Review Paper

Microbial degradation of polyethylene terephthalate: a systematic review

Cesar David Benavides Fernández[1] · Michelly Paola Guzmán Castillo[1] · Silvia Andrea Quijano Pérez[1] · Lida Vivian Carvajal Rodríguez[1]

Received: 11 January 2022 / Accepted: 25 August 2022
Published online: 08 September 2022

Abstract
Plastic pollution levels have increased rapidly in recent years, due to the accumulation of plastic waste, including polyethylene terephthalate (PET). Both high production and the lack of efficient methods for disposal and recycling affect diverse aquatic and terrestrial ecosystems owing to the high accumulation rates of plastics. Traditional chemical and physical degradation techniques have caused adverse effects on the environment; hence, the use of microorganisms for plastic degradation has gained importance recently. This systematic review was conducted for evaluating the reported findings about PET degradation by wild and genetically modified microorganisms to make them available for future work and to contribute to the eventual implementation of an alternative, an effective, and environmentally friendly method for the management of plastic waste such as PET. Both wild and genetically modified microorganisms with the metabolic potential to degrade this polymer were identified, in addition to the enzymes and genes used for genetic modification. The most prevalent wild-type PET-degrading microorganisms were bacteria (56.3%, 36 genera), followed by fungi (32.4%, 30 genera), microalgae (1.4%; 1 genus, namely *Spirulina* sp.), and invertebrate associated microbiota (2.8%). Among fungi and bacteria, the most prevalent genera were *Aspergillus* sp. and *Bacillus* sp., respectively. About genetically modified microorganisms, 50 strains of *Escherichia coli*, most of them expressing PETase enzyme, have been used. We emphasize the pressing need for implementing biological techniques for PET waste management on a commercial scale, using consortia of microorganisms. We present this work in five sections: an Introduction that highlights the importance of PET biodegradation as an effective and sustainable alternative, a section on Materials and methods that summarizes how the search for articles and manuscripts in different databases was done, and another Results section where we present the works found on the subject, a final part of Discussion and analysis of the literature found and finally we present a Conclusion and prospects.

Keywords Bioremediation · Plastics · PET · Hydrolysis · Degradation · Microorganisms

1 Article Highlights

- Many soil microorganisms can degrade PET; *Bacillus* sp., *Aspergillus* sp., and *Spirulina* sp. have demonstrated their biodegradation potential.
- PET-degrading fungi and bacteria possess enzymes such as PETase, which are hydrolases that cleave ester bonds.
- The biodegradation of PET is a slow process that leads to the use of pretreatments to increase its efficiency

✉ Lida Vivian Carvajal Rodríguez, lvivian3@gmail.com; lida.carvajal01@usc.edu.co; Cesar David Benavides Fernández, cesar2015fern@gmail.com; Michelly Paola Guzmán Castillo, plguzman4@gmail.com; Silvia Andrea Quijano Pérez, silvia.quijano00@usc.edu.co | [1]Department of Microbiology, Universidad Santiago de Cali, Cali, Valle del Cauca, Colombia.

percentage, the most used techniques for its study are Fourier-transform infrared spectroscopy (FTIR) and Scanning electron microscopy (SEM).

2 Introduction

Excessive use of plastic has had devastating effects on the environment, causing major damage to ecosystems [1, 2]. The annual environmental report on plastic pollution issued by the United Nations in 2019 has revealed extremely high amounts of this polymer on the planet, with approximately 13 million tons of plastic entering the oceans annually [3]. If this trend continues, it is expected that 26 billion tons of plastic waste will be generated and 12 billion tons will be accumulated in diverse ecosystems by 2050 [3, 4]. Of the total plastic waste, around 9% is recycled, 12% is incinerated, and 79% is disposed of in the environment [4, 5].

Polyethylene terephthalate (PET) is one of the seven major types of plastics included in the Plastics Identification System [6]. It is a long-chain polymer molecule with aromatic polyester composed of comonomers and aliphatic monomers that are susceptible to hydrolysis [5, 7, 8]. This polymer is widely used to manufacture single-use disposable products, such as bottles, food containers, jars, and pillow stuffing; therefore, its production has been higher than that of the other plastic types [4, 5, 8].

Colombia, Mexico, Bolivia, Brazil, India, and the United States have implemented a series of physical and chemical methods to process PET, which have significantly reduced PET levels [9]. However, recycling, landfilling, and incineration have led to new problems due to the generation of toxic waste, which in turn affects living beings and causes a loss of ecosystems [10, 11]. These problems and the limitations of the mentioned techniques, increase the use of biological methods based on microorganisms capable of transforming this polymer into simpler forms [2, 12–14].

Biological methods harness the metabolic capabilities of some microorganisms that naturally use polymers, such as plastic, as a source of carbon [2, 9]. These methods also use genetically modified microorganisms, whose genome has been modified by genetic engineering to introduce new traits [5, 15–17]. Microbial enzymes, such as PET hydrolase (PETase), are important players in these biological techniques since they degrade PET through the hydrolysis of ester bonds, yielding simpler forms of the polymer [18, 19].

Considering the detrimental effects on the environment caused by the use of physical and chemical methods for plastic waste management, biological methods have emerged as the best option to mitigate plastic pollution. The alarming accumulation of plastic in ecosystems, as reported by major organizations around the world, is expected to increase unless decisions are made to reduce the use and production of plastics, especially PET, which is present in many single-use products. Therefore, this review aims to present the existing publications on wild and genetically modified microorganisms with the potential of degrading PET to make them available for future work and to contribute to the eventual implementation of an alternative, an effective, and environmentally friendly method for the management of plastic waste such as PET.

3 Materials and methods

A literature search about PET degradation worldwide was carried out. Articles published between 2004 and 2022 were retrieved from different databases. The exclusion criteria were reviews on the subject, articles lacking evidence of methods of degradation by microorganisms, and articles where the molecular structure of PET had been modified. The keywords "microorganism", "biodegradation", "PET," and "PET hydrolase" and their combinations were used in English and Spanish. In addition, Boolean operators such as "AND," "OR," and "NOT" and quotation marks were used.

4 Results

A total of 137 publications focusing on PET degradation by wild or genetically modified microorganisms were used for the analysis.

The reviewed studies provided data to differentiate between microorganisms with a natural capability of degrading PET and those that were genetically modified. Among the publications analyzed, 51.8% (71 articles) used wild microorganisms (Table 1), 32.8% (45 articles) used genetically modified microorganisms (Table 3), 0.7% (1 article) used both types of microorganisms [20] and the remaining 14.6% (20 articles) corresponded to reviews (Fig. 1A). Furthermore, the articles that did not specify the genus or species but broadly refer to the group of bacteria [9, 21], actinomycetes [22], bacterial consortia [23], and/or fungal consortia [24] were also included.

4.1 Wild-type microorganisms that degrade PET

Among the publications that used wild-type PET-degrading microorganisms, 56.3% used bacteria [18, 36–38], 32.4% involved fungi [26, 31, 32, 35, 39], 7.0% both (bacteria and fungi) [40–42], 1.4% used microalgae [12] and the remaining 2.8% utilized the microbiota associated with invertebrates such as insects [43, 44] (Fig. 1B). Among the fungi, *Aspergillus* sp. was the

Table 1 Wild-type microorganisms with the ability to degrade PET, publications made in 2015 and 2019

Microorganism	Degradation percentage	Technique	References
Bacteria			
Ideonella sakaiensis	75% at 28 °C in 70 days	SEM	[25]
Bacillus subtilis	74.59–1.75% in a month	Weight loss	[13, 26]
	NA	IR	
		SEM	
Bacillus licheniformis	NA	FTIR	[27]
		SEM	
Streptococcus pyogenes	3.922–3.846% in a month	Weight loss	[26]
Thermobifida fusca	NA	HPLC	[29, 30]
Fungi			
Microsphaeropsis arundinis	3.0–2.0% in 14 days	SEM	[31]
Pleurotus ostreatus	13% In 45 days	Weight loss DSC	[32]
Penicillium sp.	NA	SEM	[33]
Mucor sp.	1.3% in 2 month	Physical changes	[34]
Aspergillus fumigatus	0.83% in 2 month		
Bipolaris sorokiniana	0.22% in 2 month		
Fusarium falciforme	NA	Physical changes	[35]
Aspergillus niger	52.94% in 1 month	Weight loss	[26]
Microalgae			
Spirulina sp.	48.61% in 112 days	FTIR, SEM, EDX	[12]

SEM Scanning electron microscopy, *FTIR* Fourier-transform infrared spectroscopy, *XRD* X-ray diffraction, *IR* Infra Red, *HPCL* High-performance liquid chromatography, *EDX* Energy dispersive X-ray spectroscopy, *DSC* Differential scanning calorimetry, *NA* not available

most frequently reported genus [14, 20, 21, 26, 34, 42]. Among the bacteria, *Bacillus* sp. was the most frequent genus [13, 27, 38, 45]. Finally, only one genus of microalgae, *Spirulina* sp., has been reported to date in an article published in Indonesia [12] (Fig. 1D).

