Water Air Soil Pollut (2023) 234:201
https://doi.org/10.1007/s11270-023-06190-2

Management of Environmental Plastic Pollution: a Comparison of Existing Strategies and Emerging Solutions from Nature

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Received: 2 August 2022 / Accepted: 23 February 2023 / Published online: 13 March 2023

Abstract The recalcitrance of modern plastics is a key driver of the accretion of plastics in both waste management streams and the environment. As a result, the management of plastic waste has become a focal point of both research and public policy. The following review summarises the effectiveness of widespread approaches to plastic management, before exploring recent developments in the use of both naturally derived products and plastic-degrading organisms to reduce the burden of plastic wastes, including the potential value of symbiotic relationships between plastic-degrading organisms in the biodegradation of plastics in the environment. To date, plastic management strategies have typically focused on interventions to influence both plastic production and consumer behaviour, improvements in effective waste management systems and increased circularity of materials, and changes to the product design to increase the lifespan of the product and its suitability for preferred waste streams. However, the relative success of these measures has been mixed. Complementary to these established approaches is the increasing exploitation of biological and biochemical processes and natural products, including the identification of organisms and enzymes which are able to biodegrade different plastics at meaningful rates. This recent research frequently focuses on microbes from soil and marine environments, identifying numerous enzymes capable of acting on polymers or specific functional groups. While questions remain as to their effectiveness outside of laboratory conditions, the distribution of identified species and their apparent effectiveness indicates the potential benefits of these microbes both individually or in symbiosis with an appropriate host species.

Keywords Microplastic · Waste management · Microbe · Enzyme · Degradation

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1 Introduction

The accumulation of plastic waste in the environment (Derraik, 2002; MacLeod et al., 2021) is the result of the combined factors of mass production of plastics (Geyer et al., 2017; Lebreton & Andrady, 2019), insufficient waste management (Borrelle et al., 2020) and the recalcitrance of plastic polymers (Ali et al., 2021). In light of these factors, and of the growing body of literature indicating the potentially harmful effects of plastic debris (e.g. Costa et al., 2020; Palmer & Herat, 2021), there has been increased interest in the development of technological, regulatory and behavioural measures to control either the annual mass of plastic waste generated or the speed at which plastic polymers degrade or are removed from the environment. However, to date, these measures have been deployed irregularly, and with mixed success. Nevertheless, the global appetite for "solutions" to the plastic problem remains high and new responses are routinely proposed.

1.1 Limiting the Production of Plastic Waste

Some of the most commonly used approaches to the management and mitigation of plastic pollution are those associated with reduced production. For example, numerous countries have introduced measures designed to reduce both plastic production and plastic waste by restricting the sale of many products, particularly non-essential single-use items (Xanthos & Walker, 2017). Common products affected by this legislation include disposable plastic bags, straws and microbead scrubs (Schnurr et al., 2018). Such legislation has been seen to yield some reduction in the use of the plastic items targeted (Lam et al., 2018). For example, Ireland's 2002 tax levy on plastic bags was reported to have reduced plastic bag use by approximately 90% (Convery et al., 2007) and Botswana's bag charge also saw usage reduction (Dikgang & Visser, 2012). However, South Africa's bag charge has been proven to be less effective, despite a sharp initial decrease after the levy introduction, demand for bags resurged after less than 2 years as customers became accustomed to the extra charge, though still at lower levels than before the levy (Dikgang et al., 2012).

The regulation of plastic products may also be associated with prior or concurrent campaigning, either to influence the type of legislative change identified above or directly affect the behaviour of industry and consumers. For example, at the industry level, businesses have endeavoured to influence behavioural change in the consumer (such as encouraging the purchase of reusable bags or promoting recycling schemes) or have altered practices at the organisational level either to reduce plastic use or to go plastic free (Lam et al., 2018).

Non-profit groups also frequently target a wide audience to petition for changes in legislation (Moss, 2021) and can use citizen-science to gather data to encourage changes in legislative, commercial, or industrial practices. For example, The Big Plastic Count, organised by Greenpeace and Everyday Plastic (https://thebigplasticcount.com/), provided materials and an online submission point for the UK public to audit 1 week of household plastic waste, the data from which is intended to be used as evidence in favour of better legislative changes. Likewise, in 2017, Lonely Whale launched "#StopSucking", a global online campaign to reduce plastic straw use. The campaign apparently reached 74 million people, saw over 50,000 pledges to stop using plastic straws and induced government and business legislation changes (https://showmethe.work/strawlessocean). In addition, media coverage has have sought to influence consumer awareness and behaviour via a combination of factual and emotive content and the highlighting of practical responses (Borg et al., 2021; Henderson & Green, 2020; Males & Van Aelst, 2021). Unfortunately, the relative impact of these measures is variable (Moss, 2021). For example, in Australia, campaigns to reduce plastic use and prevent incorrect disposal have been seen to be more impactful than the development of new public policy (Willis et al., 2018), while a Canadian store's attempt to discourage plastic bag use backfired due to people wanting the novelty printed bags which were originally designed to shame people from using them (Moss, 2021). However, the 2015 Kenya plastic bag ban campaign of photojournalist, James Wakibia, received positive responses from the then Kenyan Environment secretary, and a national plastic bag ban was passed in 2017 (Schnurr et al., 2018).

1.2 Limiting the Loss of Plastic to the Environment

Traditionally, the control of plastic materials at end-of-life is through waste management infrastructures. Waste plastics may be collected by governments, businesses, public volunteer groups and individuals, with a mix of municipal and/or private household and business waste collection. As a key part of the waste infrastructure, recycling is often highlighted for its importance in reducing the loss of plastic to the environment as well as influencing the demand for virgin plastics, oil use and associated CO_2 emissions (Gu et al., 2017). Recycling may involve both government and business in the provision of facilities and infrastructure (Xevgenos et al., 2015); however, waste infrastructure may be highly variable between countries, from national networks to local collectors. For example, 98% of local authorities in England provide kerbside collection for households (Hahladakis et al., 2018), while in Norway 70% of households have access to kerbside collection (Xevgenos et al., 2015). Furthermore, public confusion about separation of materials can contribute to contamination, lowering the quality of collected material to recyclers (Rousta et al., 2015; Thoden van Velzen et al., 2019). Recycling rates in Europe in 2020 were 13 times higher when waste was collected separately (65% recycled), compared to mixed collection methods (5% recycled) (Plastics Europe, 2022).

