synthetic polymers, with fewer studies focusing on bioplastics despite their persistence in the environment for an extended time. This issue can be potentially mitigated by applying microorganisms, plastic-eating insects, and enzymes to accelerate their degradation. Some researchers have argued that the microbial degradation of plastics has been overstated [74]. These researchers point to the lack of evidence for the substantial degradation of unadulterated PE, PP, PS, or PVC, which represent most of the global plastics production. Table 3 details the various plastic-degrading bacterial species reported and their respective biodegradation patterns for different plastics. The table summarises the advancements in identifying and cultivating microorganisms under laboratory conditions based on published reports from the ten year period 2014 to 2024.

2.2. Insect Microbiota in Plastic Degradation

Recent studies have highlighted the potential of insect microbiota to digest plastic, largely due to the microorganisms in their guts. Research into the application of insects in the breakdown of plastics is increasing, especially research linked to insect gut bacteria or associated enzymes. Recently, Ali et al. investigated how the lesser waxworm (*Achroia grisella*) larvae's stomach symbionts biodegrade low-density polyethylene plastic. The results of this study revealed that two bacterial strains, *Citrobacter freundii* (LDPE-DB1) and *Bacillus* sp. (LDPE-DB2), isolated from the insect's gut displayed notable degradation, with test plastic tensile strengths being reduced by 51.3% and 58.3%, respectively. During the course of the 30-day incubation period, cell densities rose, and the development of cavities on the LDPE surfaces verified the presence of bacteria [75].

Zophobas atratus larvae, commonly known as superworms, have emerged as standout performers in tackling plastic waste. A study unveiled the unique ability of *Z. atratus* larvae to break down PS and PU foam plastics. This study revealed that feeding on plastics changes the larvae's gut microbial communities and increases specific enzyme activities. Specifically, protease activity increased, enhancing the larvae's ability to digest these synthetic polymers. Remarkable microbial shifts in gut microflora were, characterised by *Mangrovibacter* domination in the PU-fed group, *Citrobacter* flourished in the PE-fed group, and *Dysgonomonas* and *Sphingobacterium* thrived in the PS-fed group. Across all plastic-fed groups, *Enterococcus* was found to be prominent microorganisms, suggesting its central role in the biodegradation process [76].

Building on these findings, Jiang et al. conducted a comparative analysis of polystyrene biodegradation in three insect species: *Tenebrio molitor* (yellow mealworm), *Galleria mellonella* (greater wax moth), and *Zophobas atratus*. Among these, the *Z. atratus* (common name: superworms) larvae exhibited better degradation efficiency. Across all three species, *Enterococcus* and *Enterobacteriaceae* were capable of PS plastic breakdown, yet *Z. atratus* demonstrated far greater degradation efficiency [77].

Further advancing this narrative, Peng et al. delved into the ability of *Z. atratus* larvae to biodegrade PS and LDPE. Their study provided evidence of plastic fragmentation within the larvae's gut. This process was also linked to changes in the gut microbiota, particularly the upregulation of functional enzymes such as arylesterase and serine-hydrolase. The presence of *Citrobacter* sp. was notably higher when the larvae consumed PS and LDPE, suggesting its potential contribution to enzymatic plastic degradation [78].

The use of insects could be a potential large-scale biological solution for plastic waste management [79]. While the primary mechanism of plastic degradation in insects is digestion by gut enzymes from resident bacteria, the exact enzyme(s) which facilitate depolymerisation are not clear [80].

Mealworms consume PS and PE, breaking them down into small fragments [81]. Their mechanical breakdown of plastics starts with chewing and ingesting, which increases the surface area available for microbial enzyme activity in the gut [82]. Further degradation of these fragments occurs in their gut, where bacterial communities, particularly *Psedomonas* and *Serratia* sp., play a vital role in the degradation process. This process facilitates the conversion of larger plastic particles into smaller fragments, enhancing microbial colonisation and therefore enzymatic degradation [83]. Microbial digestion in the mealworm gut enables mineralisation of plastic particles into carbon dioxide and organic matter, as shown in Figure 4.

Mealworms can degrade up to 47.7% of ingested polystyrene into metabolites within 25 h [84]. Interestingly, polystyrene is resistant to most forms of biodegradation, but mealworms have shown a significant ability to degrade both its physical and molecular structures [85]. Unlike the traditional chemical recycling process, mealworms or other insects can degrade plastic at room temperature, with less environmental waste. Moreover, the frass (insect excretion) could be investigated for potential application in agriculture as organic fertiliser, potentially opening a new area for sustainable plastic waste management [81]. The above examples show that a variety of organisms can be exploited for plastic degradation. Another approach, examined below, is to exploit the ability of isolated enzymes to degrade plastics. This approach holds the possibility of being able to recover plastic monomers and upcycle them into useful products.