Wild-type microorganisms capable of degrading PET were isolated mostly from soil (22.6%, forest soil) [5, 7, 36–38, 42, 45], followed by aquatic habitats (12.4%, salt and fresh water) [12, 46–49], from landfills (8.0%) [27, 33, 34, 40, 50] and 56.9% of the publications didn't specify (Fig. 1C). The first report on this topic was published in 2004 [21, 51], so the publications in this review cover the period from 2004 to 2022. The largest number of articles on the subject were published between 2015 and 2019, therefore, only the latter are shown in Table 1. On the other hand, some of the most recent publications are shown in Table 2, highlighting that 36 papers were published in 2021 of which most were reviews.

4.2 Microorganisms genetically modified for PET degradation

From the analysis, 32.8% of the publications (45/137 reviewed articles) used microorganisms that were genetically modified to enhance their PET degradation potential. As shown in Table 3, 50 strains of *Escherichia coli* were modified in studies from different countries, such as Germany, Austria, and Japan. In addition, the yeast species *Pichia pastoris* [54] and *Saccharomyces cerevisiae* [20], microalgae *Chlamydomonas reinhardtii* [16] and *Phaeodactylum tricornutum* [55], bacterial species *Bacillus subtilis* [53, 56] and *Clostridium thermocellum* [52] were also used as genetically modified microorganisms instead of *E. coli.*

4.3 Enzymes used to generate genetically modified microorganisms

The most widely used enzymes were PETase from *Ideonella sakaiensis* and other enzymes derived from it. The genes of these enzymes were introduced in the genome of others microorganisms [5, 16, 17, 53, 55–57, 65]. Furthermore, there were cutinase Thc_Cut1 from *Thermobifida cellulosilytica* and other recombinant enzymes derived from it, which were used to genetically modify microorganisms [61, 64]. In addition, cutinase TfCut2, whose *tfcut2* gene from *Thermobifida fusca* was introduced in seven microorganisms [28, 30, 52, 59, 29]. Figure 2 shows the frequency of use of all mentioned enzymes in the reviewed publications, classified according to their biological activity, i.e., esterases, cutinases, nonspecific hydrolases, and fungal hydrophobins.

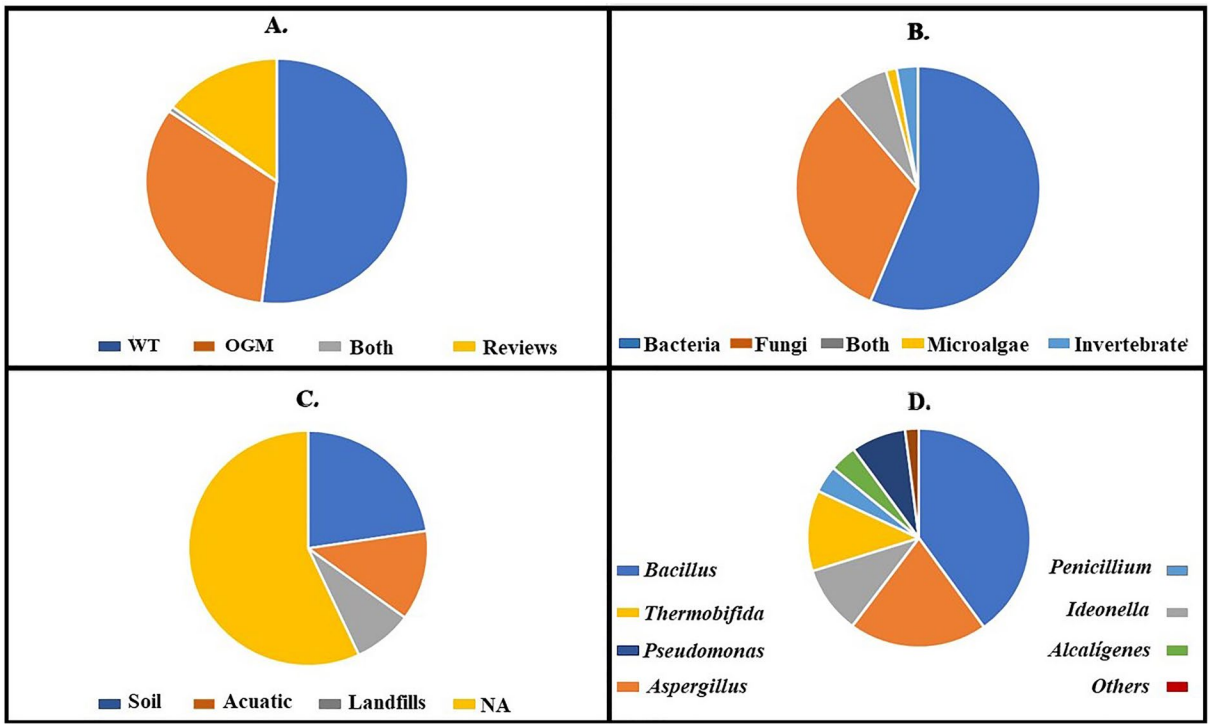

Fig. 1 Publications analyzed. **A** Percentage of publications that were used in their research: wild-type microorganisms (wt) (blue), genetically modified microorganisms (OGM) (orange), Both (wt and OGM) (grey), and those publications that were of the review type (yellow). **B** Percentage of publications that used wild microorganisms to degrade PET, some involved: bacteria (blue), fungi (orange), both (bacteria and fungi) (grey), microalgae (yellow), and microbiota associated with invertebrates (light blue). **C** Percentage of habitat type from which the wild PET-degrading microorganisms were isolated: soil (blue), water (orange), landfills (grey), and not specified in the publication (NA) (yellow). **D** Percentage of articles that used different genera of microorganisms in their research: *Bacillus* sp. (blue), *Aspergillus* sp. (orange), *Thermobifida* sp. (yellow), *Ideonella* sp. (grey), *Pseudomonas* sp. (dark blue), *Alcalígenes* sp. (green), *Penicillium* sp. (light blue), and Others genera (red) such as: *Spirulina* sp., *Streptococcus* sp., *Microsphaeropsis* sp., *Pleurotus* sp., *Mucor* sp., *Bipolaris* sp., *Fusarium* sp., *Clostridium* sp., *Hyphomonas* sp., *Alcanivorax* sp., *Halomonas* sp., *Rhizopus* sp., *Thioclava* sp

5 Discussion

5.1 Description of the literature

Few studies have been performed on PET degradation by microorganisms in comparison to those conducted on the biodegradation of other polymers, such as polyurethane, low-density polyethylene (LDPE), polyhydroxyalkanoates, or biodegradable plastics [66, 67]. The same is true when compared to the existing studies on plastic waste management in general [4, 68, 69]. Most studies on PET degradation have focused on proving the capability of some microorganisms to initiate polymer degradation by forming biofilms [70, 71]. Other published studies have focused on microbial consortia with the potential to degrade PET [25, 38, 42, 71], detecting modifications in functional groups of polymers during biodegradation for assessing the process efficiency [12, 38], identifying enzymes involved in PET degradation [25, 42, 72], intermediate hydrolysis products of PET degradation and its inhibition [28, 72], or interaction between marine microorganisms and PET microplastics [12]. In addition to research on wild microorganisms, a significant number of studies have focused on producing genetically modified microorganisms with increased potential for PET degradation. Genes encoding enzymes involved in the degradation process have been introduced and expressed mainly in *E.coli* [5, 17, 53, 57, 58, 60, 61, 63, 65, 73]. Several studies are conducted with these modified microorganisms to investigate the products or intermediate metabolites of PET degradation using recombinant enzymes [5, 8, 28, 74], and assess structural changes in enzymes to reduce their activation temperature or increase their degrading efficiency [15, 18, 56, 57, 59, 62, 75], search for amino acid sequence homology among different cutinases and compare their activity [20, 29], elucidate the thermodynamics and kinetics of the conformational and colloidal stability of a hydrolase [54], and express and measure the catalytic activity of a PETase in microalgae [16, 55].