Under certain scenarios, businesses may facilitate or undertake plastic collection and recycling services that local authorities can struggle to provide (Dumbili & Henderson, 2020), for example, the city of Rajshahi in Bangladesh had 140 recycling shops in 2012 (Bari et al., 2012); elsewhere, small recycling businesses may be seen in Nigeria (http://www.chanjadatti.com/; http://www.recyclepoints.com; https://www.wecyclers.com), Kenya (http://www.ecopost.co.ke), India (https://www.plasticsforchange.org/foundation; https://www.recykal.com) and the UK (https://stnicks.org.uk/make-a-difference/our-recycling-service/) among others. Similarly, informal litter collection is a common source of primary or additional income. For example, the Zabbaleen of Cairo, Egypt, are informal waste collectors (IWCs) who recover street materials and provide household waste collections and have been recognised as creating a highly efficient recycling system (Nzeadibe, 2013). Globally, IWCs gather waste plastics and other material in order to sell to buy-back centres and recycling businesses. In Argentina and Brazil, an estimated 200,000 and 387,910 people, respectively, are IWCs (Gutberlet & Carenzo, 2020), and in South Africa, the estimated 37,000 IWCs in 2005 (Langenhoven & Dyssel, 2007) rose to between 60,000 and 215,000 by 2016 (Godfrey & Oelofse, 2017). The proportion of domestic and business waste that is collected in this manner is variable, for example, in Nigeria, IWCs do the majority of waste collection that is not managed by local authorities (Nzeadibe, 2013), and in the metropolitan area of Metro Manila in the Philippines, 20.32 and 1.63 kg/capita/day of plastic were collected by disposal site scavengers and street collectors respectively, compared to 9.79 kg/c/d by formal collection workers (Environmental Management Bureau, 2018). Indeed, IWC cooperatives may collect and sort a wider range of material than some private recycling collection firms and can further form networks which coordinate with local governments and universities to improve worker support and integrate their labour and knowledge into formal circular economies (Gutberlet & Carenzo, 2020; Schenck & Blaauw, 2011). However, while IWCs significantly contribute to diverting and reclaiming waste from the environment, many are subject to hazardous working environments and impoverished living conditions, and more widespread working protections and support for the formation of waste collector cooperatives or unions are to be desired (Gutberlet & Carenzo, 2020; Nzeadibe, 2013; Ogando et al., 2017).

Given the information above, it is perhaps unsurprising that countries and regions differ in their recycling rates. For example, by 2020, USA plastic recycling was only at 9.3% (Law et al., 2020); meanwhile, by 2012, the Netherlands' recycling rates were 51% (Goorhuis et al., 2012) and South Africa's plastic packaging recycling rates went from 10% in the 1990s to ~46% by 2015 (Godfrey & Oelofse, 2017). Between 2018 and 2020, the percentage of overall EU post-consumer waste plastics recycled increased from 32.5 to 35% (Plastics Europe, 2022), although these figures report thermoplastics and thermosets and do not include plastics used in textiles, varnishes, paints, cosmetics and medical processes.

Despite these increases, it is estimated that just 9% of the plastic produced between 1950 and 2015 has been recycled, and only 0.9% recycled more than once, since much plastic is initially recycled into lower-grade materials (Geyer et al., 2017). More recently, Plastics Europe, (2022) estimates that 10.1% of thermoplastics and thermoset plastics produced in Europe in 2021 were from recycled sources, whilst the majority (87.6%) were from fossil fuel sources. This continued disparity must be addressed, if the European Commission wishes to succeed with their new "Circular Economy Action Plan" (Keersemaker, 2020). Additionally, recycling "in" high-income countries, such as the UK and USA, frequently means exporting plastic, sometimes illegally, to poorer countries, where a proportion may be lost to local habitats or bring about secondary negative effects during processing (Arkenbout & Bouman, 2021; Brooks et al., 2018; Law et al., 2020; Pittiglio et al., 2017; Verma et al., 2016). For example, the process of recycling (milling, washing, pelletising) can unintentionally produce micro- and nano-plastics (MNPs), which can enter aquatic ecosystems, especially if sink water does not go through a WWTP (Suzuki et al., 2022). For those plastics not destined for recycling, incineration is a widespread, large-scale method used to control otherwise low-value wastes; however, this process may produce harmful by-products. The production of potentially damaging secondary products may occur both in contained and open waste sites (UN Environment Programme, 2017), which can have detrimental health effects on local people and wildlife (Arkenbout & Bouman, 2021; Verma et al., 2016). The amount of plastic incinerated is predicted to rise and match discarded plastic amounts (12,000 million metric tons) by 2050 (Geyer et al., 2017; Plastics Europe, 2022).

1.3 Reclaiming Plastic from the Environment

In addition to limiting the production and sale of problematic plastic items and the development of waste management infrastructure, the extraction of plastics from the environment has become a widely discussed method for reducing environmental impact. The simplest of these measures are litter picks, some of which are undertaken on a voluntary basis by individuals or as part of organised events by local, national, or international groups, for example New Zealand's Love Your Coast programme (Sustainable Coastlines, 2009), and the European Surfrider Ocean Initiatives programme (https://www.initiativesoceanes.org/en/). As indicated above, some litter picks are also structured so as to generate citizen science data which may be used to influence changes in business practice and legislation, for example the PADI AWARE Foundation (Roman et al., 2020) and The Great Nurdle Hunt by Fidra (https://www.nurdlehunt.org.uk).

In addition to manual litter collection, a range of novel inventions have been created purposely for plastic recovery from aquatic environments. These include floating structures able to scoop or filter plastic debris at the water's surface such as "seabins" (https://seabinproject.com/the-seabin-v5/), offshore barrier collectors and riverine interceptors (https://theoceancleanup.com). A key consideration in mechanical plastic waste collection is the unintentional production of MNP waste, due to the increased mechanical stress (Kalogerakis et al., 2017).

