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REVIEW

# Microbial degradation of microplastics by enzymatic processes: a review

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## Abstract

Microplastics contamination is becoming a major concern worldwide. More than 1 million seabirds and 100,000 sea animals have died due to plastic contamination. In addition, plastic particles have been found in juvenile turtles. Statistical data on plastic pollution indicate that this is a serious issue. Due to their small size, microplastics have a large surface area and have more ability to absorb into biological cells. The hydrophobic surface of microplastics attracts co-contaminants such as heavy metals, pharmaceutical toxicants, flame retardants, and other plasticizers, which can then enter biological organisms. Microplastics are usually recalcitrant in the environment, causing microplastics to be transported along the food chain, with humans as the final consumer. Research has been conducted to evaluate the best way to treat and remediate microplastic pollution. Research on microplastic degradation is focused on biological and non-biological approaches. To date, microorganisms such as algae, fungi, and bacteria have attracted the attention of scientists as a tool for microplastic treatment. The degradation of microplastics is closely related to the enzymatic reactions produced by the microorganisms. Here we review microplastics degradation through enzymes from the microorganism's perspective. We present the enzymes that have been isolated from microorganisms for specific microplastics; the mechanisms of microplastics degradation by various enzymes; and the types of microplastics for which degradation mechanisms remain unclear.

**Keywords** Microplastics · Microorganisms · Enzyme · Degradation

## Introduction

Human activities are major contributors towards global contamination (López-Pedrouso et al. 2020). Contamination covers various sectors, such as air, water, and soil. Approximately 2.01 billion metric tons of municipal waste are produced each year, with a projected increase to 3.40 billion metric tons by 2050 (Ellis 2018). As previously stated, humans can impact environmental quality in many ways, such as through deforestation, agriculture, mining, industrial activities, and urbanization (Haddaway et al. 2019; Campbell 2019; Balogh and Jámbor 2020; Arshad et al. 2020). These human activities lead to various types of contamination, which can be categorized into two major groups, namely organic pollutants and inorganic pollutants (Bharagava et al. 2020). Inorganic pollution by definition is contamination that arises from the inorganic by-products of inorganic matter due to radiant energy and noise, light, or heat (Borah et al. 2020). Inorganic pollutants primarily consist of metals/metalloids (arsenic, mercury, cadmium, and lead) and radioactive elements (Wen et al. 2021). While inorganic pollutants are primarily grouped under metal contaminants, organic pollutants consist of various types of contaminants, such as phenols, azo dyes, polyaromatic hydrocarbon pesticides, plastics, and plasticizers (Bharagava et al. 2018).

Plastics are organic polymers synthesized from non-renewable resources, including natural gas, coal, and crude oil. They are easy to mold, making them suitable for a variety of uses (Rios et al. 2010; Worm et al. 2017). In general,

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plastics are categorized into thermoplastics and thermosets (Ayodeji et al. 2020). Plastic consumption has been increasing yearly. Within 10 years, global plastic production increased from 254 million tons to 359 million tons between 2008 and 2018, with an expected threefold increase by 2050 (Chia et al. 2020). Plastic waste is known for its stability and recalcitrance in the environment. Due to this, plastic waste is commonly assumed to be non-degradable. Some state that plastic degradation varies in the environment, ranging between 10 and 1000 years depending on the environmental condition, the type of plastic monomer, and the treatment applied to the plastic waste. For example, treatment analysis using thermooxidative and photodegradation toward microplastics pollutants is claimed to degrade microplastics approximately within 50 years (Mohammed et al. 2019; Ward et al. 2019; Qi et al. 2020; Chamas et al. 2020). The degradation of plastic waste in the environment will lead to the formation of secondary microplastic pollution. The presence of microplastics in the environment has been shown to cause numerous hazardous effects on vast flora and fauna species. In addition, microplastics act as carriers or chelators to various types of co-contaminants, such as heavy metals, brominated flame retardants and other types of plasticizers, and pharmaceutical toxicants. These co-contaminants easily bind to the microplastic surface due to their hydrophobicity (Chatterjee and Sharma 2019).

## Microplastics

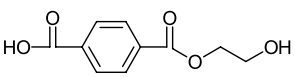
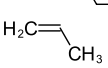
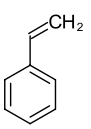
### Definition

The term microplastic itself was first mentioned by an African scientist in the 1990s in his article entitled "Plastic and other artifact on South African beaches: temporal trends in abundance and composition." The term was then recognized worldwide and has been widely used to describe small plastic particles (Alimi et al. 2021). The characteristics of microplastics, also known as tiny plastic particles, are still under debate, but most researchers agree that plastic particles ranging between 100 and 5 mm in size are considered microplastics. Plastic particles that are > 25 mm in size are known as macroplastics, those that are 5–25 mm in size are classified as mesoplastics, and those that are < 100 nm in size are classified as nanoplastics (Löder et al. 2017; Budi Kurniawan et al. 2020; Jaafar et al. 2020; Khalid et al. 2021; Yang et al. 2021b). In the environment, microplastics can be categorized into two major groups: primary microplastics and secondary microplastics. These two types of microplastics are distinguished by the source point. Primary microplastics are derived from manufacturing activity. Millimeter plastic particles are synthesized and designed for commercial products, such as personal care products, e.g., toothpaste, facial cleanser, and shower gel. Primary microplastics can be generated from the air-blasting industry due to the abrasion of materials during the preproduction of resin pellets (Suardy et al. 2020; Nava and Leoni 2020; Khalid et al. 2021). On the other hand, secondary microplastics are derived from chemical (i.e., UV radiation, the freeze–thaw cycle), physical (abrasion, wave strike, water disturbance), and biological (degradation) activities involving fragmentation and degradation of large plastics into micro-sized particles (Khalid et al. 2021; Dong et al. 2021). Microplastics are built by the polymerization of plastic monomers. Table 1 shows the monomer structure of each major microplastic present in the environment (Table 1).