Table 2 Some of the most recent publications reviewed

Microorganism	Degradation percentage	Technique	References
Alcanivorax, Hyphomonas, and Cycloclasticus	75% at 28 °C in 70 days	FTIR, SEM	[46]
Pseudomonas sp.	3% in 8 weeks	Weight loss, SEM	[38]
Bacillus sp.		ATR-FTIR	
Alcaligenes faecalis	15–21% in 10 weeks	Weight loss	[48]
		FTIR	
Clostridium thermocellum	60% in 14 days	SEM, HPLC	[52]
		SDS-PAGE	
Bacillus cereus	70–55% in 180 days	Weight loss, SEM–EDX	[36]
Bacillus subtilis		FTIR	
Bacillus subtilis ET18 Bacillus cereus ET30	NA	SEM	[45]
		Light microscope	
		SDS-PAGE	
Exiguobacterium sp. *Halomonas* sp. *Ochrobactrum* sp.	NA	SEM, FTIR	[47]
		XRD	
		HPLC–MS	
Thioclava sp. BHET1	NA	FTIR	[49]
Bacillus sp. BHET2			
Rhodotorula RHM1	NA	Enzymatic activities	[42]
Aspergillus RHM15			
Bacillus RBM2			
Bacillus pseudomycoides	> 65%	FTIR	[37]
Bacillus pumilus		HPLC	
Priestia aryabhattai			
Stenotrophomonas pavanii	91.4%	Weight loss	[15]
Comamonas thiooxydans			
Comamonas koreensis			
Fulvimonas soli			
Rhizopus oryzae	NA	FTIR	[39]
		SEM	

SEM Scanning Electron Microscopy, *FTIR* Fourier-Transform Infrared Spectroscopy, *XRD* X-ray Diffraction, *IR* InfraRed, *HPCL-MS* High-Performance Liquid Chromatography–mass spectrometry analysis, *EDX* Energy Dispersive X-ray analysis, *DSC* Differential Scanning Calorimetry, *ATR-FTIR* attenuated total reflectance-Fourier transform infrared spectroscopy, *NA* not available

5.2 Most common study techniques

All studies evaluated PET degradation through changes in the appearance or topology of the polymer surface, such as the occurrence of pores, cracks, and change in the color or crystallinity, using analytical techniques, such as electron microscopy and X-ray diffraction [14, 28, 63], through variations in polymer mass and weight [5, 69, 76], changes in PET atomic absorption spectra [50] detection of the appearance and disappearance of functional groups by Fourier-transform infrared spectroscopy (FTIR) [12, 38, 47, 63], colonization of the polymer surface by Scanning electron microscopy (SEM) [14, 16, 51, 63], or quantification of intermediate products of PET degradation, such as mono(2-hydroxyethyl) terephthalate (MHET), bis(2-hydroxyethyl) terephthalate (BHET), terephthalic acid (TPA), and ethylene glycol by high-performance liquid chromatography [16, 20, 61, 65].

SEM and FTIR are the most commonly used techniques in the determination of PET degradation. SEM images allow the study of cell division stages, individual colonization of microorganisms, and biofilm formation on a PET surface [25, 31, 33, 61, 62], a process that seemed to be a prerequisite for biodegradation and which indicates that microorganisms are able to utilize PET as a carbon source for their growth [25, 71, 77]. This result in several articles is confirmed by FTIR results showing the absorption spectra of the appearance or disappearance of functional oxidized groups during the biodegradation process of the polymers [58, 63]. SEM and FTIR are complementary techniques used in several papers that have shown a good approximation of the degree of degradation in synthetic polymers

Table 3 Genetically modified microorganisms for degradation of PET

Transformed microorganism (OGM)	Gene or enzyme	Donor microorganism	Degradation porcentage	Technique	References
Escherichia coli BL21	Cutinasa	*Moniliophthora roreri*	31%	Weight loss Titration assay, SEM	[5]
E. coli BL21 *Aspergillus niger*	PETasa	*Ideonella sakaiensis*	NA	SDS PAGE	[17]
Escherichia coli, Chlamydomonas reinhardtii	*Is*PETasa	*Idonella sakaiensis* NA	NA 35–17% In 4 weeks	HPLC	[16, 57]
Escherichia coli BL21-Gold	*pnbA*	*Bacillus subtilis*	NA	HPLC FTIR-ART	[58]
Escherichia coli BL21-(DE3)	TfH	*T. fusca*	12.9% ± 1.2%	Gravimetric Weight loss	[59]
Escherichia coli BL21-Gold	Thh_est	*Thermobifida halotolerans*	NA	SDS-PAGE	[60]
Escherichia coli BL21 Gold	Thc_Cut1	*Thermobifida cellulosilytica*	0,36%	HPLC SDS-PAGE SEM	[61]
Escherichia coli	Cut190	*Saccharomonospora viridis*	34–25% at 70 °C	SEM HPLC	[62]
Escherichia coli BL21 (DE3)	*tfcut2*	*Thermobifida fusca*	NA	RP-HPLC	[28]
Escherichia coli BL21 (DE3)	*cut5a*	*Fusarium oxysporum*	NA	FTIR-ATR SEM XPS	[63]
Escherichia coli BL21-DE3	Thc_Cut1_hfb7 Thc_Cut_hfb9b	*Thermobifida Cellulosilytica* and *Trichoderma harzianum*	NA	SDS-PAGE	[64]
Escherichia coli TOP 10	Tcur1278 Tcur0390	*T. curvata*	NA	NA	[30]

HPCL High-performance liquid chromatography, *FTIR* Fourier-transform infrared spectroscopy, *SDS-PAGE* Sodium dodecyl sulfate polyacrylamide gel electrophoresis, *RP-HPCL* Reversed- phase high-performance liquid chromatography, *XPS* X-ray photoelectron spectroscopy, *SEM* Scanning electron microscopy, *NA* not available

if are used in combination to confirm the data [12, 27, 63]. These techniques are non-invasive and allow the study of a process as slow as PET biodegradation [78].

5.3 Percentage of PET degradation

PET degradation is a slow and difficult process that depends on the structure and quantity of the polymer as well as on the interactions between the environment and the degrading microorganisms [1, 79]. Studies measuring the degradation through polymer weight loss over 30 days, 6 weeks, 6 months, and up to 1 year have observed degradation values that did not exceed 45% [2, 14, 70, 80]. Based on the present literature review, one of the highest PET degradation yields was reported by Dang et al. [81], who observed a 43.05% decrease in the weight of particulate pretreated PET by the action of *Bacillus* sp. BCBT21. The only study that used PET microplastics and a protozoan, *Spirulina* sp., reported degradation of 48.61% [12], whereas another work on microorganisms isolated from a marine environment determined degradation of 22% and 35% by *Aspergillus* sp. and *Vibrio* sp., respectively [14]. Taniguchi et al. [25] observed a decrease of 75% in carbon, which was catabolized to CO_2, using a microbial consortium composed of bacteria, yeasts, and protozoa. These two characteristics, i.e., the low degradation rates and the long time involved, are the limiting factors that have led to increased use of genetically modified microorganisms or use pretreatments.

The presence of several amorphous regions in its structure makes PET one of the polymers that are the most susceptible to attack by microorganisms [29, 82]. Different pretreatments have been performed to favor the hydrolysis of ester bonds. Among them is the addition of functional groups, such as carbonyls, alcohols, phenols, and hydroxyls [69, 76], genetic engineering of microorganisms to increase the production of surfactants, favoring cell adhesion to the surface of materials [67, 77, 80, 83], or UV irradiation of PET to favor its colonization [27, 70, 82].