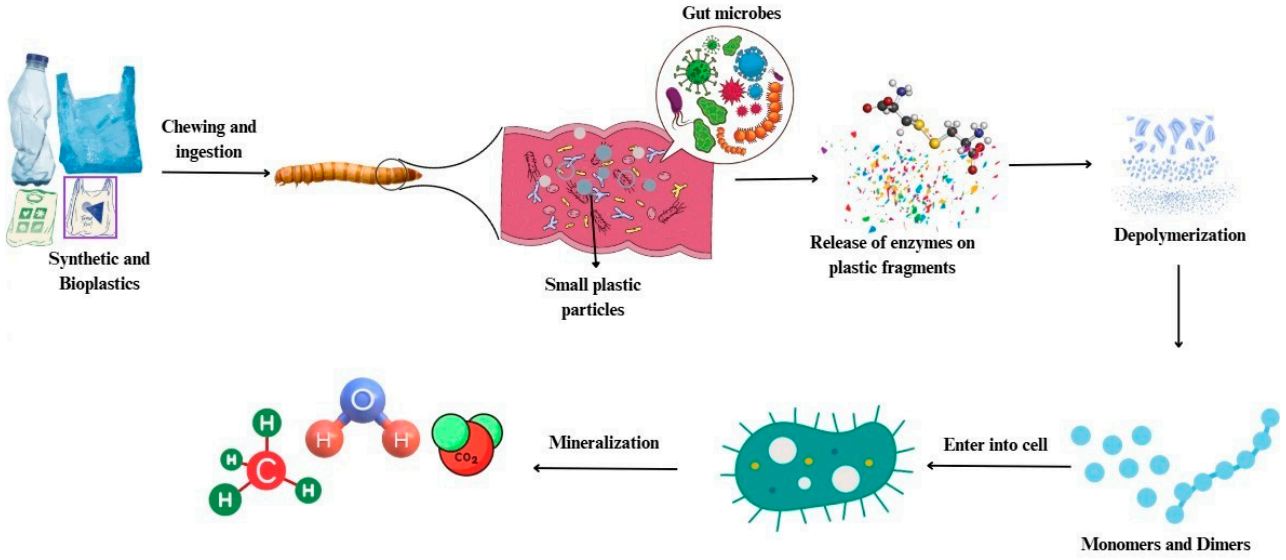


Figure 4. Role of insect gut microbiota in plastic degradation, with released enzymes facilitating depolymerisation [81,84].

2.3. Enzymatic Degradation of Polymers

Extracellular and intracellular enzymes are produced by microorganisms which are involved in the biodegradation of plastic [46,47,86]. To degrade polymers, enzymes capable of breaking ester, ether, carbon-carbon, and amide bonds will be required [34]. Among these, oxidoreductases, peroxidases, transferases, and hydrolases have been reported to facilitate depolymerisation and hydrolysis reactions [87,88]. The application of a variety of purified enzymes in plastic degradation has been studied [46,89]. The advantage of using purified enzymes lies in the easier downstream recovery of degradation products and avoiding catabolism of products (typically the monomers) [90]. Acyl hydrolases are the most extensively studied enzymes for the degradation of polymers [91–93]. Cutinase, lipase, esterase, and PETase are widely reportedto efficiently degrade polyesters like PET, PHA, and PLA [46,94,95]. They are produced by both bacteria and fungi involved in plastic degradation [46,47]. The difference between lipases, esterases, and cutinases is a function of their substrate chain lengths [96]. Esterases catalyse the breakdown of ester bonds with chain lengths of less than 10 carbon atoms, and lipases hydrolyse esters with more than 10 carbon atoms in their chains [97,98]. Cutinases can break ester bonds, and their active sites are more exposed to substrates due to the lack of a "lid" structure covering the active site [99]. Lipases also break ester bonds, but their active sites are covered by a lid which somewhat limits substrate access. The lid opens in the hydrophobic environment of the water/lipid interface [100,101]. These enzymes belong to the α/β-hydrolase superfamily [102] and contain a catalytic triad of Serine, Histidine and Aspartate. This catalytic triad facilitates nucleophilic attack on the carbonyl carbon of the ester bond, causing the hydrolysis of the polyester chain [103–105].

2.3.1. Cutinase-Catalysed Depolymerisation of Plastics

Cutinases enzymes can break down the ester bonds present in polyesters, especially polyesters like PET [103,104,106]. Cutinases have been identified in various organisms, including fungi and bacteria. The enzymatic depolymerisation reported by Lykidis et al. using the cellulolytic actinomycete *Thermobifida fusca* isolated from soil resulted in up to 50% degradation of PET at 55 °C in three weeks. After this work, many cutinases from various *Thermobifida* sp. were isolated which could degrade plastics [105]. Alongside this work, engineered cutinases were developed and employed to degrade polyester-based plastics. For example, cutinases from *Thermobifida cellulosilytica* DSM44535 and

Thermobifida fusca DSM44342 were successfully cloned and expressed in *E. coli* BL21. These enzymes from *Thermobifida*, specifically ThcCut1, exhibit favorable kinetic parameters for soluble substrates and release MHET and terephthalic acid from PET. Comparative homology modelling suggests that His-209, located in the active site, is crucial for hydrolysis activity [107]. *Thermobifida fusca* cutinase (TfC) effectively degrades PET films pretreated with *S. pavanii* JWG-G1, showing up to 91.4% degradation within 23 days. The pretreatment with *S. pavanii* JWG-G1 likely enhanced the accessibility of the PET substrate, making it more susceptible to the enzyme. This combination of microbial pretreatment and enzymatic degradation resulted in substantial degradation of PET films, suggesting the benefit of a synergetic approach for efficient PET degradation [108].