### Microplastics formation route

Microplastic contamination is commonly caused by human anthropogenic activities. Since plastics are used daily by humans, this pollution comes from a wide range of sources,

**Table 1** Polymeric microplastics and their monomers, monomer structure, chemical formula, and density

| No | Polymer name | Monomer name | Monomer structure | Chemical formula | Density (g $cm^3$) |
|---|---|---|---|---|---|
| 1 | Low-density polyethylene (LDPE) | Ethene | $H_2C{=}CH_2$ | $C_2H_4$ | 0.91–0.92 |
| 2 | High-density polyethylene (HDPE) | Ethene | $H_2C{=}CH_2$ | $C_2H_4$ | 0.93–0.97 |
| 3 | Polyethylene terephthalate (PET) | Ethylene terephthalate |  | $C_{10}H_8O_4$ | 1.37–1.38 |
| 4 | Polypropylene (PP) | Propylene |  | $C_3H_6$ | 0.89–0.92 |
| 5 | Polystyrene (PS) | Styrene |  | $C_8H_8$ | 0.28–1.04 |
| 6 | Polyvinyl chloride (PVC) | Vinyl chloride |  | $C_2H_3Cl$ | 1.10–1.47 |

from industry sectors to domestic activities. Industries such as raw plastic manufacturing and textile and laundry services are some of the major industries that have been reported to contribute to the presence of microplastics in the environment (Lechner and Ramler 2015; De Falco et al. 2019; Henry et al. 2019; Cai et al. 2020b; Tang et al. 2020). Besides industry, wastewater treatment plants (WWTPs) have been mentioned in numerous articles as the main source of microplastic contamination in the environment (Mintenig et al. 2017; Wolff et al. 2019; Funck et al. 2020; Frehland et al. 2020; Sol et al. 2020). In addition, the agricultural sector has also been reported to significantly contribute to microplastic pollution (Mohajerani and Karabatak 2020; Zhou et al. 2020; van den Berg et al. 2020; Ding et al. 2020; Crossman et al. 2020; Zurier and Goddard 2020; Kumar et al. 2020). Domestic activities such as improper littering and leachate from runoff surface water are reported to contribute to microplastic contamination (Gandara e Silva et al. 2016; Green et al. 2018; He et al. 2019; Kalnasa et al. 2019; Esquinas et al. 2020; Li et al. 2020; Shi et al. 2020). The activities mentioned above are considered to be major anthropogenic activities that cause microplastic contamination, but many human activities also contribute to this contamination.

## Microplastics toxicity

Microplastics circulate in soil and aquatic ecosystems and have been proven to impact flora and fauna. Numerous reports in ecotoxicology toward plants were mentioned in several plant species. In summary, microplastics can affect plants directly and indirectly. Microplastics have been shown to directly affect plants by blocking nutrient uptake and accumulating in roots, shoots, and leaves, while microplastics have been found to indirectly alter the properties of soil, such as the presence of soil-dwelling microorganisms and physicochemical properties (Khalid et al. 2020). A growth rate analysis in tomato plants using sludge containing microplastics indicated that the growth rate decreased significantly after exposure to microplastic sludge for 109 days. The study stated that the growth rate was significantly affected due to the alteration of the C:N ratio in the soil system, which affected the nutrient availability in the soil (Hernández-Arenas et al. 2021). An analysis using the aquatic plant *Utricularia vulgaris* showed that microplastics accumulate in several regions in plants. Microplastics were found in the root, leaves, and bladders of plants. Microplastics accumulations in plants are shown to cause oxidative damage through increment in plant antioxidative enzyme activity (Yu et al. 2020). A similar report mentioned the microplastic effect in the plant *Vicia faba*. Exposure to microplastics leads to various oxidative enzymatic responses such as catalase, superoxide dismutase, and peroxidase. These enzymes are known to be closely related to oxidative stress, which can be caused by the presence of microplastics and co-contaminants, such as heavy metals and plasticizers. Laser confocal scanning microscopy analysis showed that microplastics accumulate in the root parts of plants (Jiang et al. 2019; Abbasi et al. 2020). The ecotoxicity of microplastics has not only been observed in plants, but microplastics have also been reported to affect animals. Fish are among the common biological models used to investigate the toxicity of microplastics. Laboratory-based environments have indicated that microplastics affect nutrients by accumulating in the fish intestine. Microplastics were also found to induce inflammatory responses, reduce innate immunity, reduce reproduction rate, and promote organ failure in fish. However, data from laboratory-based environments do not provide an actual environment scenario in microplastic ecotoxicity. Reports have shown that microplastics in the environment also contain other co-contaminants, such as plasticizers and heavy metals. An analysis mimicking actual environmental conditions showed a greater effect of toxicity on fish with the toxicity effect increased with 30 times higher compared to the laboratory-based environment (Rainieri et al. 2018; Cheng et al. 2020; Wang et al. 2020b). Aquatic gastropods, bivalve, crustacean, amphipods, and insect larvae were among the biological models used for accessing the impact of microplastics on ecosystems. The same rate of toxicity was observed, with significant effects on the growth and reproductive systems of the animals tested. In addition, microplastics have been found to significantly affect regulatory enzymes, such as acetylcholinesterase, catalase, and glutathione-s-transferase (Jaikumar et al. 2019; Chagas et al. 2020; Trestrail et al. 2020). Humans are considered the top consumers in the food chain. Therefore, humans are prone to microplastic contamination. The source or point of contamination can be almost anything, such as the water source, food source, and even air. Ingestion and inhalation of microplastics from the environment promote a wide range of toxicities in humans. Microplastics have been shown to promote the inflammatory response in humans by activating the mitogen-activated protein kinase pathway. They have also been shown to have neurotoxic effects by inhibiting acetylcholinesterase activity, the inflammatory response, which can lead to the development of cancer development. The interaction between microplastics and humans has also been found to affect cell function at a molecular level (Hwang et al. 2019; Huang et al. 2020; Ju et al. 2020; Llorca et al. 2020; Wang et al. 2020a). Due to the long list of toxicities toward flora and fauna, microplastic treatment or removal from the environment is compulsory. Degradation can be separated into biological and non-biological approaches. In this review, we focus on biological degradation, especially the enzyme-based approach.