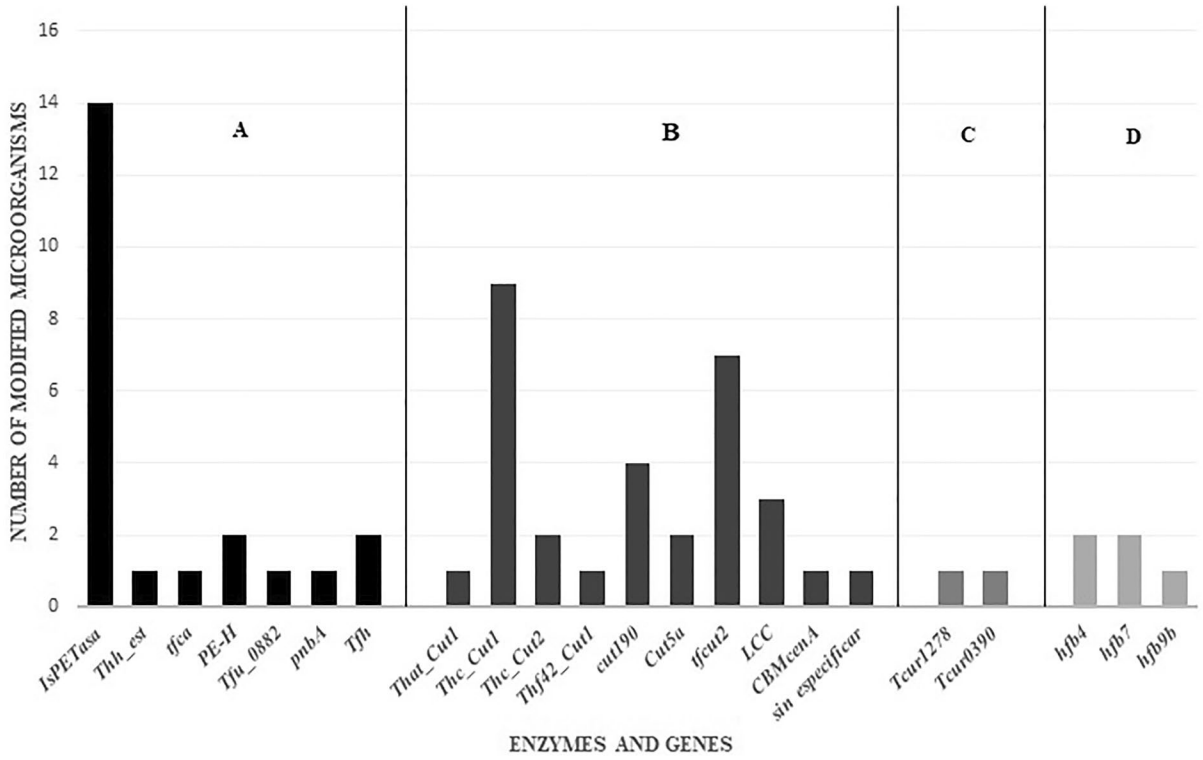

Fig. 2 Enzymes and genes used in the genetic manipulation of microorganisms to increase their capacity to degrade polyethylene terephthalate PET. **A** Esterases; **B** Cutinases; **C** Unspecified hydrolases; **D** Fungal hydrophobins

5.4 *Bacillus* sp. major PET degrader

The affinity of certain species of microorganisms for different types of polymers is evident. This review shows that species belonging to the genus *Bacillus* are able to degrade PET more efficiently than other microorganisms. *Bacillus cereus* and *Bacillus gottheilii* have been shown to adapt to other polymers, such as polyethylene (PE), polypropylene (PP), and polystyrene (PS) [76]. *Pseudomonas* sp. degraded LDPE [83, 84], *Aspergillus* sp. degraded LDPE and high-density polyethylene [85, 86], and *Acinetobacter* sp. was reported as a good polyurethane-degrading microorganism [76, 87]. Altogether, the results indicate that these microorganisms possess specific enzymatic mechanisms for the transformation of polymers into simpler forms [69, 76, 83]. The ability of *Bacillus* sp. to utilize these substrates as a source of carbon and energy is evinced in their adaptation to PET-contaminated environments [76, 88, 89], and it could have been favored by evolutionary strategies specific to this genus, the so-called "*Bacillus lifestyle*". Zeigler and Nicholson [90] have stated that "organisms with the *Bacillus* lifestyle have not only survived but also thrived on the Earth—and perhaps beyond" [90]. Among the *Bacillus*-specific characteristics are their ability to form endospores [90, 91], persistence and ability to colonize surfaces through the formation of multicellular communities, such as biofilms and swarming [92, 93], and ability to produce surfactants such as surfactin [79, 80], and peculiar cell wall structure [70, 94, 95]. Endospore and biofilm formation are evolutionarily ancient strategies found in several species of bacteria and archaea that allow them to survive in low-nutrient environments such as the surface of polymers like PET [89–91]. The mechanism of endospore formation, production of exopolysaccharides (EPS) for biofilm formation, and production of biosurfactants are finely regulated in *Bacillus* sp. by two-component signal transduction systems (TCSs). TCSs consist of 36 histidine kinase (HK) sensor proteins and 35 response regulators (HK/RR) [88, 89] are activated during the stationary phase of growth and sense various physical and chemical stimuli from the environment [96, 97]. *B. subtilis* harbors at least three coupled HK/RR systems that control the expression of genes involved in the competition, synthesis of degrading enzymes, and endospore formation called ComP/ComA, DegS/DegU. and Spo0F/Spo0B/Spo0A, respectively [89, 98]. During the stationary phase of a *Bacillus* sp. culture, cell subpopulations able to import and export DNA from and into the medium are also generated [90, 99], leading to extensive taxonomic differentiation at the species (sp.) level in this bacterial genus. This could explain why several species of isolated microorganisms with the potential to degrade PET are not determined and reported in some publications,

appearing instead as *Bacillus* sp. BCBT21, *Bacillus* sp. AIIW2, or simply *Bacillus* sp. [42, 49, 81].

As previously mentioned, another evolutionary strategy of *Bacillus* sp. to adapt to hostile environments or to grow upon a limited carbon source is its relatively hydrophobic cell wall [70, 95], which is one of the key factors in the degradation of plastics in general [79, 83]. The cell wall composition of microorganisms is known to be directly involved in bioremediation processes by enabling cell adhesion to the surface of the material [67, 100]. Species of the genus *Bacillus*, in particular *Bacillus* sp. C.I.P. 76-1 11 and *B. subtilis*, have a distinctive structure that differs from that of other gram-positive bacteria. Their cell wall contains a high percentage of very long polysaccharides, other than peptidoglycan, which favors polymer hydrolysis [94, 95].

5.5 Enzymes that transform PET

Some authors state that polymer biodegradation is determined by the extracellular enzymes secreted by microorganisms and the amount of these secreted enzymes, rather than by the cell wall and the production of biosurfactants [77, 82]. Such enzymes act according to the surface properties of the polymer and lead to hydrolytic cleavage, breaking down the material into monomers, dimers, and oligomers that can then be used by the microorganisms as an energy source [69, 79, 86, 81]. In this review, numerous thermophilic and mesophilic microorganisms were found and some of them were isolated from compost, such as *I. sakaiensis*, *Bacillus* sp. BCBT21, *T. fusca*, and *Saccharomonospora viridis* AHK190 [25, 68, 81]. These microorganisms produced hydrolase-type enzymes, such as esterases, lipases, and cutinases, which oxidize PET ester bonds [1, 79, 83] at temperatures near 55 °C as *Bacillus* sp. BCBT21 167 or at 30 °C as the PETase from *I. sakaiensis* [2]. Other enzymes that also act at high temperatures are p-nitrobenzylesterase (BsEstB) from *B. subtilis* whose optimal temperature is 40 °C [58] and TfH from *T. fusca* whose activation temperature is 60 °C [73]. Therefore, in parallel with this work, cutinases were found to be the enzymes most widely used to modify microorganisms for enhancing their potential for PET degradation [5, 15, 19, 29, 73]. According to Taniguchi et al. [25], the mechanism of PET degradation into monomers involves the activity of PETase and a mono(2-hydroxyethyl) terephthalate hydrolase (MHETase), which has only been studied in *I. sakaiensis* to date [2, 72, 74].

5.6 Major habitat for PET degrading species

In terms of habitats, the soil was the most cited in the reviewed articles [5, 7, 36, 37, 42, 45]. The wide variety of microorganisms in the soil makes it an environment of high biodiversity; one gram of soil is estimated to harbor millions of culturable bacteria [7, 101]. These microorganisms participate in different processes such as nutrient cycling and production of metabolites that promote plant growth and soil mineralization [102], and soil fertility [101, 103]. Microorganisms are responsible for the high rates of metabolic activity observed in soil [104]. Among soil microorganisms, bacteria stand out, being one of the largest groups including a large number of species, followed by actinomycetes, fungi, soil algae, and protozoa [101]. Hug et al. [105], in their approach to a new tree of life, showed that the domain Bacteria includes the largest number of described lineages (92 phyla), followed by the domain Archaea (23 phyla), and are a part of terrestrial habitats such as soil. The high diversity of bacterial species increases the probability of finding bacterial genera with the potential to degrade PET as evinced in this study [106]. Some researchers have reported that fungi possess a higher enzymatic potential to degrade plastics compared to that bacteria [39, 68]. Nevertheless, bacteria grow faster and have lower nutritional and environmental requirements than fungi and are therefore preferable for research.

Several microorganisms that compose the soil microbiome remain unknown [107]. Soils are exposed to numerous contaminants, mainly heavy metals, hydrocarbons and their derivatives, and plastic waste [108, 109]. Some microorganisms have adapted to these polluted environments and use those contaminants as a source of carbon and nitrogen for their survival [2, 9]. Bacterias have largely developed the ability to adapt to these habitats and diverse environmental conditions, showing, in some cases, changes in their structure as a survival strategy [110, 111].