The cutinases (FoCut5a) from *Fusarium oxysporum* and *Thermobifida alba* AHK119 fungus, expressed in *E. coli* BL21, show optimal catalytic activity on synthetic esters at 40 °C and a pH of 8.0 [109]. Their successful expression in *E. coli* BL21 is an advantage which allows for high yield production using a well-established and cost-effective microbial expression system. The *Fusarium oxysporum* enzyme represents a promising approach for hydrolysing PET-like substrates and other synthetic polymers [110]. A purified lipase from the yeast *Cryptococcus* sp. showed sequence homology with proteins in the cutinase family rather than the lipase family, and this enzyme demonstrated effective degradation of the high molecular weight polymer PLA, as well as other biodegradable polymers including PBS, PCL, and PHB [95]. Din et al. demonstrated the potential of an extracellular cutinase-like enzyme from the biofilm forming-bacterium *Stenotrophomonas maltophilia* PRS8 in PET breakdown [111]. This enzyme's stability and activity were maintained during various environmental changes (including temperature, pH level, substrate concentration, and the presence of inhibitors or activators), and it was effective in the hydrolysis of PET. The depolymerisation process generated terephathalic acid (TPA), mono(2-hydroxyethly) terephthalate (MHET), and bis(2-hydroxyethyl) terephthalate (BHE) from PET flakes, indicating its potential for managing PET waste and recovering value-added products [111].

Cutinases could be a promising tool in combating plastic pollution and recovering various plastics monomers. Mutation and engineering of these enzymes may enhance their functional activity and stability over a wider range of pH levels and temperatures. However, it is important to note that while cutinases are effective in the degradation of polyester, a single enzyme is not sufficient for all types of polymers. Multi-enzyme systems are needed to target a wide range of plastics. This aspect needs further exploration and research [112].

2.3.2. Lipase-Catalysed Depolymerisation of Plastic

Lipase enzymes, like cutinases, catalyse the hydrolysis of ester bonds in triglycerides to liberate fatty acids [113]. These enzymes have been identified as a sustainable and effective means for both the synthesis and degradation of polymers. Lipases can be used to degrade different types of plastics, particularly biodegradable plastics [114]. For example, a lipase isolated from *Rhizomucor miehei* (formerly *Mucor miehei*) was used to efficiently degrade synthetic polymers such as PC and PET in an aqueous medium at 37 °C [115]. Additionally, a lipase from *Crytococcus* sp. can degrade biodegradable polymers such as polybutylene succinate (PBS) sheets of 200 µm in 72 h when incubated in 100 mM phosphate buffer, pH 7.0 at 30 °C [116].

Furthermore, a lipase extracted from *Pseudomonas cepacian* caused 80% degradation of PBS in less than 24 h when incubated at 50 °C [117]. The same lipase showed greater degradation of PBS sheets when shaking (rather than under static conditions) at 37 °C in phosphate buffer pH 7.2–7.4, suggesting that shaking enhances mass transfer efficiency during the degradation process [118]. *Candida antarctica* lipase B was chemically modified to enhance its stability and activity. This modified lipase showed the ability to depolymerise PLA into its monomers within 40 h at 90 °C [119].

Deep eutectic solvents (DESs) are mixtures of a hydrogen donor and acceptor which can create a favorable environment for protein chemical modification. Few studies have been conducted on the use of DESs to enhance enzymatic plastic degradation. One such study used the *Humicola insolens* cutinase (HiC) in a DES environment for PET degradation and showed that the DES solution increased the hydrolysis yield by 1.5 times [120]. DESs are promising for the stabilisation of enzymes and enhancement of their catalytic activity [121]. This approach can be beneficial for efficient enzymatic degradation processes and can be scaled up for industrial application.

2.3.3. Esterase-Catalysed Depolymerisation of Plastics

Esterases released by both bacteria and fungi play a role in plastic degradation by acting on the polymer surface, creating micro-fractures in the polymer structure which leads to further degradation [93,94]. This mechanism has been observed in various microorganisms, showing the diverse sources and strategies for plastic degradation. For instance, some thermophilic bacteria secrete an esterase-like enzyme which targets the amorphous regions of PET and PLA polymers [122]. Similarly, the *Comamonas acidovorans* bacterium produces an esterase capable of degrading low molecular weight PLA [123]. The fungal species *Aspergillus flavus* and *Aspergillus tubingensis* also secrete esterases which can degrade plastic [124,125].