## Enzymes in microplastic degradation

Microplastic pollution is currently becoming a worldwide concern. This is due to its toxicity, which contributes to numerous diseases, especially those in humans. Anthropogenic microplastic pollution is one of the environmental stressors that is causing ecotoxicology. The technologies and methodologies in removing microplastics in the environment were extensively reviewed by Padervand et al. (2020). Chemical, physical and biological approaches were critically discussed of their advantages and disadvantages toward microplastics removal. This article did mention the microplastics removal by microorganisms through their adaptation to the microplastics-existence ecosystem (Padervand et al. 2020). The existence of microplastics in the environment leads to the adaptation of microorganisms to survive stressful conditions caused by this pollutant (Oberbeckmann and Labrenz 2020; Yang et al. 2020a). Microorganisms respond to this stress in several aspects, such as growth rate, energy reproduction (metabolism rate), and the synthesis of new macromolecules for cellular protection purposes (NicAogáin and O'Byrne 2016; Guan et al. 2017; Guan and Liu 2020). These stress responses are closely related to enzyme activity since such enzymes play a major role in regulating cell functions (Cooper 2000; Cheng et al. 2011; Winkel 2017). Enzymes are not only involved in cell function and cell regulation, but they are also involved in the degradation of anthropogenic pollutants, including microplastics. For example, the degrading enzyme from microorganism can specifically target the polymer structure of microplastic and degrade it into its monomer, later will be used as a carbon source in the microorganism energy production cycle (Fig. 1) (Gong et al. 2018; Islam et al. 2019; Kawai et al. 2019; Ganesh Kumar et al. 2020). Each enzyme shows unique interaction mechanisms when degrading microplastics. In general, the mechanism is divided into two major mechanisms. Enzyme surface modification mechanisms by enzyme hydrolases (lipases, carboxylesterases, cutinases, and proteases) were said to be responsible for modifying microplastic polymer surfaces prone to the degradation process (Vertommen et al. 2005). This situation was intensively reviewed by Kawai et al. (2019) who claimed that certain microplastic hydrolases only react as a surface modifier to a microplastic. This type of enzyme is called a surface modifying enzyme, as suggested by the author. As such, this enzyme increases the hydrophilicity of the microplastic surface and does not degrade the building blocks of the microplastic (Kawai et al. 2019). The interaction mechanism between the enzyme and microplastic surface has been proven and explained by elemental spectroscopy chemical analysis (ESCA). Changes in C–O bonding were observed when comparing the control and the enzyme-treated microplastic. From this analysis, the author concluded that the bonding change was due to the enzyme surface interaction (Vertommen et al. 2005). As a consequence of the surface modification activity, only a few cutinase enzymes were reported to be able to degrade the inner block of the microplastic (Austin et al. 2018).

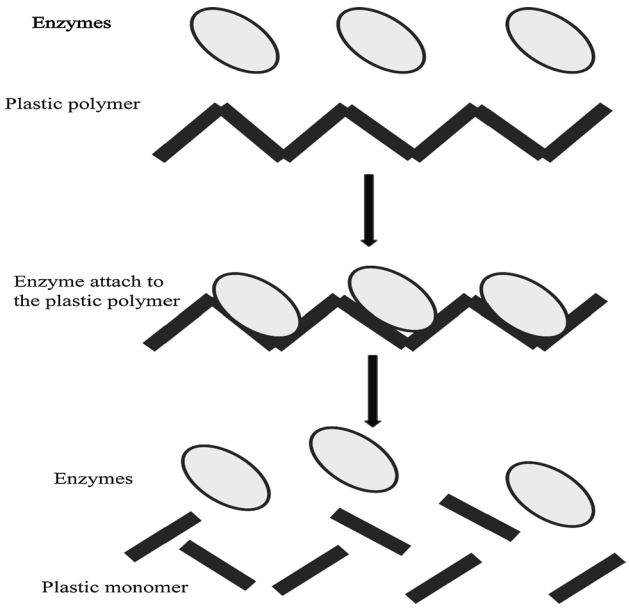



**Fig. 1** General mechanism of enzymes degrading microplastics into monomers

To find a novel enzyme that can degrade microplastics, a large amount of research has been conducted in the last decade. Several groups of enzymes are claimed to have the ability to degrade polymers into their monomer forms. Oxidases, amidases, laccases, hydrolases, and peroxidases are groups of enzymes that are involved in polymer degradation (Álvarez-Barragán et al. 2016; Ashter 2016; Gómez-Méndez et al. 2018). Due to the enzyme-specific characteristic towards its substrate, the next subchapter will discuss the identified enzyme that is responsible for degrading specific microplastic polymers based on the types of major microplastic presence in the environment.

## Microplastic-degrading enzyme

### Polyethylene-group-degrading enzyme

Polyethylene (PE) group microplastics can be categorized into the following two major groups based on their density: high-density polyethylene (HDPE) and low-density polyethylene (LDPE) (Restrepo-Flórez et al. 2014; Wu and Montalvo 2020; Patel et al. 2020). Chosen due to its excellent chemical and physical properties, PE is the largest plastic commodity presence in the various types of industries. Therefore, microplastic pollution caused by PE is common

in terrestrial environments (Chen et al. 2015; Nuawi et al. 2016; Gao et al. 2021).

The PE microplastic group commonly contaminates the ecosystem in the form of HDPE and LDPE. It is commonly known that the PE microplastic is associated with numerous illnesses and significant toxicity effect on animals, plants, and humans (Kalčíková et al. 2017; Shaikh et al. 2018; Mateos-Cárdenas et al. 2019; Bellas and Gil 2020; Silva et al. 2021; Abbasi and Turner 2021). Therefore, treatment of PE contaminant in the environment is crucial. Biodegradation using the enzyme activity of microorganisms is a current research trend. LDPE is commonly found in plastic bags. Its low density property is mainly due to the small branching molecule in the polymer backbone (Kumar Sen and Raut 2015). The biodegradation of LDPE using microorganisms has been performed for more than 50 years. The degradation mechanism is related to the enzyme degradation mechanism. SDS-PAGE analysis of *Staphylococcus epidermis* supernatant exposed to LDPE for three months revealed that the degradation of LDPE is enzyme mediated (Chatterjee et al. 2010). Later, in 2015, a review on an LDPE-degrading enzyme explained the mechanism involved. This review suggests that enzyme-based degradation is divided into two stages. First, depolymerization of the polymer takes place extracellularly, where extracellular enzymes act as a key player in the process. In this stage, the LDPE polymer is broken down into shorter chains (oligomer, dimer, and monomer). The depolymerization stage mainly facilitates the absorption of LDPE into the cell through the permeable membrane lipid. The second stage of the process is called mineralization. In this stage, the shorter LDPE chain is mineralized to the end product, such as $CO_2$, $H_2O$, and $CH_4$. These end products will be used as a carbon source for microorganism metabolism in general. In the same review article, two enzymes (laccase and alkane hydrolase) that showed significant reaction towards LDPE are mentioned by the author. Laccase and alkane hydrolase are from the *AlkB* family enzyme. Between these two enzymes, alkane hydrolase gets more attention in the discussion due to its novel activity in the degradation of PE (Kumar Sen and Raut 2015; Ghatge et al. 2020; Montazer et al. 2020).