In environments such as soil, PET degradation is favored by aerobic conditions that accelerate the oxidation of the polymeric molecule to form a polar complex of carbonyl groups and generate water and CO_2 as final products [66]. Plastic biodegradation in general can occur under both aerobic and anaerobic conditions, depending on the microorganism involved and the environmental conditions [11, 66].

Certain microorganisms with the potential to degrade PET have been isolated in the aquatic environment, including *Spirulina* sp., *Alcanivorax* sp., *Hyphomonas* sp., *Cycloclasticus* sp., *Alcaligenes faecalis*, *Exiguobacterium* sp., *Halomonas* sp., *Ochrobactrum* sp., *Vibrio* sp., *Thioclava* sp. [12, 46–49]. Although there are not many publications on microorganisms from this habitat, there is a microbiota to be explored.

6 Conclusion and perspectives

The present systematic review revealed that among wild microorganisms, bacterial and fungal genera such as *Bacillus* sp. and *Aspergillus* sp., showed the greatest enzymatic

potential for degrading PET. Further studies using these two microorganisms together are warranted to obtain increased polymer degradation rates. An alternative could be the use of compost where these two microorganisms, in association with others, might show enhanced degradation. Janczak et al. [7] showed the biodegradation capacity of rhizosphere microorganisms in the compost where a fungal strain (*Laccaria laccata*) and a bacterial strain (*Serratia plymuthica*) were able to degrade biodegradable polymers such as polylactic acid and conventional polymers such as PET.

Our review reveals that the world is working at an accelerated pace to address this issue by taking fundamental actions, banning single-use products at the national level, and creating public–private partnerships for waste management. Additionally, this work demonstrates the exceptional potential of microorganisms in substantially reducing PET emissions to the environment; therefore, we propose their use for the management of this type of waste. For example, composting plants enriched with microbial consortia having a high PET-degrading potential could be implemented through partnerships between government and private companies. In particular, different microalgae species should be included to exploit their high diversity in different countries. Furthermore, it is worth studying whether enzymes such as PETase or similar ones are present in other PET-degrading microorganisms, such as *Bacillus* sp. and *Aspergillus* sp., to confirm their involvement in the degradation process and to thoroughly elucidate the mechanism of PET degradation by microorganisms.

We believe that the benefits of using biological methods for the degradation of polymers such as PET should be further explored to replace the physical and chemical methods causing harmful effects on the environment.

Lastly, our goal with this literature review is to encourage scientific-based initiatives that promote the use of biological techniques on a commercial scale for the mitigation of the high rates of plastic pollution.

Acknowledgements This research was funded by Dirección General de Investigaciones of Universidad Santiago de Cali under call No. 01-2021. We are thankful to Universidad Santiago de Cali for the support provided through the research project 934-621119-436. We are also grateful to all our professors, friends, and family for their collaboration and encouragement.

Author contributions CDBF, MPGC, LVCR: Conceptualization, LVCR: Project administration, MPGC, CDBF: Formal analysis and investigation, CDBF, MPGC: Writing—original draft preparation, CDBF, LVCR: Visualization, SAQP, LVCR: Writing—review and editing, LVCR: final review.

Funding This research was funded by the Direccion General de Investigaciones of the Universidad Santiago de Cali. The role played by the latter was only to finance the research Project.

Data availability Data sharing is not applicable to this article, as no data sets were generated or analyzed during the present study. We used articles published in different databases (ScienceDirect, Springer Link, Scopus, Pubmed, Taylor and Francis Online, Wiley Online Library, and Scielo), that are referenced throughout the paper and appear in the bibliography of the paper.

Declarations

Conflict of interest The authors declare that they have no competing interests.

Ethical approval Not applicable.

Consent to participate Not applicable.

Consent for publication Not applicable.

References

1. Sangeetha Devi R, Rajesh Kannan V, Natarajan K, Nivas D, Kannan K, Chandru S, Robert Antony A (2015) The role of microbes in plastic degradation. In: Chandra R (ed) Environmental waste management, 1ra edn. CRC Press, Boca Raton, pp 341–370
2. Yoshida S, Hiraga K, Takehana T, Taniguchi I, Yamaji H, Maeda Y, Toyohara K, Miyamoto K, Kimura Y, Oda K (2016) A bacterium that degrades and assimilates poly(ethylene terephthalate). J Res Rep 351:1196–1199
3. ONU United Nations (2019) 10 UN cifras to show the damage plastics are doing to the planet. https://expansion.mx/vida-arte/2019/07/03/10-cifras-de-la-onu-para-mostrar-el-dano-que-los-plasticos-le-hacen-al-planeta. Accessed 9 June 2020 (In Spanish)
4. Geyer R, Jambeck JR, Law KL (2017) Production, use, and fate of all plastics ever made. Sci Adv 3:25–29. https://doi.org/10.1126/sciadv.1700782
5. Vázquez-Alcántara L, Oliart-Ros RM, García-Bórquez A, Peña-Montes C (2021) Expression of a cutinase of *Moniliophthora roreri* with polyester and PET-plastic residues degradation activity. Microbiol Spectr 9(3):e00976-e1021
6. Muñoz L (2012) Study of the use of Polyethylene terephthalate (PET) as a replacement material in soils with low load-bearing capacity. Dissertation, the National Autonomous University of Mexico (In Spanish)
7. Janczak K, Hrynkiewicz K, Znajewska Z, Dąbrowska G (2018) Use of rhizosphere microorganisms in the biodegradation of PLA and PET polymers in compost soil. Int Biodeterior Biodegrad 130:65–75. https://doi.org/10.1016/j.ibiod.2018.03.017