Esterase activity is typically limited to short-chain acyl esters [94], but recombinant technology allows fine-tuning of enzymes through site-directed mutagenesis, which has shown promising enhancement in their degradation capabilities [126]. A notable approach can be observed in the case of *Tenebrio molitor*, where five genes were cloned into an *E. coli* expression system, with the feruloyl esterase-like enzyme (TmFae) exhibiting the most PET degradation at 50 °C. Through site-directed mutagenesis of TmFae, two amino acids, Leucine at position 95 (L95) and Proline at position 122 (P122), which were mutated along with the hydrophobic amino acid Tryptophan (W), resulting in increased interaction with PET [127]. Another esterase which was originally found in *Ideonella sakaiensis* was expressed in *E. coli*, and a double mutation, S238F and W159H, produced a narrow active site, like *Thermobifida fusca* cutinase (TfCut). This mutant showed enhanced catalytic activity against PET [128]. Similarly, an engineered recombinant esterase from *Pseudomonas aeruginosa* demonstrated 60% enhanced depolymerisation activity [129]. These mutations are examples of how site-directed mutagenesis can optimise enzyme activity for applications in plastic degradation.

2.3.4. PETase-Catalysed Depolymerisation of Plastics

Hydrolases are a class of enzymes that catalyse the hydrolysis of bonds, often through the addition of water [130]. They include esterases, lipases, and cutinases, and each one is specialised in breaking down different ester bonds [69]. The difference between these enzymes is primarily a function of their substrate chain length and the type of bond length cleaved (as explained in Section 2.3). A PET hydrolase, termed PETase, which was originally isolated from *Ideonella sakaiensis* exhibited optimal degradation activity at 40 °C. PETase has the catalytic triad S160-D206-H237 and an α and β hydrolase fold structure, with the core domain comprising nine β-sheets encircled by seven α-helices. In contrast to other hydrolases (i.e., lipases and cutinases), PETase possesses three additional residues (N244, S245, and N246) in the β8-α6 region, extending the substrate binding pocket's cleft and expanding it to accommodate the PET substrate [113,131]. PETase enzymes are named for their ability to hydrolyse PET, thereby differentiating PETase from other hydrolases, which typically have no, or less, structural adaptations necessary to effectively degrade PET. Figure 5A depicts the 3D structure and catalytic triad residues of PETase, while Figure 5B shows the structure and catalytic triad of a cutinase. This cutinase showed efficient degradation against PCL and PBS, but could not degrade PET.