HDPE is one of the microplastics that is commonly found in the environment. HDPE density is between 0.94 and 0.97 g $cm^3$ which is lower than water density. Therefore, HDPE floats in the water environment and contributes to almost 46% of total microplastics contamination worldwide (Lee and Chae 2021). Being the most abundant microplastics in the environment, the degradation of HDPE has attracted the attention of scientists looking for potential natural degraders of this pollutant. Over the last few years, numerous microorganisms capable of degrading HDPE in the environment were isolated. Fungi and bacteria are the most common microorganisms reported to degrade this microplastic, with bacteria phyla divided into three major groups. Proteobacteria, Firmicutes, and Actinobacteria are the common phyla reported to be related to microplastics degradation (Sangeetha Devi et al. 2015, 2019; Ojha et al. 2016; Bonilla et al. 2020; Matjašič et al. 2021). Laccase is the most reported enzyme associated with HDPE degradation. Categorized under the oxidase group enzyme, laccase is found to depolymerize polymers through oxidative cleavage of the amorphous region of HDPE, providing an easily accessible carbonyl region within the polymer chain (Kang et al. 2019; Ghatge et al. 2020). Physical analysis using scanning electron microscopy (SEM) revealed that in the presence of the laccase enzyme, the HDPE surface developed pits and cracks after 90 days of incubation (Kang et al. 2019). Several other enzymes were reported to be involved in microplastic degradation through either direct or indirect degradation. Manganese peroxidase from the fungi *Phanerochaete chrysosporium* was reported to be able to reduce and decrease the tensile strength and total molecular weight of PE. In addition, the enzyme soybean peroxidase with the presence of hydrogen peroxide has been shown to reduce the hydrophobicity of the PE surface Although the ability of certain enzymes involved in microplastic degradation has been discussed, the actual mechanism is still unclear (Ghatge et al. 2020). The degradation scheme of LDPE and HDPE is simulated in Fig. 2. In summary, few enzymes were identified by researchers related to LDPE and HDPE degradation. Those enzymes were identified as laccase and alkane hydrolase. Manganese peroxidase and soybean peroxidase were claimed to reduce tensile strength and reduce hydrophobicity of PE surface, respectively. Although depolymerization and intake of the microplastics were discussed, the complete mineralization of microplastics monomer inside the microorganisms is still unclear and unexplored. In author opinion, LDPE and HDPE degradation will undergo almost similar mechanism due to the similar monomer structure of these two microplastics. Thus, this can provide a potential research gap in understanding the metabolism pathway involved in microplastics biodegradation.

#### Polyethylene terephthalate-degrading enzyme

Polyethylene terephthalate (PET) is categorized under thermoplastics. Linked by an ester bond, this plastic polymer is used in various industries, such as fiber, bottle, and film industries. The PET structure consists of an amorphous semi-crystalline structure. PET melts at high temperatures (260 °C). The PET half-life is approximately 700 years in the normal environment (Abdelaal et al. 2008; Zulkifley et al. 2014; Horvath et al. 2018). Similar to other types of microplastics, PET has been shown to have toxicity toward living cells. PET has been shown to significantly reduce the zooplankton population and egg production when exposed

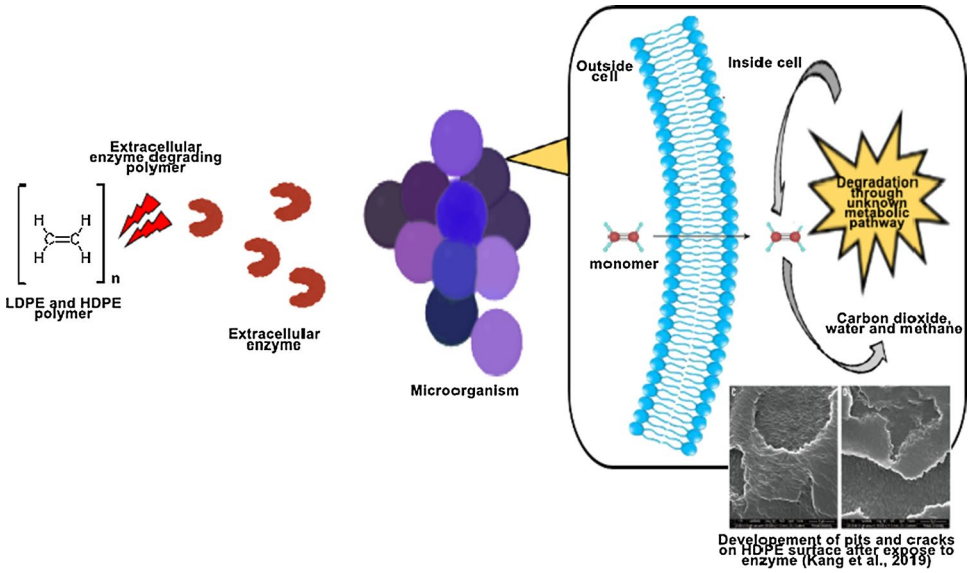



**Fig. 2** Degradation scheme of low-density polyethylene (LDPE) and high-density polyethylene (HDPE) microplastics. An extracellular enzyme secreted by microorganisms will degrade microplastics polymer and produce monomer. Microplastic monomer uptake by the microorganism is facilitated by a permeable membrane bilayer. Microplastics mineralization inside the cell through unknown metabolic pathway produces $CO_2$, $H_2O$ and $CH_4$. An The scanning electron microscopy (SEM) image shows the formation of pits and cracks on the HDPE surface after exposure to the microorganism's enzyme

to PET from the environment (Heindler et al. 2017). A toxicity effect has been observed in higher organisms, such as benthic grazer organisms (Parolini et al. 2020). PET toxicity in humans has raised concerns on the effect of PET leachate from bottles on the human endocrine system. Research has shown that exposure to PET that has leached from containers affects the human endocrine system, such as human estrogenic regulation. Additionally, there has been a 78% increase in breast cancer development after exposure to PET (Sax 2010). Several steps have been taken to reduce the negative impact of PET on the environment, including reducing usage quantity, recycling, and degradation PET from the environment. Of these, PET degradation has received more attention from researchers since it is believed to solve PET contamination in the environment (Chowdhury et al. 2018; Sang et al. 2020).