8. Venkatachalam S, Shilpa G, Jayprakash V, Prashant R, Krishna R, Anil K (2012) Degradation and recyclability of poly (ethylene terephthalate). Polyester. https://doi.org/10.5772/48612
9. Gómez J, Oliveros C (2016) Polyethylene terephthalate biodegradation by microorganisms isolated from sites of final disposal of solid waste, Tachira, Venezuel. Redieluz 6:57–62
10. Kang MJ, Yu HJ, Jegal J, Kim HS, Cha HG (2020) Depolymerization of PET into terephthalic acid in neutral media catalyzed by the ZSM-5 acidic catalyst. Chem Eng J 398:1–9. https://doi.org/10.1016/j.cej.2020.125655
11. Rodríguez DK, Silva J, Rueda JP, Guedes E (2020) A mini-review: current advances in polyethylene biodegradation. World J Microbiol Biotechnol 36:1–10. https://doi.org/10.1007/s11274-020-2808-5
12. Khoironii A, Anggoro S, Sudarno, (2019) Evaluation of the interaction among microalgae *Spirulina* sp. plastics polyethylene terephthalate and polypropylene in freshwater environment. J Ecol Eng 20:161–173. https://doi.org/10.12911/22998993/108637
13. Nakkabi A, Elmoualij N, Saad IK, Fahim MF (2015) Biodegradation of poly (ethylene terephthalate) by *Bacillus Subtilis*. Int J Recent Adv Multidiscip Res 2:1060–1062
14. Sarkhel R, Sengupta S, Das P, Bhowal A (2020) Comparative biodegradation study of polymer from plastic bottle waste using novel isolated bacteria and fungi from marine source. J Polym Res 27:1–8. https://doi.org/10.1007/s10965-019-1973-4
15. Huang QS, Yan ZF, Chen XQ, Du YY, Li J, Liu ZZ et al (2022) Accelerated biodegradation of polyethylene terephthalate by *Thermobifida fusca* cutinase mediated by *Stenotrophomonas pavanii*. Sci Total Environ 808:152107
16. Kim JW, Park SB, Tran QG, Cho DH, Choi DY, Lee YJ, Kim HS (2020) Functional expression of polyethylene terephthalate-degrading enzyme (PETase) in green microalgae. Microb Cell Fact 19:1–9. https://doi.org/10.1186/s12934-020-01355-8
17. Sánchez Bermúdez JC (2021) Construcción de los plásmidos pIN-PETasa, pET-PETasa, pGLAam7-PETasa para la expresión de la PETasa de *Ideonella sakaiensis* en *Escherichia coli* y *Aspergillus niger*, para la degradación de PET (politereftalato de etileno) (Master's thesis, Tesis (MC)—Centro de Investigación y de Estudios Avanzados del IPN Departamento de Biotecnología y Bioingeniería), México D.F.
18. Boneta S, Arafet K, Moliner V (2021) QM/MM study of the enzymatic biodegradation mechanism of polyethylene terephthalate. J Chem Inf Model 61(6):3041–3051
19. Gao R, Pan H, Lian J (2021) Recent advances in the discovery, characterization, and engineering of poly (ethylene terephthalate)(PET) hydrolases. Enzyme Microb Technol 150:109868
20. Heumann S, Eberl A, Pobeheim H, Liebminger S, Fischer-Colbrie G, Almansa E, Cavaco-Paulo A, Gübitz GM (2006) New model substrates for enzymes hydrolysing polyethyleneterephthalate and polyamide fibres. J Biochem Biophys Methods 69:89–99. https://doi.org/10.1016/j.jbbm.2006.02.005
21. Fischer-Colbrie G, Heumann S, Liebminger S, Almansa E, Cavaco-Paulo A, Guebitz GM (2004) New enzymes with potential for PET surface modification. Biocatal Biotransform 22:341–346. https://doi.org/10.1080/10242420400024565
22. Diaz R (2016) Textile microbiology. Biocatalytic modification of polyester. Dissertation, Higher School of Textile Engineering (In Spanish)
23. Shabbir S, Faheem M, Ali N, Kerr PG, Wang LF, Kuppusamy S, Li Y (2020) Periphytic biofilm: an innovative approach for biodegradation of microplastics. Sci Total Environ 717:1–13. https://doi.org/10.1016/j.scitotenv.2020.137064
24. Gutierrez J, Flores L, Villagomez J (2018) Study of PET degradation by fungal consortia. Young People Sci 4:941–946 (**In Spanish**)
25. Taniguchi I, Yoshida S, Hiraga K, Miyamoto K, Kimura Y, Oda K (2019) Biodegradation of PET: current status and application aspects. ACS Catal 9:4089–4105. https://doi.org/10.1021/acscatal.8b05171
26. Asmita K, Shubhamsingh T, Tejashree S (2015) Isolation of plastic degrading micro-organisms from soil samples collected at various locations in Mumbai, India. Int Res J Environ Sci 4(3):77–85
27. Markandan M, Umamaheswari S, Anuradha S (2019) Bacterial (*Bacillus licheniformis*) biodegradation of UV exposed PET (polyethylene terephthalate). Int J Recent Sci Res 10:34310–34314. https://doi.org/10.24327/ijrsr.2019.1008.3866
28. Barth M, Oeser T, Wei R, Then J, Schmidt J, Zimmermann W (2015) Effect of hydrolysis products on the enzymatic degradation of polyethylene terephthalate nanoparticles by a polyester hydrolase from *Thermobifida fusca*. Biochem Eng J 93:222–228. https://doi.org/10.1016/j.bej.2014.10.012
29. Wei R, Oeser T, Schmidt J, Meier R, Barth M, Then J, Zimmermann W (2016) Engineered bacterial polyester hydrolases efficiently degrade polyethylene terephthalate due to relieved product inhibition. Biotechnol Bioeng 113:1658–1665. https://doi.org/10.1002/bit.25941
30. Wei R, Oeser T, Then J, Kühn N, Barth M, Schmidt J, Zimmermann W (2014) Functional characterization and structural modeling of synthetic polyester-degrading hydrolases from *Thermomonospora curvata*. AMB Express 4:1–10. https://doi.org/10.1186/s13568-014-0044-9
31. Malafatti-Picca L, de Barros Chaves MR, de Castro AM, Valoni É, de Oliveira VM, Marsaioli AJ, De Angelis D, Attili-Angelis D (2019) Hydrocarbon-associated substrates reveal promising fungi for poly (ethylene terephthalate) (PET) depolymerization. Braz J Microbiol 50:633–648. https://doi.org/10.1007/s42770-019-00093-3
32. de Faria PC, Wisbeck E, Dias LP (2015) Biodegradation of recycled polypropylene (ppr) and poly (ethylene terephthalate) recycled (petr) by *Pleurotus ostreatus*. Materia J 20:452–459. https://doi.org/10.1590/s1517-707620150002.0045(InPortuguese)
33. Umamaheswari S, Murali M (2015) Potential of soil fungi (*Penicillium* sp.), to form biofilm on polyethylene terephthalate surface. J Pure Appl Microbiol 9:1–9
34. Iparraguirre K, Vivanco M (2015) Isolation and characterization of biodegradable filamentous fungi made of Terephthalate polyethylene and low-density polyethylene. Dissertation, National University San Luis de ICA (In Spanish)
35. Sooksai T, Bankeeree W, Sangwatanaroj U, Lotrakul P, Punnapayak H, Prasongsuk S (2019) Production of cutinase from *Fusarium falciforme* and its application for hydrophilicity improvement of polyethylene terephthalate fabric. 3 Biotech 9:1–11. https://doi.org/10.1007/s13205-019-1931-1
36. Dąbrowska GB, Janczak K, Richert A (2021) Combined use of *Bacillus* strains and *Miscanthus* for accelerating biodegradation of poly (lactic acid) and poly (ethylene terephthalate). PeerJ 9:e10957
37. Dhaka V, Singh S, Ramamurthy PC, Samuel J, Swamy Sunil Kumar Naik T, Khasnabis S et al (2022) Biological degradation of polyethylene terephthalate by rhizobacteria. Environ Sci Pollut Res. https://doi.org/10.1007/s11356-022-20324-9
38. Roberts C, Edwards S, Vague M, León-Zayas R, Scheffer H, Chan G, Swartz NA, Mellies JL (2020) Environmental consortium containing *Pseudomonas* and *Bacillus* species synergistically degrade polyethylene terephthalate plastic. mSphere 5(6):e01151-e1220. https://doi.org/10.1128/mSphere.01151-20
39. Seenivasagan R, Karthika A, Poonkuzhali K (2022) In vitro and silico study of the efficacy of fungi in low-density polyethylene