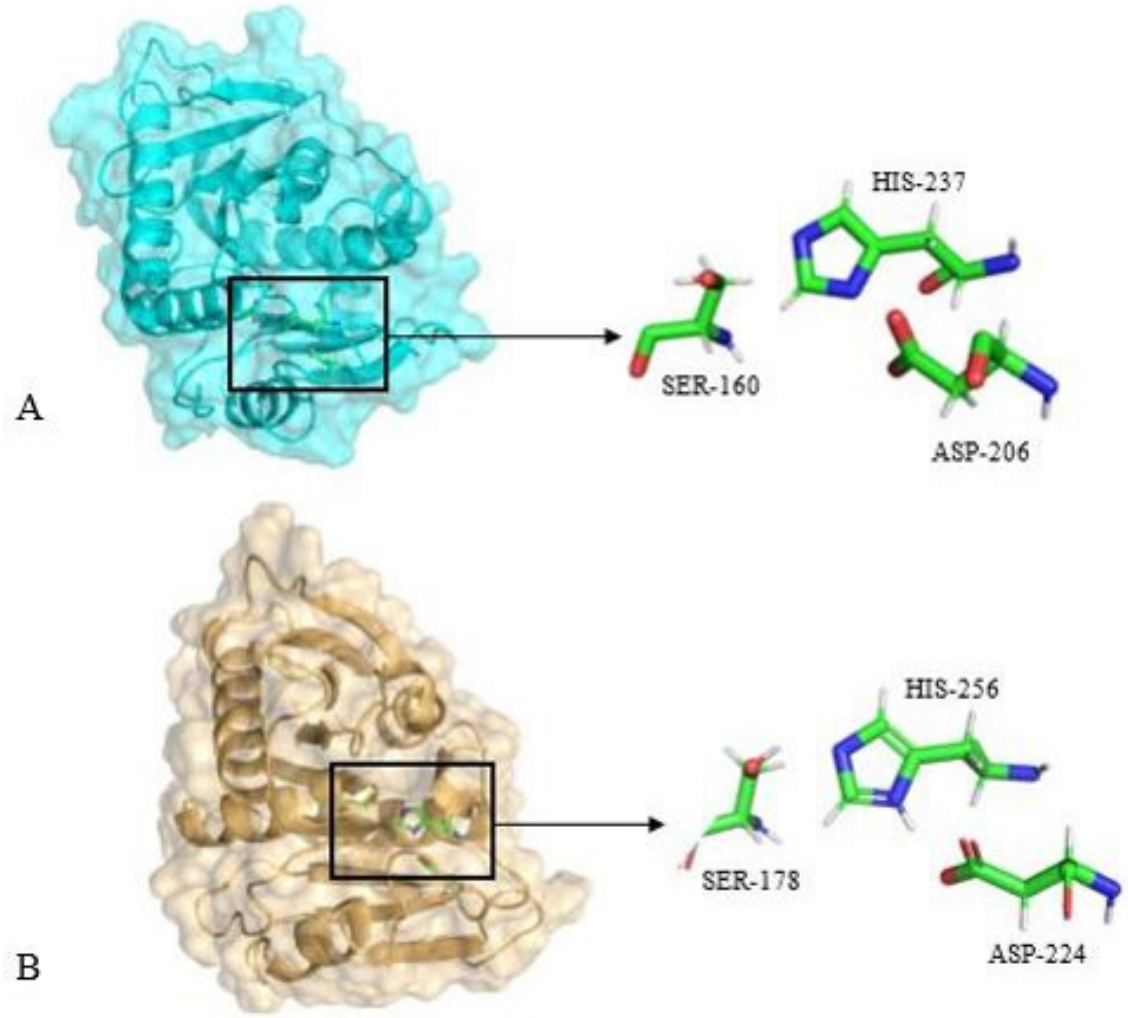


Figure 5. Structure of PETase and *Amycolatopsis mediterranei* cutinase, (**A**) Structure and catalytic triad representation of PETase from *Ideonella sakaiensis* (PBD ID code: 6EQE) [128]. (**B**) Modelled structure and catalytic triad representation of the cutinase from *Amycolatopsis mediterranei* [46].

Figure 6 shows the enzymatic degradation pathways of PET in *Ideonella sakaiensis*. PETase initiates the reaction by hydrolysing the ester bonds (green highlight) in PET, breaking it down into BHET and MHET monomers [132]. Further hydrolysis is carried out by MHETase converting MHET into terephthalic acid (TPA) and ethylene glycol. Esterases and lipases are also involved in this process; these enzymes can further hydrolyse the ester bonds in both the primary polymer and the intermediates, enhancing the overall degradation process [97]. Yoshida et al. reported *Ideonella sakaiensis* breaking down 75% of PET in 6 weeks using both PETase and MHETase [133]. The PET degradation pathway suggests that multiple enzymes can act synergistically to break down polymers more efficiently than a single enzyme [134]. An enzyme cocktail would be a promising approach to improving effective polymer degradation and could be a suitable option for continuous industry-scale plastic recycling processes.

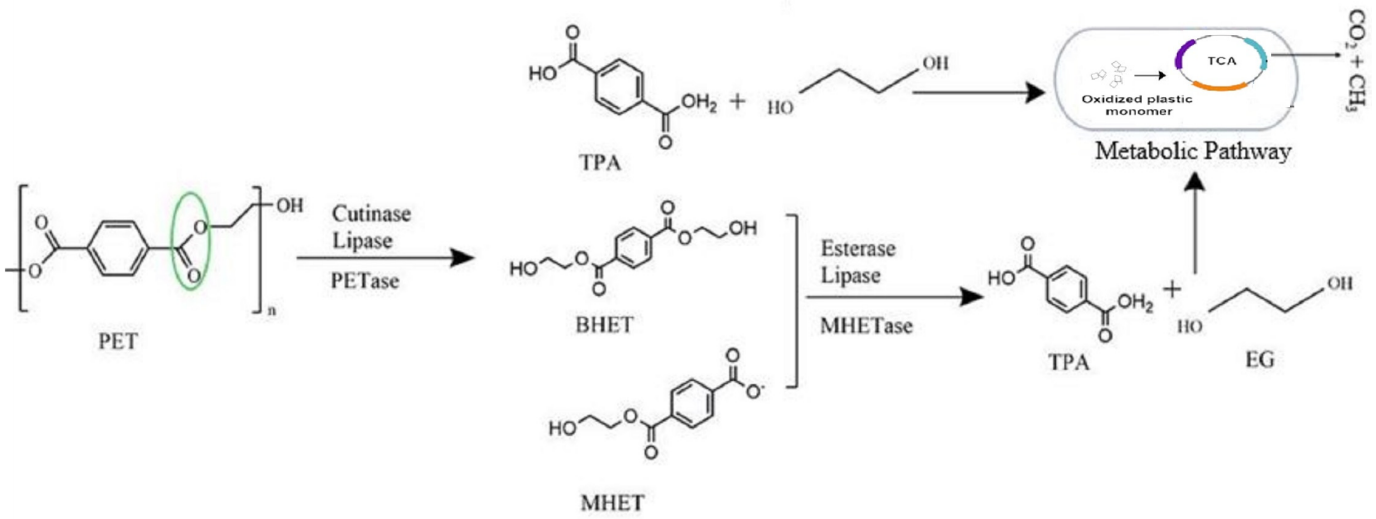


Figure 6. Enzymatic degradation mechanism of PET degradation through cutinase, lipase, and MHETase producing terephthalic and ethylene glycol (adapted from [135]).

2.3.5. Overview of Plastics Biodegradation

Biodegradation of plastics has been extensively studied, focusing on a variety of plastic types, microorganisms, and enzymes involved in their degradation. Polyethylene, in both low- and high-density form (LDPE and HDPE), and PET are among the most studied polymers for biodegradation [135–137]. These plastics are widely used in packaging, construction, and industrial applications, leading to their widespread accumulation in the environment. The degradation of these plastics typically includes specific microbial strains and enzymatic processes that vary from plastic to plastic, depending upon its chemical structure [138,139]. The biodegradation process is monitored using various qualitative and quantitative analytical techniques, such as FTIR, SEM, HPLC, and GC-MS, providing information on the rate of degradation [138,139]. Chemical and physical modifications of polymers such as HDPE and LDPE with degradation are monitored using FTIR and SEM to know the extent of surface erosion and chemical bond breaking during microbial degradation [140]. Table 3 illustrates the range of microorganisms and enzymes involved in the biodegradation of different types of plastics, detailing the growth media used, the time required for biodegradation, and the extent of biodegradation achieved.

