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Co-consumption for plastics upcycling: A perspective

Michael Weldon, Sanniv Ganguly, Christian Euler *

Department of Chemical Engineering, University of Waterloo, Canada

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ABSTRACT

The growing plastics end-of-life crisis threatens ecosystems and human health globally. Microbial plastic degradation and upcycling have emerged as potential solutions to this complex challenge, but their industrial feasibility and limitations thereon have not been fully characterized. In this perspective paper, we review literature describing both plastic degradation and transformation of plastic monomers into value-added products by microbes. We aim to understand the current feasibility of combining these into a single, closed-loop process. Our analysis shows that microbial plastic degradation is currently the rate-limiting step to "closing the loop", with reported rates that are orders of magnitude lower than those of pathways to upcycle plastic degradation products. We further find that neither degradation nor upcycling have been demonstrated at rates sufficiently high to justify industrialization at present. As a potential way to address these limitations, we suggest more investigation into mixotrophic approaches, showing that those which leverage the unique properties of plastic degradation products such as ethylene glycol might improve rates sufficiently to motivate industrial process development.

1. Introduction

The advent of plastics has significantly improved quality of life globally by enabling the development of lightweight, durable, and efficient products with a wide array of applications. In particular, plastics have played a significant role in feeding the growing human population by making farming activities more efficient and helping to prevent food spoilage (Hofmann et al., 2023). However, their resistance to degradation, coupled with linear, "take-make-waste" use economics has led to an increasingly dangerous plastics end-of-life crisis. 400 megatonnes of plastic were produced in 2022 alone (Statista Research Department, 2024), and only ~9% of all the plastic ever produced has been recycled, with an estimated 22% having ended up in the environment (D'ambrieres, 2019), where it physically degrades into persistent micro- and nanoplastic particles which threaten environmental systems worldwide (Du et al., 2020), and contributes to CO_2 emissions (Stegmann et al., 2022).

Cleaning up environmental microplastics, especially those in drinking water supplies, is a critical task to address the *acute* problem of environmental plastic pollution. A number of new technologies motivated by this need have been rapidly developed, though deployment lags. Of these technologies, those which leverage microbial degradation pathways are particularly interesting because of their low environmental impact, and their potential to transform plastic waste into an array of valuable feedstocks for upgrading (Lee et al., 2023), or directly into valuable products (Diao et al., 2023). Though the history of investigation into biological degradation of plastics extends back to as early as 1976 (Watanabe et al., 1976), this field has recently exploded with the discovery and engineering of both polyethylene terephthalate (PET) plastic-degrading enzymes and pathways (Yoshida et al., 2016; Jerves et al., 2021; Son et al., 2019), and microbial consortia capable of degrading recalcitrant plastics (Syranidou et al., 2017). Microbial plastic degradation not only has potential in addressing microplastic accumulation, but also in the transformation of bulk plastic waste via novel recycling processes.

Preventing plastics from accumulating in the environment in the first place – that is, solving the *chronic* problem of environmental plastic pollution – is of similar importance to addressing the acute problem. Modern society is dependent on plastics, so it is unlikely that we will avoid using them altogether. Drastically reducing or completely ending the flux of persistent plastics into the environment will require increasing recycling rates significantly and/or shifting to biodegradable plastics wherever possible (Stegmann et al., 2022). Achieving these changes in the plastic economy will in turn require significant technological development to make recycling more economical, and to establish biodegradable drop-in replacements with similar properties to

* Corresponding author.
E-mail address: ceuler@uwaterloo.ca (C. Euler).

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existing plastics (Vidal et al., 2024). In this regard, microbial upgrading technologies are also of special interest, because of their specificity, potentially high yields, and, again, low environmental impact. For example, polyhydroxyalkanoates (PHAs), a natural carbon storage intermediate in many microbes, have been extensively explored as drop-in replacements for polypropylene (PP) and other plastics (Muthuraj et al., 2021). Microbial transformation of petroleum-derived plastics to PHAs or other biopolymers represents one attractive route of many to increase the value of bulk plastic waste through chemical transformation – i.e. to "upcycle" these streams. Ultimately, completely addressing the plastics problem will require coupling degradation and 54 upcycling steps, as in Fig. 1, to make closing the plastics loop economically viable.

The purpose of this perspective paper is not to comprehensively review microbial plastic degradation and upcycling literature, since many such reviews already exist (see (Chow et al., 2023) as an example). Rather, we aim to examine broad trends in the rates of plastic breakdown by microbes and valorization of plastic breakdown products, with motivation to understand the progress toward feasibility of industrially relevant, closed-loop microbial degradation-valorization processes. Our focus is on the rate of input consumption, and efficiency of transformation of these inputs, not the scope of products that can be made, since these too have been reviewed extensively (see (Choi et al., 2023) as an example). As such, we examine a targeted subset of the literature primarily limited to polyethylene (PE), polypropylene (PP), polyurethane (PU), and polyethylene terephthalate (PET) related works, since these plastics make up the volume majority of plastic production (Stegmann et al., 2022).

We find that, while progress toward microbial circularization in the plastic economy has been made, significant barriers remain. In particular, the productivity of both microbial degradation and upcycling pathways is, at present, far too low for either of these to be of industrial use and moreover, gains in productivity have not been made over time except in the case of polyethylene terephthalate (PET) degradation. Furthermore, the demonstrated degradation rates are generally at least one order of magnitude smaller than those of upcycling pathways, indicating that there are potentially insurmountable barriers to the development of fully microbial plastic degradation-upcycling loops. Based on these broad observations and on specific examples from the reviewed literature, we suggest further investigation into mixotrophic approaches as a potential route to alleviate the challenges we have highlighted. To this end, we present a case study of butyrate production using co-consumption of ethylene glycol, showing that productivity above an industrially-relevant threshold could be achieved by engineering microbes to consume both plastic monomers and other carbon sources simultaneously. We suggest that this case study should motivate further economic analysis of novel mixotrophic bioprocesses for plastic circularization.