degradation in a disposal paper cup. Water Air Soil Pollut 233(3):1–12
40. Avendaño Toledo CA, Castro Velazco AM (2020) Determinación del pretratamiento más efectivo sobre el polietileno tereftalato para el aumento en la eficiencia del proceso de degradación realizado por hongos y bacterias autóctonas de lixiviado de relleno sanitario. Universidad Libre, Socorro Santander
41. Bermúdez Morera, D. C. (2021). Evaluación de microorganismos (*Trichoderma* spp y *Pseudomonas* aeruginosa) para la degradación del PET (Bachelor's thesis, Fundación Universidad de América)
42. Salinas J, Martínez-Gallardo MR, López-González JA, Jurado MM, Suárez-Estrella F, Lopez MJ (2021) Screening and selection of microorganisms for oil-based plastics biodegradation. Department of Biology and Geology, University of Almeria, Spain
43. Ali SS, Elsamahy T, Koutra E, Kornaros M, El-Sheekh M, Abdelkarim EA et al (2021) Degradation of conventional plastic wastes in the environment: a review on current status of knowledge and future perspectives of disposal. Sci Total Environ 771:144719
44. Arribas Arias H (2021) Microorganismos de la plastisfera y la biodegradación del plástico por la microbiota digestiva de diferentes insectos. Universidad de Salamanaca, España, Facultad de Biología
45. Demirkan E, Güler BE, Sevgi T (2020) Analysis by scanning electron microscopy of polyethylene terephthalate and nylon biodegradation abilities of *Bacillus* sp. strains isolated from soil. J Biol Environ Sci 14(42):107–114
46. Denaro R, Aulenta F, Crisafi F, Di Pippo F, Viggi CC, Matturro B et al (2020) Marine hydrocarbon-degrading bacteria breakdown poly (ethylene terephthalate) (PET). Sci Total Environ 749:141608
47. Gao R, Sun C (2021) A marine bacterial community capable of degrading poly(ethylene terephthalate) and polyethylene. J Hazard Mater. https://doi.org/10.1016/j.jhazmat.2021.125928
48. Nag M, Lahiri D, Dutta B, Jadav G, Ray RR (2021) Biodegradation of used polyethylene bags by a new marine strain of *Alcaligenes faecalis* LNDR-1. Environ Sci Pollut Res 28(30):41365–41379
49. Wright RJ, Bosch R, Langille MG, Gibson MI, Christie-Oleza JA (2021) A multi-OMIC characterization of biodegradation and microbial community succession within the PET plastisphere. Microbiome 9(1):1–22
50. Nowak B, Pajak J, Labuzek S, Rymarz G, Talik E (2011) Biodegradation of poly(ethylene terephthalate) modified with a polyester "Bionolle Ò" by *Penicillium funiculosum*. Polymer 56:35–44
51. Zhang J, Wang X, Gong J, Gu Z (2004) A study on the biodegradability of polyethylene terephthalate fiber and diethylene glycol terephthalate. J Appl Polym Sci 93:1089–1096. https://doi.org/10.1002/app.20556
52. Yan F, Wei R, Cui Q, Bornscheuer UT, Liu YJ (2021) Thermophilic whole-cell degradation of polyethylene terephthalate using engineered *Clostridium thermocellum*. Microb Biotechnol 14(2):374–385
53. Huang X, Cao L, Qin Z, Li S, Kong W, Liu Y (2018) Tat-Independent secretion of polyethylene terephthalate hydrolase PETase in *Bacillus subtilis* 168 mediated by its native signal peptide. J Agric Food Chem 66:13217–13227. https://doi.org/10.1021/acs.jafc.8b05038
54. Shirke AN, White C, Englaender JA, Zwarycz A, Butterfoss GL, Linhardt RJ, Gross RA (2018) Stabilizing leaf and branch compost cutinase (LCC) with glycosylation: mechanism and effect on PET hydrolysis. Biochemistry 57:1190–1200. https://doi.org/10.1021/acs.biochem.7b01189
55. Moog D, Schmitt J, Senger J, Zarzycki J, Rexer KH, Linne U, Erb T, Maier UG (2019) Using a marine microalga as a chassis for polyethylene terephthalate (PET) degradation. Microb Cell Fact 18:1–15. https://doi.org/10.1186/s12934-019-1220-z
56. Wang N, Guan F, Lv X, Han D, Zhang Y, Wu N, Xia X, Tian J (2020) Enhancing secretion of polyethylene terephthalate hydrolase PETase in *Bacillus subtilis* WB600 mediated by the SPamy signal peptide. Lett Appl Microbiol 71:235–241. https://doi.org/10.1111/lam.13312
57. Seo H, Kim S, Son HF, Sagong HY, Joo S, Kim KJ (2019) Production of extracellular PETase from *Ideonella sakaiensis* using sec-dependent signal peptides in *E. coli*. Biochem Biophys Res Commun 508:250–255. https://doi.org/10.1016/j.bbrc.2018.11.087
58. Ribitsch D, Heumann S, Trotscha E, Herrero Acero E, Greimel K, Leber R, Birner-Gruenberger R, Deller S, Eiteljoerg I, Remier P, Weber T, Siegert P, Maurer KH, Donelli I, Freddi G, Schwab H, Guebitz GM (2011) Hydrolysis of polyethyleneterephthalate by p-nitrobenzylesterase from *Bacillus subtilis*. Biotechnol Prog 27:951–960. https://doi.org/10.1002/btpr.610
59. Then J, Wei R, Oeser T, Barth M, Belisário-Ferrari MR, Schmidt J, Zimmermann W (2015) Ca^{2+} and Mg^{2+} binding site engineering increases the degradation of polyethylene terephthalate films by polyester hydrolases from *Thermobifida fusca*. Biotechnol J 10:592–598. https://doi.org/10.1002/biot.201400620
60. Ribitsch D, Acero EH, Greimel K, Eiteljoerg I, Trotscha E, Freddi G, Schwab H, Guebitz GM (2012) Characterization of a new cutinase from *Thermobifida alba* for PET-surface hydrolysis. Biocatal Biotransform 30:2–9. https://doi.org/10.3109/10242422.2012.644435
61. Gamerith C, Gajda M, Ortner A, Herrero Acero E, Guebitz GM, Ulbricht M (2017) Enzymatic hydrolysis of poly(ethyleneterephthalate) used for and analysed by pore modification of track-etched membranes. New Biotechnol 39:42–50. https://doi.org/10.1016/j.nbt.2017.06.007
62. Oda M, Yamagami Y, Inaba S, Oida T, Yamamoto M, Kitajima S, Kawai F (2018) Enzymatic hydrolysis of PET: functional roles of three Ca^{2+} ions bound to a cutinase-like enzyme, Cut190*, and its engineering for improved activity. Appl Microbiol Biotechnol 102:10067–10077. https://doi.org/10.1007/s00253-018-9374-x
63. Kanelli M, Vasilakos S, Nikolaivits E, Ladas S, Christakopoulos P, Topakas E (2015) Surface modification of poly(ethylene terephthalate) (PET) fibers by a cutinase from *Fusarium oxysporum*. Process Biochem 50:1885–1892. https://doi.org/10.1016/j.procbio.2015.08.013
64. Ribitsch D, Acero EH, Przylucka A, Zitzenbacher S, Marold A, Gamerith C, Tscheließhing R, Jungbauer A, Rennhofer H, Lichtenegger H, Amenitsch H, Bonazza K, Kubicek C, Druzhinina I, Guebitz GM (2015) Enhanced cutinase-catalyzed hydrolysis of polyethylene terephthalate by covalent fusion to hydrophobins. Appl Environ Microbiol 81:3586–3592. https://doi.org/10.1128/AEM.04111-14
65. Chen Z, Wang Y, Cheng Y, Wang X, Tong S, Yang H, Wang Z (2020) Efficient biodegradation of highly crystallized polyethylene terephthalate through cell surface display of bacterial PETase. Sci Total Environ 709:1–9. https://doi.org/10.1016/j.scitotenv.2019.136138
66. Sangale MK (2012) A review on biodegradation of polythene: the microbial approach. J Biorem Biodegrad 3:1–9. https://doi.org/10.4172/2155-6199.1000164
67. Sangeetha Devi R, Rajesh Kannan V, Nivas D, Kannan K, Chandru S, Robert Antony A (2015) Biodegradation of HDPE by *Aspergillus* spp. from the marine ecosystem of Gulf of Mannar. India Marine Pollut Bull 96:32–40. https://doi.org/10.1016/j.marpolbul.2015.05.050