Table 3. Microorganisms and enzymes involved in the biodegradation of different types of plastics. The table is categorised by plastic polymer type.

Polymer Type	Microorganisms and Enzymes	Media	Time	Degradation Extent	Reference
Polyethylene terephthalate (PET)	*Paracoccus* sp. (Enzyme not specified)	Mineral Basal Medium	40 days	Change in PET characteristics	[136]
	Ideonella sakaiensis (PETase and MHETase)	M9 Media	6 weeks	75% of PET	[133]
	Streptomyces species (Esterase, MHETase, PETase)	MSM	18 days	49.2–68.8% of PET	[137]
	16 genera of *Bacilli*, 5 genera of *Proteobacteria*, and one genus of *Actinobacteria* (Enzyme not specified)	Bushnell-Haas broth (BHB)	90 days	18% weight loss	[138]
	Rhococcus sp. *SSM1* (Esterase)	Modified Minimal Medium	-	Presence TPA in fermentation media which can only come only by degradation of PET	[139]
	Bacillus altitudinis B538 and *Alcaligenes faecalis B947* (Esterase)	Minimum Media	10 days	0% PET and 2.49% PCL	[140]
Polyethylene (PE)	*Achromobacter xylosoxidans* (Enzyme not specified)	Davis Minimal Broth medium	90 days	9.38% of HDPE	[141]
	Acinetobacter sp. strain NyZ450 and *Bacillus* sp. strain NyZ451 (Laccase, Alkane Hydroxylase)	LB broth	30 days	18% of PE film	[142]
	Pseudomonas aeruginosa (MHETase)	Aquatic microcosm	30 days	6.25% of PE	[143]
	P. knackmussii N1-2 and *P. aeruginosa* RD1-3 (Esterase and Peroxidase)	Nutrient rich growth medium	8-week	PE mulch lost 5.95% and 3.62%	[144]
	Bacterial and Fungal consortia (Esterase)	Basal MSM medium	90 days	LDPE weight reduction (22.4% and 55.6%)	[145]
	Rhodococcus opacus R7 (Laccase)	M9 mineral medium	24 h	10% of PE	[146]
	Klebsiella pneumoniae (Laccase-Like Multi-Copper Oxidase)	Liquid carbon-free basal medium (LCFBM) and Luria-Bertani (LB) medium	90 days	1.68% of LDPE	[53]

Table 3. *Cont.*

Polymer Type	Microorganisms and Enzymes	Media	Time	Degradation Extent	Reference
Polylactic acid (PLA)	*Amycolatopsis* sp. SCM_MK2-4 (Protease and Lipase)	Basal media (MM)	14 days	36% of PLA	[147]
	Brevibacillus brevis (Hydrolase)	Submerged Conditions	60 days	21.9% of PLA film and 42% reduction in molecular weight	[148]
Polystyrene (PS)	*Gordonia* and *Novosphingobium* (Hydrolase)	Marine Broth 2216	30 days	7.73% of PS	[149]
Polyvinyl chloride (PVC)	*P. citronellolis* and *B. flexus* (Enzyme not specified)	MSM	30 days	4.2% by weight loss	[150]
Polyhydroxybutyrate (P(3HB))	*Nocardioides marinisabuli* DSM 18965 (Esterase (C4) and Esterase Lipase (C8))	Mineral Medium	15 days	Change in P(3HB) surface characteristics	[151]
Polycarbonate (PC)	*Pseudoxanthomonas* sp. strain NyZ600 (Hydrolase-PETase)	Liquid Enrichment Media	30 days	Mw from 45.67 to 31.97 kDa and 23.55 to 16.75 kDa	[54]

3. Factors Affecting Plastic Biodegradation

Plastic biodegradation is affected by the physical and chemical properties of polymers. The main influencing factors are the surface area, molecular weight, hydrophilicity, hydrophobicity, chemical structure, melting temperature, and crystallinity [152]. Furthermore, the hydrophobic properties of plastic polymers inferred by their chemical structures reduce microbial activity by preventing water absorption [153]. For example, plastics such as PE and PS have long hydrophobic chains which resist water penetration, creating a barrier that inhibits microbial colonisation on the plastic's surface [154]. These factors could be broadly classified into extrinsic factors and polymer properties.