The degradation of PET can be classified into two groups: abiotic degradation and biotic degradation. Abiotic degradation, such as hydrolysis, thermal degradation, and chemical degradation, is commonly mentioned in articles (Arhant et al. 2019; Wu et al. 2019; Das and Tiwari 2019). Biotic degradation, or biodegradation, attracts researcher's attention due to its complete mineralization, especially in microorganism degradation. A long list of bacteria and fungi are associated with PET degradation (Herrero Acero et al. 2011; Ribitsch et al. 2011; Kawai et al. 2014; Yoshida et al. 2016; Sangale et al. 2019; Danso et al. 2019; Bollinger et al. 2020; da Costa et al. 2020; Denaro et al. 2020). Out of the microorganisms associated with PET degradation, *Ideonella sakaiensis* 201-F6 bacterium has been shown to successfully express the enzyme related to PET degradation. Isolated in 2016 by Yoshida et al., this bacterium strain led to further research in understanding the mechanism of the reaction (Yoshida et al. 2016). The PET-degrading enzyme, known as PETase, became the center of attention related to PET degradation. The early mechanism explained the involvement of two major enzymes. First, PETase converts PET into mono(2-hydroxyethyl) terephthalic acid (MHET), with trace amounts of terephthalic acid (TPA) and bis(2-hydroxyethyl)-TPA (BHET) as secondary products. Second, the involvement of a secondary enzyme, known as MHETase, converts MHET to terephthalic acid and ethylene glycol (EG). Ethylene glycol, on the other hand, can be used as a precursor in the tricarboxylic acid (TCA) cycle substrate depending on the metabolic route. Ethylene glycol can be converted either to acetate via acetyl CoA or converted to isocitrate. The terephthalic acid molecule will undergo a series of reactions, including protocatechuate (PCA) synthesis from terephthalic acid. Protocatechuate then undergoes a typical metabolic pathway for toxic and recalcitrant aromatic molecules, known as the β-ketoadipate pathway (Fig. 3) (Yoshida et al. 2016; Chen et al. 2018; Salvador et al. 2019). Further analysis focused on the PETase structure and mechanism was done in 2018. Austin et al. 2018 through X-ray crystallography analysis, showed that PETase structure is expressed by the common α/β hydrolases, which consists of six α-helicase and eight β-sheets. A comparison between the cutinase enzyme structure (previously mentioned as the PET-degrading enzyme) indicated that PETase and cutinase are distinctively different, with PETase having a polarized surface compared to cutinase and isoelectric point (pI) values of 9.6 and 6.3, respectively. The interaction between the PETase enzyme and its substrate was determined in this analysis. PETase was found to interact with PET through an induced fit mechanism. Due to this, the author suggested that the PETase mechanism could be wider, with other types of polyaromatic microplastics is possible for PETase substrate. This was later proven by the analysis that PETase can bind

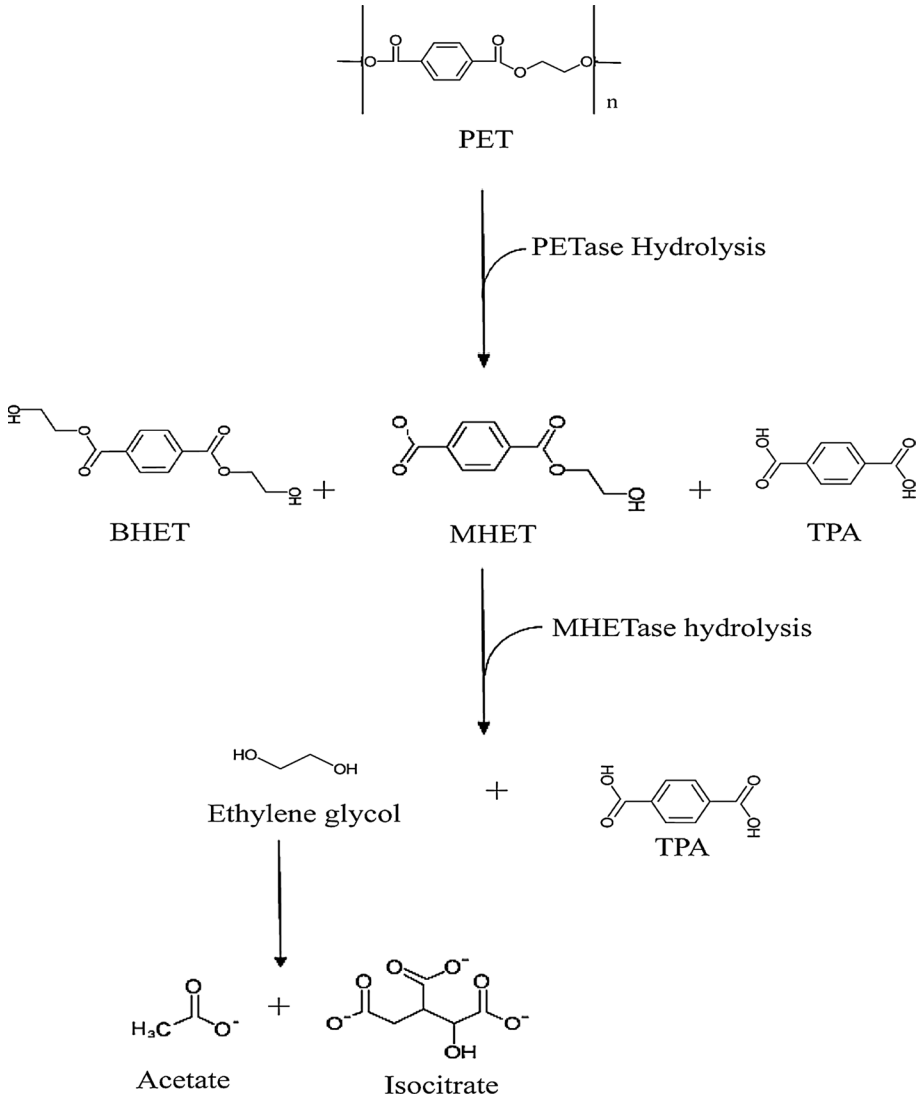



**Fig. 3** Enzymatic degradation mechanism toward the polyethylene terephthalate monomer. Mineralization of polyethylene terephthalate (PET) produces acetate and isocitrate, which are used in the tricarboxylic acid (TCA) cycle. TPA: terephthalic acid, BHET: bis(2-hydroxyethyl)-terephthalic acid, MHET: mono(2-hydroxyethyl) terephthalic acid

and degrade polyethylene-2,5-furandicarboxylate (PEF) (Austin et al. 2018). Furthermore, the PETase structure was determined using higher X-ray crystallography resolution (2.02 Å). The PETase active site showed high flexibility due to the presence of a disulfide bond (Fecker et al. 2018). The understanding of PETase structure and mechanism leads to an improvement of PETase performance. Several analyses including mutation and overexpression were conducted to improve PETase performance. Microalgae are one of the microorganisms chosen for overexpression of PETase since microalgae are considered the best model organism due to several advantages, such as being safe and eco-friendly toward the environment, easy to cultivate and capture $CO_2$ from the environment through their photosynthetic ability. The transformation of PETase in microalgae has been successfully expressed and proved to be able to degrade PET through overexpression of PETase enzyme and its activity (Moog et al. 2019; Kim et al. 2020b). The PETase mutation was evaluated and compared with the wild-type performance. The mutant PETase was found to increase the activity rate up to 2.5-fold (Ma et al. 2018). PET degradation is regulated by two major enzymes. MHETase acts as a secondary enzyme that uptakes MHET and converts it to terephthalic acid and ethylene glycol. MHETase structure reminisces of feruloyl esterases. Similar to PETase, MHETase consists of an α/β hydrolase domain in addition to a lid domain structure, differentiating between MHETase and PETase. The lid domain is also crucial in MHET hydrolysis. MHETase has been shown to share the same mechanism (induced fit) with PETase toward its substrate. A comprehensive analysis of the MHETase structure through structure modification is needed to enhance its performance (Palm et al. 2019; Knott et al. 2020). PET mainly originated from food container was found to be completely mineralized by the microorganisms. PETase and MHETase were two enzymes involved in degrading PET polymer to

its monomer. Complete mineralization of PET involving two major pathways (TCA cycle and β-ketoadipate pathway) depends on the metabolic substrates formed from the degradation. Though PET-degrading enzymes (PETase and MHETase) have been extensively explored, few other enzymes have been reported to contribute to PET degradation, such as lipase and esterase, which are still unexplored. The potential showed by other enzymes can be a new baseline for PET degrading enzyme analysis in the future.