68. Bhardwaj H, Gupta R, Tiwari A (2012) Microbial population associated with plastic degradation. Open Acess Sci Rep 1:1–4. https://doi.org/10.4172/scientificreports.272
69. Lucas N, Bienaime C, Belloy C, Queneudec M, Silvestre F, Nava-Saucedo JE (2008) Polymer biodegradation: mechanisms and estimation techniques—a review. Chemosphere 73:429–442. https://doi.org/10.1016/j.chemosphere.2008.06.064
70. Arkatkar A, Juwarkar AA, Bhaduri S, Uppara PV, Doble M (2010) Growth of *Pseudomonas* and *Bacillus* biofilms on pretreated polypropylene surface. Int Biodeterior Biodegrad 64:530–536. https://doi.org/10.1016/j.ibiod.2010.06.002
71. Miao L, Yu Y, Adyel TM, Wang C, Liu Z, Liu S, Huang L, You G, Meng M, Qu H, Hou J (2021) Distinct microbial metabolic activities of biofilms colonizing microplastics in three freshwater ecosystems. J Hazard Mater 403:1–40. https://doi.org/10.1016/j.jhazmat.2020.123577
72. Yoshida S, Hiraga K, Taniguchi I, Oda K (2021) *Ideonella sakaiensis*, PETase, and MHETase: from identification of microbial PET degradation to enzyme characterization. Methods Enzymol 648:187–205
73. Müller RJ, Schrader H, Profe J, Dresler K, Deckwer WD (2005) Enzymatic degradation of poly(ethylene terephthalate): rapid hydrolyse using a hydrolase from *T. fusca*. Macromol Rapid Commun 26:1400–1405. https://doi.org/10.1002/marc.200500410
74. Mathew JJ, Mathews AI, Sajeshkumar NK, Vazhacharickal PJ (2021) Microbial degradation of polyethylene terephthalate (PET): an outlook study. Journal of Medicinal Plants 9(5):31–40
75. Zhang Y, Wang L, Chen J, Wu J (2013) Enhanced activity toward PET by site-directed mutagenesis of *Thermobifida fusca* cutinase-CBM fusion protein. Carbohyd Polym 97(1):124–129. https://doi.org/10.1016/j.carbpol.2013.04.042
76. Auta HS, Emenike CU, Fauziah SH (2017) Screening of *Bacillus* strains isolated from mangrove ecosystems in Peninsular Malaysia for microplastic degradation. Environ Pollut 231:1552–1559. https://doi.org/10.1016/j.envpol.2017.09.043
77. Montazer Z, Habibi-Najafi MB, Mohebbi M, Oromiehei A (2018) Microbial degradation of UV-pretreated low-density polyethylene films by novel polyethylene-degrading bacteria isolated from plastic-dump soil. J Polym Environ 26:3613–3625. https://doi.org/10.1007/s10924-018-1245-0
78. Matjašič T, Simčič T, Medvešček N, Bajt O, Dreo T, Mori N (2021) Critical evaluation of biodegradation studies on synthetic plastics through a systematic literature review. Sci Total Environ 752:141959
79. Arkatkar A, Arutchelvi J, Sudhakar M, Bhaduri S, Uppara PV, Doble M (2009) Approaches to enhance the biodegradation of polyolefins. Open Environ Eng J 2:68–80. https://doi.org/10.2174/1874829500902010068
80. Vimala PP, Mathew L (2016) Biodegradation of polyethylene using *Bacillus subtilis*. Procedia Technol 24:232–239. https://doi.org/10.1016/j.protcy.2016.05.031
81. Dang TCH, Nguyen DT, Thai H, Nguyen TC, Hien Tran TT, Le VH, Nguyen HV, Tran XB, Nguyen TG, Thao T, Nguyen QT (2018) Plastic degradation by thermophilic *Bacillus* sp. BCBT21 isolated from composting agricultural residual in Vietnam. Adv Nat Sci 9:1–11. https://doi.org/10.1088/2043-6254/aaabaf
82. Restrepo-Flórez JM, Bassi A, Thompson MR (2014) Microbial degradation and deterioration of polyethylene—a review. Int Biodeterior Biodegrad 88:83–90. https://doi.org/10.1016/j.ibiod.2013.12.014
83. Wilkes R, Aristilde L (2017) Degradation and metabolism of synthetic plastics and associated products by *Pseudomonas* sp.: capabilities and challenges. J Appl Microbiol 3:582–593. https://doi.org/10.1111/jam.13472
84. Sharma A, Sharma A (2004) Degradation assessment of low-density polyethylene (LDP) and polythene (PP) by an indigenous isolate of *Pseudomonas stutzeri*. J Sci Ind Res 63:293–296
85. Aswale P, Ade A (2011) Polythene degradation potential of *Aspergillus niger*. In: Sayed IU (ed), Scholarly Articles in Botany. Pune
86. Usha R, Sangeetha T, Palaniswamy M (2011) Screening of polyethylene degrading microorganisms from garbage soil. Libyan Agric Res Cent J Int 2:200–204
87. Howard GT, Norton WN, Burks T (2012) Growth of *Acinetobacter gerneri* P7 on polyurethane and the purification and characterization of a polyurethanase enzyme. Biodegradation 23:561–573. https://doi.org/10.1007/s10532-011-9533-6
88. Galicia-Jiménez MM, López-Garrido SJ, Ávila-Serrano NY, Murialdo SE (2017) Component system: a molecular dialogue between ruminal bacteria and food particles (forage plants). Trop Subtrop Agroecosyst 20:413–418 (**In Spanish**)
89. Msadek T, Kunst F, Rapoport G (1995) A signal transduction network in *Bacillus subtilis* includes the DegS/DegU and ComP/ComA two-component systems. In: Hoch, Silvahy (eds) Two-component signal transduction. ASM Press, Washington, pp 447–471
90. Zeigler DR, Nicholson WL (2017) Experimental evolution of *Bacillus subtilis*. Environ Microbiol 19:3415–3422. https://doi.org/10.1111/1462-2920.13831
91. Ostrov I, Harel A, Bernstein S, Steinberg D, Shemesh M (2016) Development of a method to determine the effectiveness of cleaning agents in removal of biofilm derived spores in the milking system. Front Microbiol 7:1–9. https://doi.org/10.3389/fmicb.2016.01498
92. Oosthuizen MC, Steyn B, Theron J, Cosette P, Lindsay D, Von Holy A, Brözel VS (2002) Proteomic analysis reveals differential protein expression by *Bacillus cereus* during biofilm formation. Appl Environ Microbiol 68:2770–2780. https://doi.org/10.1128/AEM.68.6.2770-2780.2002
93. Ostrov I, Sela N, Belausov E, Steinberg D, Shemesh M (2019) Adaptation of *Bacillus* species to dairy-associated environment facilitates their biofilm-forming ability. Food Microbiol 82:316–324. https://doi.org/10.1016/j.fm.2019.02.015
94. Hayhurst EJ, Kailas L, Hobbs JK, Foster SJ (2008) Cell wall peptidoglycan architecture in *Bacillus subtilis*. PNAS 105:14603–14608
95. Leduc M, Rousseau M, Van Heijenoort J (1977) Structure of the cell wall of *Bacillus* Species C.I. p. 76–111. Eur J Biochem 80:153–163
96. Galperin MY (2005) A census of membrane-bound and intracellular signal transduction proteins in bacteria: bacterial IQ, extroverts and introverts. BMC Microbiol 5:1–19. https://doi.org/10.1186/1471-2180-5-35
97. Pelosi LA, Ohemeng KA, Barrett JF (2004) Bacterial signal transduction: two-component signal transduction as a model for therapeutic intervention. In: Fairweather I (ed) Cell signalling in prokaryotes and lower metazoa, 1ra edn. Springer, Cham, pp 347–402
98. Mäder U, Antelmann H, Buder T, Dahl MK, Hecker M, Homuth G (2002) *Bacillus subtilis* functional genomics: genome-wide analysis of the DegS-DegU regulon by transcriptomics and proteomics. Mol Genet Genom 268:455–467. https://doi.org/10.1007/s00438-002-0774-2
99. Norman TM, Lord ND, Paulsson J, Losick R (2015) Stochastic switching of cell fate in microbes. Annu Rev Microbiol 69:381–403. https://doi.org/10.1146/annurev-micro-091213-112852
100. Perpetuo EA, Souza CB, Oller Nascimento CA (2011) Engineering bacteria for bioremediation. In: Carpi A (ed) Progress in molecular and environmental bioengineering-from analysis

and modeling to technology applications. IntechOpen, Rijeka, pp 605–633
101. Johns C (2017) Living soils: the role of microorganisms in soil health, Future Directions International pp. 1–7
102. Gan Y, Siddique KHM, Turner NC, Li XG, Niu JY, Yang C, Liu L, Chai Q (2013) Ridge-furrow mulching systems-an innovative technique for boosting crop productivity in semiarid rain-fed environments. In: Lewis D (ed) Advances in agronomy. Elseiver, Amsterdam, pp 429–476
103. Zhang K, Adams JM, Shi Y, Yang T, Sun T, He D, Ni Y, Chu H (2017) Environment and geographic distance differ in relative importance for determining fungal community of rhizosphere and bulk soil. J Stomatol Soc 19:3649–3659. https://doi.org/10.1111/1462-2920.13865
104. Furtak K, Gajda AM (2018) Activity and variety of soil microorganisms depending on the diversity of the soil tillage system. In: Oliveira De (ed) Sustainability of agroecosystems. CRC Press, London, pp 45–61
105. Hug LA, Baker BJ, Anantharaman K, Brown CT, Probst AJ, Castelle CJ, Butterfield CN, Hernsdorf AW, Amano Y, Ise K, Suzuki Y, Dudek N, Relman DA, Finstad KM, Amundson R, Thomas BC, Banfield JF (2016) A new view of the tree of life. Nat Microbiol 1:1–6. https://doi.org/10.1038/nmicrobiol.2016.48
106. DeLong EF, Pace NR (2001) Environmental diversity of bacteria and archaea. Syst Biol 50:470–478. https://doi.org/10.1080/106351501750435040
107. Buerkert A, Joergensen RG, Ludwig B, Schlecht E (2011) Nutrient and carbon fluxes in terrestrial agro-ecosystems. In: Marschner P (ed) Marschner's mineral nutrition of higher plants, 3rd edn. Elseiver, Amsterdam, pp 473–482
108. Gan S, Lau E, Ng H (2009) Remediation of soils contaminated with polycyclic aromatic hydrocarbons (PAHs). J Hazard Mater 172(2–3):532–549. https://doi.org/10.1016/j.jhazmat.2009.07.118
109. Puga S, Sosa M, Lebgue T, Quintana C, Campos A (2006) Heavy metal contamination in soil caused by the mining industry. Appl Ecol 5:149–155 (**In Spanish**)
110. Campilongo R, Fung RKY, Little RH, Grenga L, Trampari E, Pepe S, Chandra G, Stevenson C, Roncarati D, Malone G, Malone JG (2017) One ligand, two regulators and three binding sites: How KDPG controls primary carbon metabolism in *Pseudomonas*. PLoS Genet 13:1–29. https://doi.org/10.1371/journal.pgen.1006839
111. Li Y, Powell DA, Shaffer SA, Rasko DA, Pelletier MR, Leszyk JD, Scott AJ, Masouidi A, Goodlett DR, Wang X, Raetz C, Ernst RK (2012) LPS remodeling is an evolved survival strategy for bacteria. Proc Natl Acad Sci USA 109:8716–8721. https://doi.org/10.1073/pnas.1202908109