3.1. Extrinsic Factors

Extrinsic factors refer to the external conditions which influence the growth of microorganisms. Microbes require specific conditions to grow and thrive. The temperature and pH level are prominent influences. Extremes of temperature can hinder microbial growth and activity to slow the biodegradation process [155]. For instance, extremely high temperatures may denature microbial enzymes and disrupt cellular structures, while extremely low temperatures can reduce metabolic rates and enzyme activity. However, some cold-adapted microbes can effectively degrade polymers at low temperatures due to specialised enzymes which remain active in cold environments. Despite this, the overall rate of degradation is typically slower at low temperatures. For example, *Penicillium* sp. has shown a degradation efficiency of just 3.53% for LDPE at low temperatures [58] compared with *P. simplicissimum* from the *Penicillium* genus which demonstrated a significantly higher degradation efficiency of 38% for PE [156]. These examples underscore the importance of considering environmental factors when evaluating the potential for microbial biodegradation. However, while certain specialised microorganisms can operate in more extreme conditions, most microbes and purified enzymes prefer neutral to slightly alkaline conditions [49,157] The primary consideration for effective biodegradation must be the environment in which it will occur.

3.2. Polymer Properties

The hydrophobicity of polymers is strongly influenced by the presence or absence of functional groups. When non-polar groups dominate in the polymer structure, the polymer is more hydrophobic and more resistant to microbial attacks [154]. For example, PE and PP, which consist of long chains of non-polar carbon and hydrogen atoms, are highly hydrophobic and resistant to biodegradation [158]. Another important factor is the polymer's structural complexity. For instance, crystalline polymers have an ordered structure at the molecular level and are therefore more difficult to degrade, as it is difficult for enzymes to access suitable regions of the substrate to begin degradation. The degree of crystallinity is determined by the functional groups, polymer chain length, degree of branching, and tacticity of the monomers. In general, branched and interlinked polymers are resistant to degradation compared with the same polymers without interlinking [125]. Similarly, ester bonds break down more quickly than ether or amide bonds because they have a lower bond dissociation energy [159]. The sequence of bond breakability is as follows: ester > ether > amide > urethane [160]. Higher-density polymers are often more resilient to microbial attacks as they have tighter molecular packing, which inhibits the entry of enzymes or microorganisms [161]. Along the same reasoning, amorphous plastic is more prone to degrade than crystalline plastic [162]. These factors significantly vary between polymers, influencing not only their biodegradability but also their susceptibility to abiotic degradation processes such as photo- and thermal- degradation, which rely on the presence of reactive sites.

Engineering novel enzymes or microbial strains for more specificity and activity towards plastics requires a multidisciplinary approach. For studying and designing protein thermostability, the ProthermaDB database is a valuable online resource [163]. The database comprises over 14 million protein sequences which can be viewed according to their

thermal stability and protein family. These experimentally derived data, when combined with advancing machine learning and artificial intelligence, can be beneficial to increase our understanding of protein stability towards creating new mutational and evolutional strategies to make enhanced enzymes. Based on known, experimentally measured changes in temperature stability (ΔT) mutations, the database recommends mutations for protein families to improve their thermostability. However, the application of this knowledge to plastic degrading enzymes is still in the early stages.

Furthermore, protein glycosylation produced in eukaryotic microbial cells can also improve enzyme thermostability [164] There are some examples of successful glycosylation for enhancing enzyme stability. For example, the lipase from *Geobacillus zalihae* was expressed in a yeast *Pichia* sp. strain, producing a lipase with improved thermostability [165]. These more stable enzymes could potentially be more useful to degrade plastic compared to their native forms.

Enzyme-mediated plastic degradation can be accelerated by altering the enzyme's surface properties. However, in this approach, the enzymes must first be identified based on their catalytic properties and may require mutation to improve substrate specificity or stability under specific conditions, such as pH or temperature [166].

4. Biodegradable Plastic and the Circular Economy

Plastic valorisation is the process of turning waste plastic into energy, useful chemicals, or other usable resources to reduce resource depletion and environmental impact. Enzymatic valorisation is an environmentally friendly approach when compared with traditional chemical or mechanical recycling because it operates under milder conditions, such as lower temperature and pressure, and typically does not require harmful chemicals [167].

High-purity product recovery is also possible since enzymes can be highly selective [168], resulting in the production of valuable byproducts upon degradation [168]. Koller et al. reported biodegradation of PHA into 3-hydroxyalkanoates (3HAs), which can be used to make new plastics [169]. Creating a closed loop re- and up-cycling system, where the degraded products from plastic are repolymerised into new materials and other products such as butanol or biofuels, is currently of significant interest [170]. To make bio-based valorisation more effective, bioreactors are employed for enzymatic degradation in controlled environments. The degradation of PLA in non-sterile soil environments is influenced by both abiotic and biotic factors. Microorganisms present in the soil can catalyse the hydrolysis of PLA. Therefore, the observed 16% degradation after 180 days is likely a combined effect of both intrinsic polymer properties and microbial activity in the soil environment (see Table 2). However, employing enzymatic degradation in a controlled environment, such as a bioreactor, could enhance degradation and favour product recovery. For example, enhanced PET waste conversion into monomers has been demonstrated by enzyme systems like PETase/MHETase (see Section 2.3), indicating the possibility for multienzyme systems (i.e., enzyme cocktails) which can break down PET and possibly polyolefins and other plastic additives [171]. An example of industry-scale enzymatic valorisation was commercialised by CARBIOS [172] for recycling PET by employing specifically engineered enzymes, effectively breaking PET down into ethylene glycol and terephthalic acid. These monomers can then be repolymerised to produce high-value, food-grade PET [173]. Applying such models to biodegradable plastics can lead to more effective and sustainable valorisation strategies [174].