1.4 Gaps in the System: Natural Processes and Biotechnologies to Control "Unmanageable" Plastics

Whilst the measures for the management of plastic waste outlined above are necessary to reduce both the mass of plastic wastes and the volume lost to the environment, they appear to be insufficient in isolation (Lau et al., 2020). Additionally, the approaches above are best suited to the management of large plastic wastes, rather than of MNPs. Currently, the only waste management measure widely shown to have a quantifiable effect on the flow of MNPs to the environment is wastewater treatment (WWT), with secondary and tertiary treatment able to capture in excess of 90% of microplastics. Nevertheless, WWT facilities remain a major source of MNPs, predominantly fibres and fragments, into the aquatic environment (Acharya et al., 2021; Collivignarelli et al., 2021; Lares et al., 2018; Mintenig et al., 2017; Park et al., 2020; Prajapati et al., 2021), whereas WWT sewage sludges represent a substantial source of MNPs into the terrestrial environment (Collivignarelli et al., 2021). As a result, millions of tonnes of plastics continue to enter the environment each year (Jambeck et al., 2015).

Fortunately, in addition to the reduction of plastic inputs and the removal of existing marine debris, there are a number of methods by which we may reduce the resistance of plastic polymers to degradation, thus limiting their accumulation in the environment. Although not a novel method, there has been a significant recent development in bio-based approaches to the formulation of novel polymers and fillers, and of the identification of new or increasingly efficient modes of biodegradation. Here we review recent developments in these measures and contrast them to established plastic management approaches.

2 Methods

In order to map recent developments in these novel approaches to plastic management, as well as to determine recent publication trends, a systematic review was undertaken. The targets of this review were novel, nature-based, developments in both bioplastics and biodegradation. Articles were identified via Web of Science using the search terms in Table 1. Initial terms were deliberately broad, and publications were initially filtered to only include publications from between January 2012 and December 2021. Remaining documents were then restricted to remove those from unrelated research areas, for example "entomology", "geology" and "neurosciences", review articles, and those not written in English. It is important to note at this point that restricting our publication to English-language only may result in some omissions; however, it is our belief that the predominant trends in the research have been preserved.

After download, articles were sorted by title and abstract to include only those studies which considered either (i) the development or application of novel bioplastics, blends, or fillers (rather than measurement of efficacy or optimisation alone), or (ii) the identification/observation of substances or organisms responsible for the biodegradation of plastics and bioplastics. The final number of publications is given in Fig. 1.

3 Results and Discussion

Observations of the annual number of studies published indicate an increasing number of articles per year which explore the development of biobased plastics and fillers; however, the number of publications per year which report novel drivers of biodegradation of plastics shows no clear trend (Fig. 2).

After removing the search terms specified in Table 1, the combined titles from each of collections of sorted papers were analysed to determine common themes. Common terms from each dataset are displayed in Fig. 3. Papers concerning the development of bioplastics, blends and fillers most frequently used the following keywords: starch (49) and cellulose (34), chitosan (16), lignin (12) and alginates (7). Of the papers exploring modes of biodegradation, focal areas included soil (63) and marine (13) environments and, while invertebrates are mentioned, these studies most frequently focus on either individual microbial organisms or consortia, most commonly fungi (35) and bacteria (14), with specific mention of *Aspergillus* (16) and *Pseudomonas* (15). The application of the approaches outlined in these papers is presented and expanded on in the following sections.

3.1 Bioplastics, Blends and Fillers: Reducing Polymer Recalcitrance

3.1.1 Synthetic and Biobased Polymer Blends

Biodegradability of traditional polymers may be increased by direct modification of the polymer, to make it more chemically accessible to microorganisms. For example, poly(butylene terephthalate) (PBT), similar in structure to PET, produces a hydrolytically degradable copolymer, when combined with poly(ethylene glycol) (PEG), partly due to PEG's hydrophilicity (Chao et al., 2007; Wang et al., 2005). Similarly, PET_{70}-NT_{30}, a copolymer of both pure PET and that modified with nitrate and different bonding positions of the benzene ring to the carbon–carbon backbone, was more susceptible to degradation by *Aspergillus niger* than pure PET (Marqués-Calvo et al., 2006). Nevertheless, this method has not always achieved greater rates of plastic biodegradation, with polymer blends still outperforming them (Webb et al., 2013). Subsequently, a variety of bio-based approaches have been taken to influence the degradation time of plastics. To increase the degradation rates of traditional plastic polymers, many plastic fillers and additives have been developed, although these are often primarily used to improve other characteristics of a product (Civancik-Uslu et al., 2018). For example, $Mg(OH)_2$ and $Al(OH)_3$ are used as flame retardants for different plastics (Titelman et al, 2002), and biobased fillers, such as wood (Xu et al., 2008), reed (Corbière-Nicollier et al., 2001),

Table 1 Search terms

Research question	Search terms
Bioplastics	(Bioplastic* OR Biopolymer*) AND Degrad*
Biodegradation of plastics	(Plastic OR Polymer) AND Biodegrad*