#### Polystyrene-degrading enzyme

Polystyrene (PS) was first synthesized by BASF in the 1930s. Constructed from an aromatic styrene monomer, a liquid hydrocarbon, which originated from a petroleum base, polystyrene is considered an aromatic polymer. Having unique characteristics, such as hard, rigid, and solid at room temperature, transparently makes this plastic a major plastic used in food and packaging industries (Koerner et al. 2006; Dağ et al. 2019). Polystyrene presence in the environment or water body leads to numerous toxicities. Polystyrene in a form of microparticle or nanoparticle is proved to be toxic towards animals, humans and plants. Animals, especially aquatic animals are one of the common species studied for polystyrene toxicity. Polystyrene is shown to significantly affect fish reproduction systems over time (Wang et al. 2019; Zhu et al. 2020; Qiang and Cheng 2021). The absorption of polystyrene is also reported to affect the molecular level. Absorption of polystyrene in the cell promotes DNA damage in erythrocytes and brain tissue (Zhang et al. 2011; Farrelly and Shaw 2017; Sökmen et al. 2020; Guimarães et al. 2021). Although polystyrene is considered less toxic or not harmful towards humans, excess exposure to certain particle sizes may lead to certain immune responses in human cells. Depending on the site of exposure, polystyrene can enter human systems through air, food and skin contact. Polystyrene is found to accumulate in human alveoli tissue through inhalation, penetration through skin and food consumption result in polystyrene accumulation in cells and bloodstream. Analysis in the human bloodstream showed that excess of polystyrene in the red blood cells (RBCs) can promote hemolysis. Polystyrene also is proved to promote the expression of local proinflammatory cytokine (Interleukin-6) which indicates local inflammation in human cells (Farrelly and Shaw 2017; Kik et al. 2020; Hwang et al. 2020). Different from animals and humans, absorption of polystyrene in plants is assessed through the root part. Root in plants is a major nutrient uptake point. Numerous analysis reports, plants that were exposed to polystyrene in the environment showed deficiency in their biomass. This situation is due to the accumulation of polystyrene in plant root tissue. The accumulation promotes blockage in the nutrient transportation in the plants. In addition to that, the accumulation of polystyrene in plant tissue leads to inhibition of seed germination, gene expression and induce cytogenotoxicity (Jiang et al. 2019; Maity and Pramanick 2020; Taylor et al. 2020; Gao et al. 2020). Polystyrene in the environment is proved not only to affect higher organisms, a group of protist phyla or known as algae are reported to be affected by the presence of polystyrene. Several analyses in different types of microalgae showed that interaction between polystyrene and microalgae reduced microalgae growth rate. Polystyrene is found to agglomerate at the microalgae cell wall in general. This situation is reported to take place when exposed to small size (micro) polystyrene (Sjollema et al. 2016; Nolte et al. 2017; Libralato et al. 2017; Reynolds et al. 2021).

Adaptation towards microplastic environments promotes the biodegradation process in general. Degradation study by living organisms covers a broad range of organisms' types and species. Numerous studies report on the association of decomposer animals towards polystyrene degradation. Removal of microplastics by organisms such as zooplankton was associated with their uptake and ingestion factors. A high concentration of zooplankton in the environment able to remove polystyrene (Padervand et al. 2020) Recently, the utilization of snail and larvae is used to determine the biodegradation rate of polystyrene in the environment. *Achatina fulica* land snail is reported to reduce approximately 30.7% of ingested polystyrene in 4 weeks (Song et al. 2020). Additional to this, various types of mealworm larvae are reported to be able to degrade polystyrene from the environment. Each of these larvae showed different degradation rates with *Zophobas atratus* larva claimed to be the super worm by degrading polystyrene in less than 1 month. Even though these studies report in different organisms related to polystyrene degradation, one similar fact that these reports are that polystyrene degradation takes place in the gut of these organisms and this condition is regulated by the presence of intestine microbiota (bacteria and fungi) in the gut (Yang et al. 2020b, 2021a; Billen et al. 2020; Cucini et al. 2020; Peng et al. 2020). High throughput next gene sequencing analysis of gut microbiota in *Tenebrio molitor* and *Alphitobius diaperinus* larva showed that several bacteria and fungi strain identified able to use diverse types of plastics as a sole carbon source. Those strains belong to *Klebsiella*, *Pseudomonas, Serratia* and *Trichoderma* (Urbanek et al. 2020; Cucini et al. 2020). Although polystyrene degradation by microorganisms is abundantly mentioned (O'Leary et al. 2002; Oikawa et al. 2003; Hwang et al. 2008; Mor and Sivan 2008; Atiq et al. 2010; Atiq 2011; Bhardwaj et al. 2013), data on the related enzyme involved in the degradation mechanism are still scarce. In 1997, the first polystyrene degrading enzyme was reported. Hydroquinone peroxidase from *Azotobacter beijerinckii* HM121 is claimed to degrade polystyrene. Dichloromethane is used to convert water-insoluble polystyrene into a small water-soluble