The potential for obtaining biodegraded products from mixed plastic is still challenging and currently requires plastic sorting and segregation prior to degradation. This "sorting problem" is an expensive part of the recycling process. However, promising methods are being developed, including the use of metal-promoted autoxidation to chemically oxidise mixed plastics such as HDPE, PET, and polystyrene [175,176]. In this approach, the polymers are treated to become water-soluble intermediates, which are subsequently broken down for re- and up-cycling through enzymatic degradation by engineered *Pseudomonas putida* [177].

End-of-life biodegradable plastics can be valorised through a circular lifecycle concept, specifically by upcycling biodegradable plastics into chemical and molecular intermediates, which can then be converted into more valuable products. For example, in agricultural mulching fields, plastic mulch films are widely used for weed control, moisture retention, and soil temperature regulation. However, these films often persist in the environment after use. According to EU guidelines, all polymer products used in agriculture must be biodegradable [36]. Therefore, in the context of agriculture, increasing the rate of biodegradation of mulching films in situ will save time and provide organic fertiliser for the soil, leading to increased soil fertility. An interesting example of recycling plastic waste involves PLA, which is a biodegradable plastic that can be depolymerised into lactate monomers (see Figure 7). The hydrolytic depolymerisation of PLA into its monomeric units is catalysed by enzymes such cutinases, lipases, and proteinase K [178,179]. These lactate esters are considered green solvents due to their biodegradability and low toxicity [180]. They can be converted into lactide, which can be used again to produce PLA, thus becoming an important part of a circular bioprocess [181].

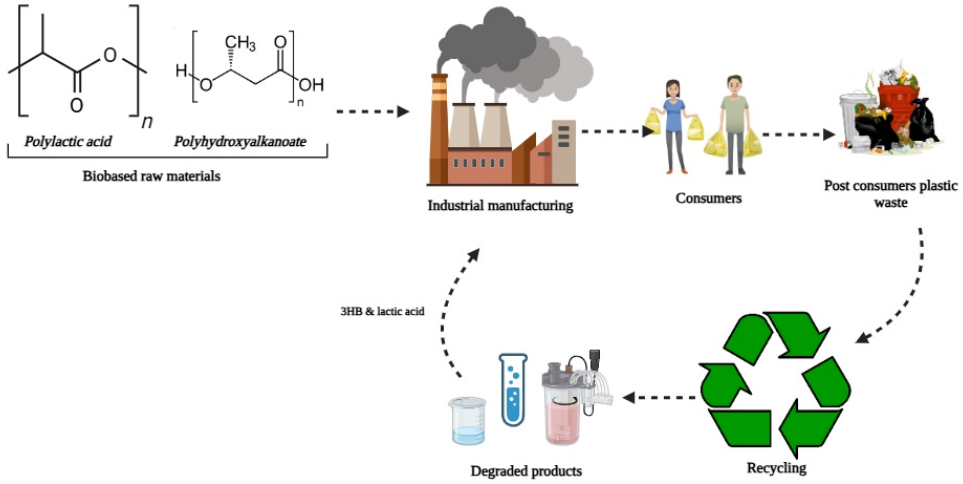


Figure 7. Lifecycle of biodegradable PLA and PHB contributing to a circular economy.

5. Conclusions and Future Directions

Traditional waste management methods are costly and hazardous. However, microbial and enzymatic degradation of plastic presents a viable and sustainable solution to global plastic waste problems. Biodegradation by microorganisms, which produce enzymes like cutinase, lipases, esterases, and PETases, offers a more sustainable approach. PHA and PLA are promising bioplastics which not only degrade under specific conditions but also produce valuable products following degradation (e.g., 3-hydroxyalkanoates and lactic acid). These products can be upcycled (to enhance their value) and recycled into various industrial applications contributing to a circular economy. A circular economy is a closed-loop system where products can be easily extracted, recycled, and reused. However, in the context of soil, it becomes challenging, as once plastics enter the soil, they become difficult to retrieve and reuse.

Additionally, investigating the interactions between the polymer structure, composition, and enzymatic degradation mechanisms will further aid in developing enzymes which effectively degrade specific plastics. This will provide critical information for further rational enzyme design and improvements in the biocatalytic performance of enzymes in terms of selectivity, activity, stability, and scalability. In addition, the development of specific enzymes capable of digesting one plastic in the presence of another will contribute towards addressing the expensive sorting step. Selective hydrolysis of plastic mixtures would greatly ameliorate the costs associated with plastic sorting. The cost and impact of the production of degradative enzymes also needs to be considered as part of a circular

economy. One approach is to enhance enzyme affordability by economies of scale. Another approach is via increasing the activity of enzymes by mutagenesis or solvent engineering.

Integrating biological processes into the entire lifecycle of plastic products would enhance sustainability and favour environmental remediation. Creating a closed loop from production to end of use for plastics in non-polluting and regenerative ways is a must to achieve this goal of a circular economy. This requires continued technological advancements, the development of appropriate infrastructures, and policy support to integrating biological solutions into global waste management.

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