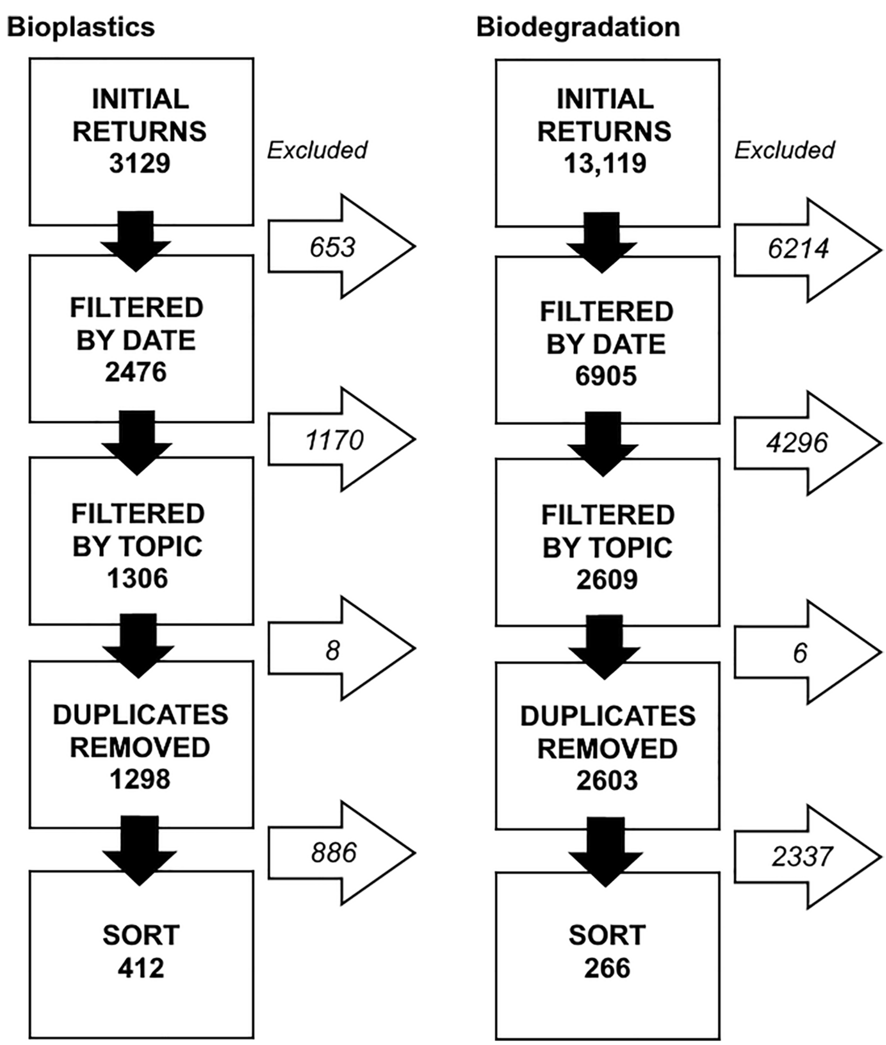
chitosan (Sunilkumar et al., 2012), cotton, or rice husks (Vidal et al., 2009), can maintain the tensile strength required of a product whilst reducing environmental impacts, such as greenhouse gas and heavy metal emissions, from the overall product life cycle (Chuayjuljit et al., 2009).

Similarly, the recalcitrance of plastic products may also be altered by mixing plastic polymers with naturally occurring biodegradable ones. For example, cotton-based microcrystalline cellulose combined with polyvinyl chloride (PVC) to make MCC-PVC films has been seen to exhibit improved tensile strength than that of pure PVC and could partially biodegrade, as have LDPE-chitosan composites plasticised with palm oil (Sunilkumar et al., 2012). The increased biodegradability of such blended products may be solely due to the incorporation of material that is already biodegradable, resulting in a partially biodegradable product (Khoramejadian, 2013; Leja & Lewandowicz, 2010); however, Zykova et al., (2021) found FTIR evidence of PE polymer breakdown from PE-wood flour composites buried in soil.

Nevertheless, some blends have negligible degrading capacity, such as PP and sugarcane bagasse (Cardoso et al., 2014); furthermore, the biodegradable component may not breakdown as swiftly as when in isolation, if it is encapsulated in the plastic, since access for the biodegrading microorganisms can be obscured until mechanical breakdown liberates it again (Sunilkumar et al., 2012; Vidal et al., 2009).

Nonetheless, the chemical incorporation, via cross-linkage, of a naturally biodegradable polymer

Fig. 1 Paper sorting and exclusion



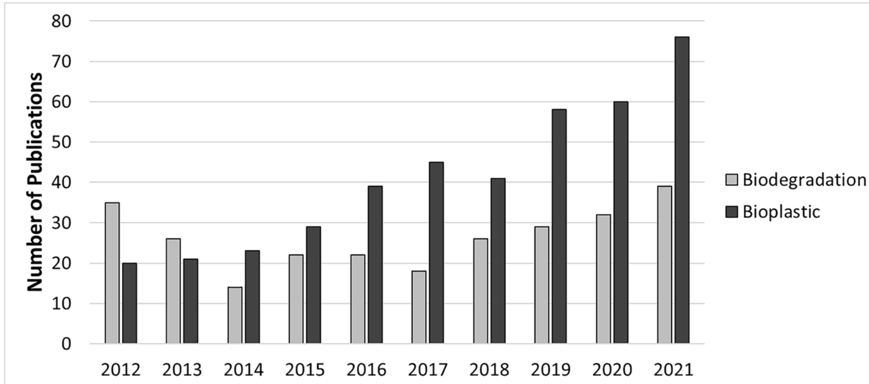


Fig. 2 Distribution of the sorted publications by year

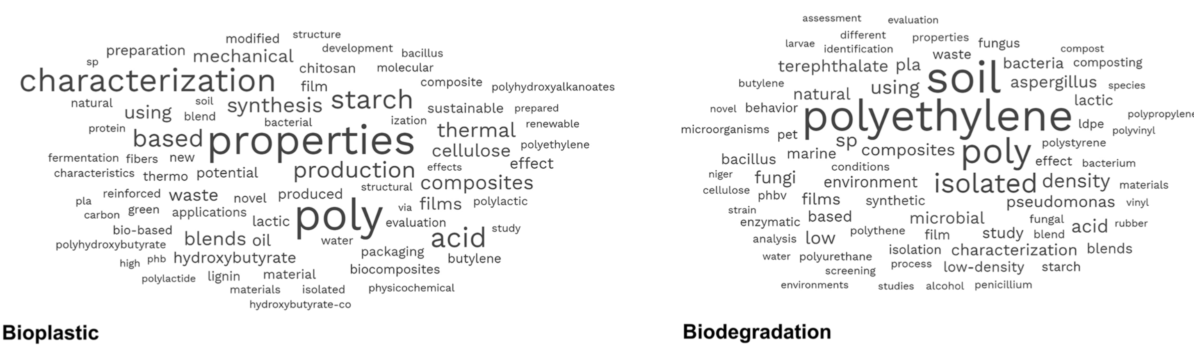


Fig. 3 Common keywords across the sorted papers

to a synthetic plastic polymer, can facilitate the biochemical breakdown of the plastic polymer itself. Starch cross-linked with LDPE facilitates microbial attachment and attack of the LDPE and its oligomer breakdown products, via increasing water permeability and providing hydrophilic binding points for microbes (Borghei et al., 2010; Bulatović et al., 2022; Oromiehie et al., 2013); a similar process has been indicated with LDPE-chitosan, with palm oil plasticiser enhancing composite biodegradation (Sunilkumar et al., 2012).