molecule. Water-soluble polystyrene is later degraded by the hydroquinone peroxidase (Nakamiya et al. 1997). More than two decades later, a study report on polystyrene degradation involving sets of enzymes reaction. Mineralization of polystyrene is reported to be used as a substrate in TCA cycle (Fig. 4). The mechanism is initiated by degrading the polystyrene backbone by hydrolytic activity into styrene monomer. Styrene monomer is oxidized to styrene oxide in the presence of styrene monooxygenase. Next, styrene oxide undergoes isomerization into 3-phenyl acetaldehyde by styrene oxide isomerase. 3-phenyl acetaldehyde was then converted to 4-phenylacetic acid by phenylacetaldehyde dehydrogenase. Lastly, 4-phenylacetic acid is converted to 5-phenylacetyl coenzyme A in the presence of phenylacetyl coenzyme A ligase enzyme. 5-phenylacetyl coenzyme A undergoes β-oxidation to yield acetyl-CoA which is fed to TCA cycle (Ho et al. 2018; Danso et al. 2019). To date, another enzyme-mediated mechanism is reported performed by bacteria *Pseudomonas* sp. DSM 50,071 isolated from *Zophobas atratus* guts. Serine hydrolase (SH) is claimed to show a significant effect in polystyrene degradation. Analysis using serine hydrolase inhibitor (SH inhibitor) indicates that at low SH inhibitor concentration (10 µM), polystyrene degradation is dropped from 2.6% (control) to 1.3% after 15 days of incubation. Incubation at high SH inhibitor concentration (50 µM) showed complete inhibition SH activity with no polystyrene degradation observed (Kim et al. 2020a). In summary, polystyrene degradation is proved by enzymatic degradation. The polystyrene monomer mineralization will produce acetyl-coenzyme A (CoA) through β-oxidation. Acetyl-CoA produced will be used as a feeder for TCA cycle in microorganism metabolism. Another enzyme known as serine hydrolase is proven to be involved in polystyrene degradation. Though enzyme mechanisms aforementioned can be a baseline for researchers to understand polystyrene degradation, further extend analysis is needed especially for serine hydrolase to support and provide mass knowledge related to the enzyme mechanism in polystyrene degradation.

### Polypropylene degrading enzyme

Polypropylene (PP) can be derived from primary and secondary microplastic reactions. Primary polypropylene microplastic is commonly found in cosmetics and personal care products (Uheida et al. 2020). Polypropylene is considered as low-density plastic with an average density is 0.94 g/cm$^3$. Building blocks for polypropylene are a straight chain

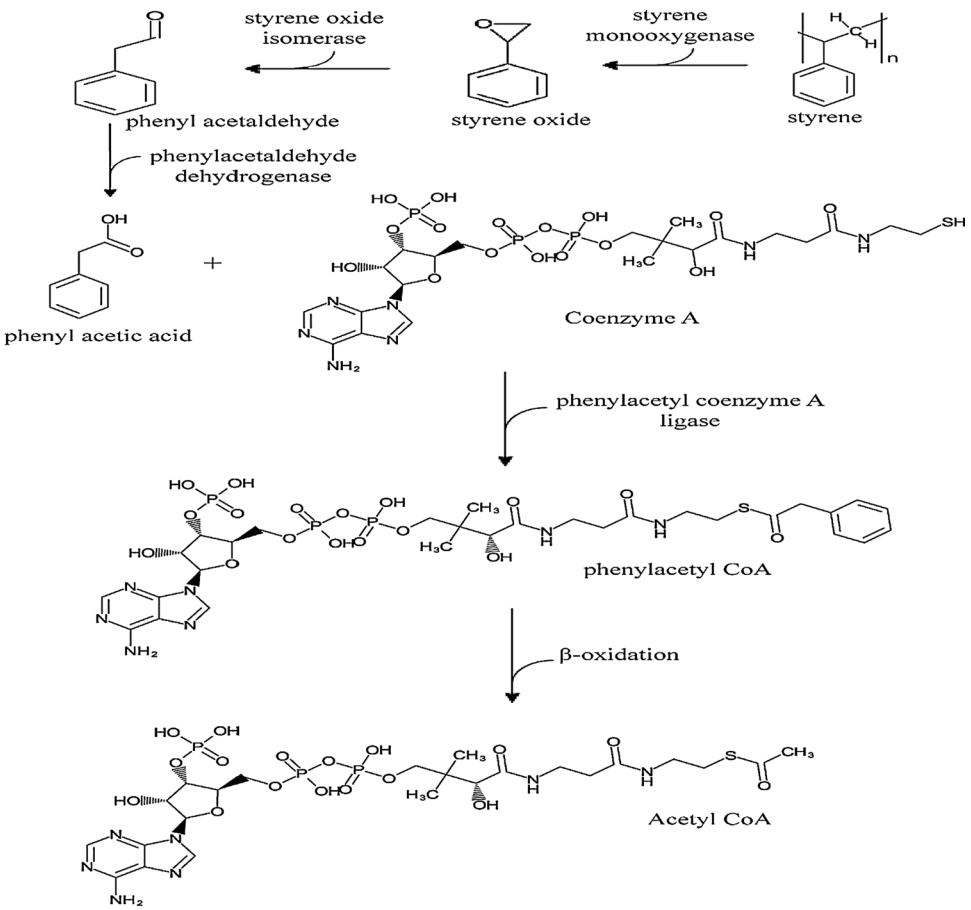



**Fig. 4** Enzymatic degradation mechanism of the styrene monomer. Mineralization of the styrene monomer produces acetyl-CoA, which is used as a substrate in the tricarboxylic acid (TCA) cycle

of hydrocarbon structure with only carbon atoms in its main ring structure. Due to this hydrocarbon arrangement, polypropylene has a hydrophobic surface. There are three stereoisomers for polypropylene (isotactic, syndiotactic, and atactic) with isotactic polypropylene is the most abundant plastic used mainly in food and medical industries. Having hydrophobic property and rough surface, making it one of the resilient and recalcitrant in the environment (Khoironi et al. 2020). The distribution of polypropylene is reported to be ubiquitous and scattered around the world from east to west regions. A marine water sampling was conducted by two different groups, sampling site in Zhubi Reef from South China Sea and Chesapeake Bay in USA. Act as the main water basin in both regions, numbers of samples are taken from these areas and analyzed for microplastic content. In both regions, it is reported that polypropylene is the most abundant microplastic found in these regions (Huang et al. 2019; Bikker et al. 2020). Similar to other types of microplastic, cells exposed to polypropylene will show toxicity. Analysis using PBMCs, RAW 264.7, and HMC-1 human-derived cells showed that exposure to polypropylene stimulated immune response and enhanced hypersensitivity via increment in cytokines and histamine level in respected cells (Hwang et al. 2019).

The reports on microbial degradation associated with polypropylene are extensively discussed by Ru et al. (2020). In this report, the author mentioned the degradation of polypropylene polymer is not only targeting the backbone of the polypropylene but also targeting the plasticizers that exist on the surface of the polypropylene (Ru et al. 2020). Two species of bacteria are associated with polypropylene degradation. *Rhodococcus* sp. strain 36, *Bacillus* sp. strain 27 and *Bacillus gottheilii* are the bacteria reported to have the ability in degrading polypropylene from the environment (Auta et al. 2017, 2018). Although the research did mention bacteria species able to degrade polypropylene, no enzyme was identified with respect to the degradation mechanism (Chandra et al. 2020; Ganesh Kumar et al. 2020). Even though there is no clear explanation related to the enzyme and its mechanism in polypropylene degradation, the polypropylene degradation facilitated by the enzyme is proved in 2019, but the actual enzyme and its characteristic are never mentioned (Pires et al. 2019). Compared to other microplastics, information on polypropylene degradation and removal is still lacking. Through various sources of literature search, only three bacteria species were said to be able to degrade polypropylene from the environment. In the authors' opinion, the lack of information in microorganisms degrading polypropylene is due to the resilient characteristic showed by the polypropylene. The resilient characteristic might cause difficulty in the degradation process, with that, only certain microorganisms can show the ability in degrading polypropylene. Due to this, the research area for responsible enzymes from microorganisms that can degrade polypropylene from the environment is something that can be looked at in-depth in the future.