3.1.2 Bioplastic Substitution of Synthetic Polymers

Another way to reduce the production of recalcitrant plastic waste is to use an already highly biodegradable naturally sourced material. This is especially important for short-lifespan products which are left out in the environment, such as agricultural mulch (Manfra et al., 2021). Polylactic acid (PLA) is a widely used bioplastic, especially in practical medicine and in anticancer drug delivery research (Ashothaman et al., 2021; Jelonek et al., 2016) and can be further chemically modified to alter its qualities (Veccharelli et al., 2016). Starch biofilms are used in some packaging and can be sourced from potatoes. The incorporation of glycerol and sorbitol acts as plasticisers, able to alter water permeability and biodegradability (Ng et al., 2022) to suit product requirements. Other chemical enhancements of starch include acetylation of hydroxyl groups, creating ester links, which also act as internal plasticisers (Jayasekara et al., 2005). Animal-based biopolymers include chitin, from which chitosan films, used in food packaging, can be made. Chitin films can be as impermeable to water vapour as commercial PVC, and modification via glutaraldehyde cross-linking can both reduce the degree of swelling when submerged in water and retain biodegradability (Pavoni et al., 2021). Both chitin and cellulose-based films can have lower oxygen permeability (OP) than synthetic plastic packaging, due to the degree of polymer hydrogen bonding, with variation of OP possible depending on production methods. Chitosan can be further blended with glycerol and Na-montmorillonite (clay-based) to improve mechanical properties and reduce water permeability (Yu et al., 2020). Chitin nanowhiskers can also reinforce PLA, creating a nanocomposite with greater tensile strength and thermal stability whilst remaining biodegradable (Mohd Asri et al., 2020). Bacteria produce a range of biodegradable polyesters, including poly-ß-hydroxyalkanoate (PHB) (Jayasekara et al., 2005), a member of a wider group of poly(hydroxyalkanoate)s (PHAs). These are also used for some commercial products (Boey et al., 2021); however, the production costs are typically higher than petroleum-based materials; hence, synthetic plastics have continued to dominate markets over PHAs (Sabapathy et al., 2020; Yu et al., 2020). Bioplastics are continuously being developed into useful synthetic plastic replacements and feedstocks from algae, seaweed and even fish scales are being explored (Rajendran et al., 2012; University of Sussex, 2019).

3.1.3 The Drawbacks of Bioplastics

Bioplastics can be biobased (from biomass) and/or biodegradable (able to be converted to biomass, CO_2, H_2O and CH_4 by microorganisms), but not always both. For example, PE can be created with biobased feedstocks, but still presents a biochemical challenge for breakdown, as petrochemical-based PE does (Dilkes-Hoffman et al., 2019). Unfortunately, biobased feedstocks may have further negative environmental impacts of their own, such as the use of more land and pesticides besides that for food production (Vidal et al., 2009), especially if managed unsustainably. Other critiques of bioplastics, such as PLA, are that they can induce similar toxicological effects in marine animals as synthetic plastic does (Manfra et al., 2021), can emit methane in landfills, and are not as biodegradable under typical domestic conditions or in the environment as they are in industrial composting or laboratory trials (Haider et al., 2019; Yu et al., 2020). For example, Dilkes-Hoffman et al. (2019) point out that PLA should technically be referred to as an "industrially compostable" polymer, due to its specific temperature requirements and abiotic hydrolysis degradation. Nevertheless, a study screening Arctic microorganisms found many able to biodegrade bioplastics even at such low temperatures (Urbanek et al., 2017), an encouraging indicator that biodegradation of bioplastics could be feasible outside of optimised temperatures.

A final potential drawback of polymer blends and bioplastics is that some recycling facilities may not accommodate variants from purer synthetic polymers, since the addition of fillers can produce lower-quality recycled materials (La Manila, 2003; Soroudi & Jakubowicz, 2013). Usual plastic recycling facilities are not the ideal destination for biodegradable plastics, but most countries do not have waste management systems designed for the appropriate separation of biodegradable plastics, and surveys indicate the public generally believe recycling bins to be the correct disposal point (Dilkes-Hoffman et al., 2019). This may lead to the rejection of the accompanying "purer" synthetic plastic from the recycling process, if a company deems a batch of collected plastic as too "contaminated" with blended or biodegradable plastics (Soroudi & Jakubowicz, 2013).

3.2 Enhancing Biodegradation

3.2.1 Biodegrading Microbes and Enzymes

Although by far the least explored approach to plastic management, the identification of plastic-degrading organisms has created significant interest in the past few years. Despite the persistence of plastics in the environment, many plastic-biodegrading microorganisms (PBMs) and plastic-biodegrading enzymes (PBEs) have been identified. Recognised as early as the 1970s (Jones & Prasad, 1974; Suzuki et al., 1973), these organisms and enzymes can target a range of synthetic plastic. This biochemical degradation generates opportunities to eradicate waste plastics from our environment without the drawbacks of traditional waste management measures such as incineration, since microorganisms are capable of degrading complex (Ndeh & Gilbert, 2018) or toxic (Ismail et al., 2022; Sher & Rehman, 2019) compounds. Table 2 provides exemplars of PBM's and PBEs from the literature, including the organism or environment from which they were isolated and the plastic on which they have been found to be effective (Ahmaditabatabaei et al., 2021; Amobonye et al., 2021; Danso et al., 2018; Francis et al., 2021; Pathak & Navneet, 2017; Ru et al., 2020; Tiwari et al., 2020).

The process of plastic degradation is typically as follows: PBMs adhere to the surface of plastics and excrete extracellular PBEs, often forming pits and fissures detectable under microscopes. The PBEs depolymerise and chemically alter plastic polymers via oxidation of side groups and dehydrogenation of carbon chains, resulting in deformation or stretching of C = C, CO, COOH, OH, CN bonds within the polymer chain and depolymerised products (Abdulhay, 2020; Leja & Lewandowicz, 2010; Santo et al., 2013; Sepperumal et al., 2013; Woo et al., 2020; Yang et al., 2014).

Some plastics, such as polyurethane (PUR) are heteropolymers, made up of several different starting monomers and so need different species of enzymes to attack the relevant groups. Polyurethane contains ester and amide-type bonds (urethane groups) and was more effectively depolymerised by both amidase E4143 and esterase E3576 than either alone. Another esterase, TfCut2 polyester hydrolase from *Thermobifida fusca*, also catalyses polyester-PUR depolymerisation via hydrolysis (Magnin et al., 2019; Schmidt et al., 2017). PETase and MHETase from *Ideonella sakaiensis* catalyse different stages of PET biodegradation, with PETase first catalysing conversion of polyethylene terephthalate (PET) to bis-2-hydroyethyl terephthalate (BHET), terephthalic acid (TPA) and mono(2-hydroethyl)terephthalic acid (MHET). MHETase then hydrolyses MHET to TPA and ethylene glycol (EG), the different monomers for PET production (Knott et al., 2020; Yoshida et al., 2016).

Genetic cloning studies have clarified the identities of a number of PBEs via their ability to transform a none-PBM into a PBM (Howard et al., 2001; Marconi et al., 1996; Sulaiman et al., 2011; Vega et al., 1999), for example, a polyester hydrolase (PE-H) from *Pseudomonas aestusnigri* allowed *Escherichia coli* to biodegrade PET (Bollinger et al., 2020). Alkane hydroxylase (alkB) and alkane monooxygenase (alkB1, alkB2) from *Pseudomonas* sp. expressed in *Escherichia coli* allowed it to mineralize 19.3%, 19.6% and 27.6% of PE into CO_2, respectively (Jeon & Kim, 2016; Yoon et al., 2012). Further study identified potential regulatory genes of alkB1, called rubA1 and rubA2, which increased the biodegradability of *E. coli*-expressing alkB1 from 18.5 to 26.3% (Jeon & Kim, 2015).

3.2.2 Rates of Biodegradation

Questions are regularly raised about the real-world practicalities of such PBMs and PBEs outside of laboratory conditions, and whether biodegradation rates achieved will prove meaningful (Haider et al., 2019). First to note, whilst some PBMs show very low plastic biodegradation rates (Ru et al., 2020), studies of both wildtype and purposely site-mutated PBMs reveal that many can biodegrade plastic at substantial rates, even if often within laboratory settings. *T. fusca* hydrolase biodegraded PET by 50% after 3 weeks (Müller et al., 2005) and TfCut2 expressed in *B. subtilis* could induce amorphous PET weight loss of 22.2% in 24 h and 97% in 120 h, with chemical analysis confirming biodegradation (Wei et al., 2019). *I. sakaiensis* assimilated PET in 6 weeks with its PETase impressively biodegrading commercial, highly crystalised PET bottles (Yoshida et al., 2016). Mutation accelerated biodegradation rates further; three *I. sakaiensis* PETase mutants biodegraded PET 1.6, 2.1 or 2.5 times faster than wildtype PETase (Ma et al., 2018) and a PE-H mutant hydrolysed commercial PET bottles, which wildtype PE-H could not (Bollinger et al., 2020). An engineered adhesive fusion polyester-UR enzyme was 6.6-fold more effective at PUR MP biodegradation than the wildtype (Islam et al., 2019), and artificially made chimeric (physically linked) PETase and MHETase were more effective PET biodegraders than the separate enzymes in solution (Knott et al., 2020). Blue-green algae *Anabaena spiroides* biodegraded LDPE by 8.18% in one month (Kumar et al., 2017) and *R. ruber* laccase catalysed a 20% molecular weight loss of PE after 2 weeks, with Fourier transform infrared (FTIR) microscopy confirming chemical changes to the plastic (Santo et al., 2013).

3.2.3 Occurrence and Distribution of PBMs

When considering the real-world applicability of PBM/Es, it is notable that these PBMs are not extremophiles found in only specific niches; they are in garden soil, landfill sites, wastewater, rivers, urban structures, surface biological litter and on ocean-floating plastic (Jacquin et al., 2019; Oberbeckmann et al., 2016; Ru et al., 2020; Tiwari et al., 2020). Remarkably, Asmita et al., (2015) found PS and PET could degrade by 29% and 5% in just soil samples, over 4 months, respectively, and Roberts et al., (2020) isolated a bacteria consortium from soil able to biochemically degrade post-consumer PET bottle fragments after 6 weeks. Microbial isolates from

Table 2 A selection of organisms and PBEs, according to plastic target. Polyethylene terephthalate (PET), bis-2-hydroyethyl terephthalate (BHET) and mono(2-hydroethyl)terephthalic acid (MHET) are PET break-down products; polyethylene (PE), high-density PE (HDPE), low-density PE (LDPE), polypropylene (PP), polystyrene (PS), high impact PS (HIPS) made of PS and polybutadiene; polyurethane (PUR) often comes in two forms: polyester PUR or polyether PUR; polyvinyl alcohol (PVA). Sources are provided within the table