### Polyvinyl chloride degrading enzyme

Polyvinyl-based microplastic consists of vinyl backbone polymer. The repetition of vinyl (ethenyls) monomers in the formation of polymer chains consist of variation in its branch that represents the uniqueness of polyvinyl-integrated β-diketonebased polymer. The incorporation of chlorine in its branch is known as polyvinyl chloride (PVC), as one of the most plastic produced in the industry. Changing in branch molecules will give different properties of the polyvinyl polymer, e.g. incorporation of acetate will give plastic material named polyvinyl acetate/polyvinyl alcohol (PVA). When a butyral molecule is added to the branch, it is known as polyvinyl butyral (PVB) (Akovali 2012). PVC toxicity is well reported in numerous sources including scientific articles and mainstream articles. PVC is known to cause angiosarcoma in the human liver, other than that PVC also proved in targeting lung, brain and lymphohematopoietic function (Wagoner 1983). As years passed and awareness related to PVC toxicity increased, PVA was introduced to the industry as an alternative plastic replacing PVC or as an additive to PVC, mainly to increase the hydrophilicity of PVC (Cai et al. 2020a). PVA is said to be less toxic compared to PVC. PVA toxicity is very low even if orally administered, PVA also showed poorly absorbed by the gastrointestinal tract (DeMerlis and Schoneker 2003).

Oxidases are a group of enzymes involved in catalyzing the oxidation of C–N and C–O bonds in the presence of the oxygen molecule. Three major principal substrate classes for oxidase enzymes are amino acids, amines, and alcohols. The end product for amino acids and amines is imine, while alcohol end product will be ketones and aldehydes (Turner 2012). One of the oxidase enzymes reported in PVA degradation is PVA oxidase which present in Gram-negative bacteria, *Pseudomonas* sp. including *Pseudomonas* sp. O-3, *P. vesicularis* PD and *Pseudomonas* sp. VM15C (Wilkes and Aristilde 2017). PVA oxidase activity is mentioned to correlate with PVA dehydrogenase enzyme. PVA oxidase oxidizes the PVA through its serine hydrolase active site. The mechanism is initiated by the product from PVA dehydrogenase reaction introducing β-diketone group into the PVA polymer molecule. Later, PVA oxidase hydrolyzes the integrated β-diketone group within the PVA molecule to produce PVA monomer (Shimao et al. 2000).

However, data on PVC degradation by enzymes are still scarce. A review article released in 2020 by Ru et al. and his colleagues concluded that no scientific report mentioned the ability of biological components in degrading PVC (Ru et al. 2020). However, when searching through wider sources of

publications, we found that (to the very best that we can do) few articles report the ability of fungi in degrading PVC (Ali et al. 2014a,b; Sumathi et al. 2016). These articles were later reviewed in 2019 (Glaser 2019). Even though these reports claimed to succeed in isolating fungi that may be beneficial in degrading PVC, detail mechanisms, especially enzyme/s involved in the reaction and fate of the PVC monomer were never mentioned in detail. In the same review article, it is mentioned that the recalcitrant feature showed by PVC can be the major factor for PVC to be resistant to biodegradation process (Glaser 2019). Thus, this leaves a research gap that is worth paying attention to the scientist. Research specifically on the microorganism degrading PVC is a potential area in the future and can be beneficial in microplastics treatment.

## Conclusion

As reviewed above, microplastics are categorized based on their monomer types. The enzymes responsible for their degradation from microorganisms were mentioned and discussed for their mechanism in this review based on previously published articles. Several conclusions can be extracted from this review and mentioned below.

(a) PE can be grouped into two major groups: LDPE and HDPE. With the most widespread pollution in the environment, PE has attracted the interest of researchers trying to understand degradation mechanisms through enzymes. Laccase, alkane hydrolase, manganese peroxidase, and soybean peroxidase were the enzymes reported to be responsible for PE degradation in the environment.
(b) The presence of PET in the environment is mostly from the leachate of plastic bottles. Two types of enzymes were closely related to the degradation of PET. PETase and MHETase work continuously after one another. PETase breaks the PET polymer into MHET. MHETase uptakes MHET and converts it into TPA and ethylene glycol. Nonetheless, the mechanism of PETase and MHETase is well understood. The existence of other enzymes that can degrade PET, such as lipase and esterase, remains unclear.
(c) Polystyrene is mainly used in food packaging industries. The degradation of polystyrene has been widely explored. Numerous organisms have been reported to degrade this pollutant. A series of enzymes (styrene monooxygenase, styrene oxide isomerase, phenylacetaldehyde dehydrogenase, and phenylacetyl coenzyme A ligase) were reported to be associated with polystyrene degradation, with acetyl-CoA as a final monomer that is utilized in the TCA cycle. Another enzyme that can degrade polystyrene is serine hydrolase, with little knowledge known about the mechanism.
(d) PP is a low-density plastic that is commonly found in cosmetics and personal care products. Numerous microorganisms are claimed to be able to degrade PP. With numerous reports related to the microorganism's degradation, there are no data on the enzyme-based mechanism.
(e) PVC is categorized under the thermoplastic group. PVC degradation data is considered to be the scarcest among those mentioned above, with fungi as a sole microorganism reported to be able in degrading PVC. In addition, the enzyme that is responsible for PVC degradation has not been mentioned (until this article was written).

Although some microplastics (PE, PET and PS) degradation by enzyme was fully understood, the information on other microplastics (PP and PVC) degradation through enzyme reaction is still unexplored. Therefore, further effort to understand the enzyme-based degradation of these microplastics is needed, such as those listed below:

(a) The purification and identification of enzymes responsible for PP and PVC degradation.
(b) Mechanism elucidation of each enzyme that has been reported to degrade microplastics.
(c) Enhancing the performance of the identified enzymes through various advanced engineering approaches.

Based on the important points aforementioned in this review, understanding the enzymatic reaction plays great importance in microplastics degradation. Enzyme identification and elucidating the mechanism are challenging, current advancement in protein analysis through proteomic approach can be the potential technique in solving this obstacle. If we manage to address these issues, we can provide a novel finding in this research area and a sustainable solution for the current pollution issue.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

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