Plastic	*Genus/source*	*Species*	Strain	Enzyme	References
PET	*Streptomyces*	*scabies*	NA	Suberinase	(Jabloune et al., 2020)
PET	*Ideonella*	*sakaiensis*	NA	PETase	(Yoshida et al., 2016)
PET	*Thermobifida*	*fusca*	NA	TfCutinase2	(Wei et al., 2019)
PET	*Saccharomonospora*	*viridis*	AHK190	Cutinase190	(Kawai et al., 2014)
PET	Leaf Compost Library	NA	NA	LC-cutinase	(Sulaiman et al., 2011)
PET	*Bacillus*	*gottheilii*	NA	NA	(Auta et al., 2017)
PET	*Homo*	*sapiens*	NA	Neprilysin	(Hu et al., 2021)
PET	*Cryptococcus*	*sp.*	S-2	Cutinase-like	(Hu et al., 2021)
PET	*Pseudomonas*	*sp.s*	B10 SW136	Autotransporter lipase Carboxylesterase Triacylglycerol lipase-like	(Roberts et al., 2020)
PET	*Bacillus*	*thuringiensis* *albus*	C15 PFYN01	Triacylglycerol esterase/lipase	(Roberts et al., 2020)
BHET	*Bacillus*	*thuringiensis* *albus*	C15 PFYN01	Hydrolase FrsA	(Roberts et al., 2020)
MHET	*Ideonella*	*sakaiensis*	NA	MHETase	(Yoshida et al., 2016)
PE	*Bacillus*	*gottheilii*	NA	NA	(Auta et al., 2017)
HDPE	*Glycine*	*max*	NA	Soybean peroxidase	(Zhao et al., 2004)
LDPE	*Alcaligenes*	*faecalis*	NA	NA	(Nag et al., 2021)
LDPE	*Pleurotus*	*ostreatus*	NA	Laccase Manganese peroxidase Lignin peroxidase	(Gómez-Méndez et al., 2018)
LDPE	*Pseudomonas*	sp.	E4	Alkane hydroxylase	(Yoon et al., 2012)
LDPE	*Pseudomonas*	*aeruginosa*	E7	Alkane hydroxylase	(Jeon & Kim, 2015)
LDPE	*Rhodococcus*	*ruber*	C208	Laccase	(Santo et al., 2013)
PP	*Engyodontium*	*album*	NCIM1170	Laccase indicators	(Jeyakumar et al., 2013)
PP	*Phanerochaete*	*chrysosporium*	MTP091	Laccase indicators	(Jeyakumar et al., 2013)
PP	*Bacillus*	*gottheilii*	NA	NA	(Auta et al., 2017)
PP	*Bacillus*	sp.	27	NA	(Auta et al., 2018)
PP	*Rhodococcus*	sp.	36	NA	(Auta et al., 2018)
Nylon	white rot fungus	NA	IZU-154	Manganese peroxidase	(Deguchi et al., 1998)
Nylon	*Aestuariibacter*	*halophilus*	MND-1	Extracellular	(Yamano et al., 2019)
PS	*Bacillus*	*gottheilii*	NA	NA	(Auta et al., 2017)
PS	*Lantinus*	*tigrinus*	NA	Esterase	(Tahir et al., 2013)
PS	*Azotobacter*	*beijerinckii*	HM121	Hydroquinone peroxidase	(Nakamiya et al., 1997)
HIPS	*Pseudomonas*	sp.	NA	Esterase	(Mohan et al., 2016)
HIPS	*Bacillus*	sp.	NA	Lipase Esterase	(Mohan et al., 2016)
PUR	Enzyme Library	NA	NA	Esterase E3576 Amidase E4143	(Magnin et al., 2019)
PUR	*Pestalotiopsis*	*microspora*	E2712A	Serine hydrolase	(Russell et al., 2011)
PUR	*Thermobifida*	*fusca*	NA	TfCutinase2	(Schmidt et al., 2017)
PUR	*Bacillus*	*subtilis*	NA	Lipase	(Rowe & Howard, 2002)
PUR	*Pseudomonas*	*chlororaphis*	NA	PolyurethanaseA	(Stern & Howard, 2000)

Table 2 (continued)

Plastic	*Genus/source*	*Species*	Strain	Enzyme	References
PUR	*Pseudomonas*	*chlororaphis*	NA	PolyurethanaseB	(Howard et al., 2001)
PVA	*Penicillium*	*brevicompactam*	OVR-5	Lipase Laccase Manganese peroxidase	(Mohamed et al., 2021)

sewage and landfill soils biodegraded LDPE, high-density polyethylene (HDPE) and polypropylene (PP) with average weight losses of 22.6%, 21.6% and 21.6% respectively, over 140 days, with chemical and structural analysis using nuclear magnetic resonance (NMR), FTIR and scanning electron microscopes (SEM) confirming biodegradation (Skariyachan et al., 2018). Low-density polyethylene (LDPE) bags were biochemically degraded by *Alcaligenes faecalis*, isolated from sea banks, after 10 weeks in a simple soil burial set-up (Nag et al., 2021), and Yamano et al. (2019) found that nylon-4 could biodegrade by 30% in seawater in 4 weeks. Finally, recent computational analysis highlights a human-neutral endopeptidase, neprilysin, with PET-degrading characteristics (Hu et al., 2021), and Zhou et al., (2022) proposed that WWTP should be developed to include microbial biodegradation of MNPs.

3.2.4 Plastic-Biodegrading Symbionts

Another potential source of PBMs is host organisms. Previous observations have been made of aquatic and terrestrial arthropods burrowing through plastic and dispersing problematic MNPs (Cookson, 1987; Davidson, 2012), and recent studies have found some animals actively eating plastic, some of which have been seen to contain symbiotic PBMs. For example, *Zophobas atratus* (superworms) fed PS for 28 days fared as well as those fed by a normal (bran) diet, with FTIR indicating PS depolymerisation (Yang et al., 2020), and *Tenebrio molitor* (mealworm) larvae converted 47.7% of PS to CO_2 in 16 days, also showing FTIR evidence of PS depolymerisation (Yang et al., 2015a). Perhaps more impressively, *Achroia grisella* (lesser waxworm) created holes in HDPE after 45 min, resulting in a 43.3% plastic weight loss in 8 days, and were able to complete their lifecycle subsisting only on PE and produced PE-degrading offspring. FTIR and NMR assessment of egested frass revealed new OH, CO, COOH and CN group indicators, likely created by oxidising enzymes (Kundungal et al., 2019). Similarly, *Tribolium confusum* larvae (confused flour beetle) ate and biodegraded PE and PS with 46.8% and 51.9% plastic weight loss after 30 days, respectively, and FTIR assessment found chemical alterations such as new OH and COOH groups from the ingested plastics (Abdulhay, 2020). *Plesiophthalmus davidis* (darkling beetle) larvae survived on PS for 4 weeks and biodegraded 34.27% after 2 weeks and FTIR assessment showed oxidation of ingested PS (Woo et al., 2020).

Some publications highlight the importance of bacteria in this process. *Plodia interpunctella* (waxworms) (Yang et al., 2014) and *Galleria mellonella* (wax moth) (Bombelli et al., 2017) larvae have also been seen to consume PE, with FTIR analysis showing chemical alterations to the plastic after ingestion. *Enterobacter* species were active in both *P. interpunctella* and *G. mellonella*, with *Bacillus sp.* YP1 also active in *P. interpunctella* (Ren et al., 2019; Yang et al., 2014). Similarly, consortia of bacteria isolated from *Lumbricus terrestris* (earthworms) reduced LDPE MP size and produced compounds indicative of LDPE depolymerisation (Lwanga et al., 2018). *Exiguobacterium sp.* YT2 was isolated from *T. molitor* (also discussed above), able to form biofilms on and biodegrade PS by 7.4% after 60 days. Notably, this was a reduced capability when in vitro compared to when in symbiosis with the mealworm (Yang et al., 2015b). A *Serratia* sp. strain WSW was isolated from *P. davidis* (also discussed above) and formed a biofilm on and biodegraded PS, confirmed by x-ray photoelectron spectroscopy (XPS) assessment. These changes were more pronounced when the PS was treated with the full *P. davidis* gut microbiome (Woo et al., 2020), indicating again the importance of the host's gut microbial community during plastic biodegradation. Finally, and remarkably, Song et al., (2020) found evidence that eukaryotic enzymes may be capable of biodegrading

PS, as the use of broad-spectrum antibiotics in their host *Achatina fulica* snails did not hinder PS biodegradation and NMR and FTIR analysis confirmed chemical changes after passage through the gut. These studies show the potential for novel PBMs from animal microbiomes; recently Francis et al., (2021) highlighted that gut microbes might be key sources in addressing plastic pollution.

3.3 A Novel Symbiosis

The studies summarised above suggest that PBM-host symbionts may represent a novel solution to the plastic problem. The microbiome-host system can be more effective at biodegrading plastics compared to in vitro microbial isolates, and other studies found multi-bacteria consortia more effective than individual species sourced from same consortia (Roberts et al., 2020; Woo et al., 2020; Yang et al., 2015b).

A key challenge in our global plastic problem is how to address the problems of macro-, micro- and nanoplastic dispersed in rivers and oceans; our aquatic environments being major plastic sinks (Cózar et al., 2014; Jambeck et al., 2015; Peng et al., 2018). The discovery or novel creation of an aquatic PBM-host symbiont could help to biochemically eradicate free-floating plastics. Aquatic filter-feeders are ingesting MNP, with a mixture of individual and ecological consequences (Bergami et al., 2016, 2020; Berglund et al., 2019; Yan et al., 2021). Perhaps, they, in symbiosis with PBMs, could become aquatic plastic cleaners and play a key role in reducing plastic sinks. A host could provide the ideal conditions to facilitate biofilm formation on ingested plastics and actively maintain a PBM community. Filter-feeder hosts which mechanically breakdown plastic particles, such as krill (Dawson et al., 2018a), would also increase microbial access to the polymer, speeding up biodegradation rates. Additionally, a filter-feeder host would offer selectivity of what size plastic could be biodegraded; aquatic filter feeders such as krill or mussels will only be able to ingest plastic up to a certain size, meaning that large plastic infrastructure (e.g. pipes, cables or boats) should be unaffected. A similar concept has previously been postulated for earthworms, to address terrestrial bioplastic mulch (Sanchez-Hernandez et al., 2020).

The fact that such naturally occurring plastic degrading symbionts are increasingly being discovered suggests that there is already evolutionary pressure in favour of PBMs and PBEs (Francis et al., 2021) providing diverse potential for research, such as the laboratory improvement of PBEs (Lu et al., 2022; Ma et al., 2018). In this plastic era, acquiring PBE genes into the microbiome may be evolutionarily advantageous. For example, studies into shrimp microbiome alteration attest to benefits probiotics can bring to host health (Holt et al., 2020), and a host with PBMs may be able to use plastic as an energy source, instead of it being a health hazard.

Nevertheless, achieving a successful novel PBM-host symbiosis would require consideration of a multitude of factors: the compatibility of a particular microbial strain with the animal or plant species and its microbiome; the ease by which a novel symbiosis could be established during host-microbiome development; how well a novel microbe could colonise a host; what effect its presence has on the structure of the microbiome and host health; what stages of plastic biodegradation different microbes address; how rapidly the PBMs biodegrade plastic compared to gut-retention time (Dawson et al., 2018b); host health advantages; wider ecological effects; and crucially, how effectively the symbionts eradicate MNPs from a habitat. Previous findings regarding the processes underlying microbial colonisation (Holt et al., 2020; Millet et al., 2014; Stauder et al., 2012) and symbiont establishment (Dong et al., 2020; Nyholm & McFall-Ngai, 2004) will inform how a successful novel symbiosis might be established and data from PBM studies can indicate which are likely candidates. A further complicating factor concerns the biochemical breakdown of additives, plasticisers and toxic chemicals absorbed from the environment, commonly present in plastic waste (Ahmaditabatabaei et al., 2021; Kale et al., 2015). These too must be considered along with the main polymer degradation if environmentally safe plastic biodegradation is to be developed.

4 Conclusions

Plastic waste is a key factor in our current ecological and climate crisis; macro-, micro- and nanoplastic negatively impact individual and ecosystem health, reduce the aesthetic value of habitats and may result in financial losses to industries such as tourism and shipping. Measures to limit the impact of plastics include regulatory control, campaigns to change public and corporate behaviour and reclaiming and recycling plastic waste. For those plastics that are lost to the environment, the stability of common synthetic plastics is a barrier to biodegradation in most natural habitats. Over the past 10 years, there has been an increasing number of studies focussing on the sourcing of biobased materials from both plants and animals, such as cellulose, lignin and chitosan, to substitute or blend with fossil-fuel-derived plastics to enhance biodegradation. Additionally, an increasing range of microbes, commonly bacteria and fungi, and associated enzymes have been identified which are able to biodegrade different plastics at meaningful rates, from a variety of habitats. Some are in symbiosis with an animal host, which together are highly efficient. Our current knowledge can be used to create microbial solutions which eradicate collected plastic. A next step in addressing plastic pollution could be the establishment of a novel symbiosis between PBMs and a filter-feeder, which together could reduce both macroplastics and MNP in natural habitats, such as aquatic sinks.

Author Contribution All authors contributed to the document's conceptualization. RD was responsible for the writing of the original draft, and NW was responsible for outlining the scope of the systematic review and undertook the supervision of the writing process. Both authors shared responsibility for review and editing.

Data Availability Data sharing is not applicable to this article as no datasets were generated or analysed during the current study; however, further information regarding the examples discussed within the text is available via hyperlinks within the text or in the reference list below.

Declarations

Conflict of Interest The authors declare no competing interests.

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