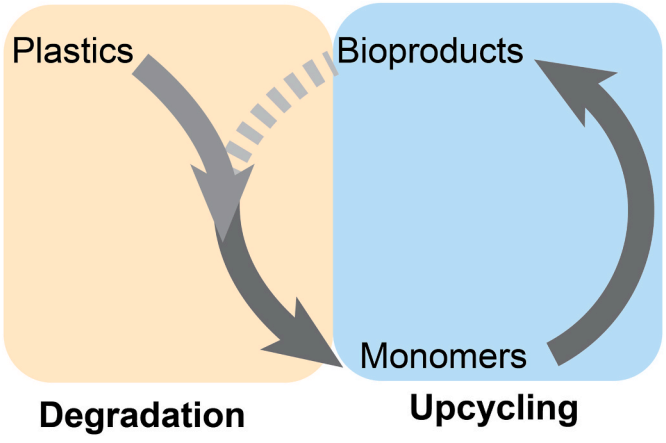

Fig. 1. Schematic of a circularized plastics economy. Microbial degradation of plastics to their monomers or other degradation products enables upcycling to value-added bio-products. These, too, may be degraded and chemically recycled (dashed line). Degradation rates must be similar to upcycling rates to enable closed-loop microbial processing of plastics.

1.1. Degradation

Work to uncover and characterize microbial plastic degradation activity has been ongoing since plastic use became widespread across industries and consumer products in the 1970s. For example, Watanabe et al. reported having purified and characterized a polyvinyl alcohol (PVA)-degrading enzyme from a *Pseudomonas* species in 1976 (Watanabe et al., 1976), demonstrating biodegradability of this plastic. PVA has since been used for a variety of applications in which biodegradability is critical. However, it was not until the 1990s that the search for plastic-degrading microbial activity began in earnest, motivated by increasing understanding of the risks posed by large-scale production of synthetic polymers. In particular, PU production had increased significantly, prompting research into PU-degrading biological activities (Cregut et al., 2013).

Early studies identified *Pseudomonas* and *Corynebacterium* as promising PU-degrading microbial families. For example, Kay et al. demonstrated 100% degradation of PU in 12 weeks using yeast extract-supported cultures of members of either family (Kay et al., 1991). Notably, these cultures were not able to use PU in minimal media: in the absence of yeast extract, no degradation of the polymer was detected. Later, Howard et al. showed that *Pseudomons chlororaphis* specifically could degrade PU, but did not report on degradation rates. However, they did measure biomass productivity on PU as a carbon source, showing relatively slow growth and low affinity for the substrate (Howard et al., 1999). The scope of PU degrading species was expanded more recently, with demonstration of degradation by specific *Streptomyces* (Pantelic et al., 2024) and *Bacillus* strains (Ji et al., 2024). Impressively, Pantelic et al. showed that *Streptomyces* strain PU10 could degrade PU samples at a concentration of 10 g/L by 96 wt% in just 48 h, and further that assimilation flux could be directed into polykyetide biosynthesis to yield products with potential economic relevance, such as the potential antimalarial compound undecylprodigiosin (Pantelic et al., 2024). In contrast, Ji et al. showed only 42.1 wt% degradation of PU in 30 days by *Bacillus* YXP1 (Ji et al., 2024).

While microbial plastic consumption rates have not increased significantly to date, the range of plastics for which microbial degradation has been demonstrated has been expanded significantly, especially in recent years. An early report of PE degradation by *Brevibacillus borstelensis* was published in 2005 (Hadad et al., 2005). Jeon et al. followed this in showing PE degradation by *Lysinibacillus* sp JJYO216 in 2021 (Jeon et al., 2021). In 2023, *Brevibacillus brevis* (Tiwari et al., 2023) and *Acinetobactor guillouiae* (Kim et al., 2023) were shown to degrade PE as well. Jeon et al. also demonstrated that *Lysinibacillus* sp JJYO216 can degrade PP, and indeed more efficiently than it degrades PE. Similarly, nylon and polyvinyl chloride (PVC) degradation has been demonstrated over many years. An early report of nylon-6 and nylon-6,6 degradation by *Bacillus cereus* was published in 2007 (Sudhakar et al., 2007), and later *B. brevis* was shown to degrade nylon-6,6 specifically (Tiwari et al., 2022). The very recent expansion and characterization of the nylonase class of enzymes will no doubt lead to improvements in microbial nylon-6 degradation in future years (Bell et al., 2024). PVC degradation by both *Pseudomonas citronellolis* and *Bacillus flexus* was reported in 2019 (Giacomucci et al., 2019), with later demonstration of degradation by a consortium of *Bacillus* and *Micrococcus* species in 2022 (Yadav et al., 2022), and by an uncharacterized consortium isolated from the gut of *Tenebrio molitor* larvae in 2023 (Xu et al., 2023).

The microbial plastic degradation literature has been summarized more thoroughly in the past. For example, Han et al., has compiled a list of characterized enzymes from various microbes which have been shown to degrade plastics ranging from PET to PU (Han et al., 2024).

Similarly, Bhaduri et al. curated a comprehensive list of microbes which have been shown to degrade both pre-treated and untreated PE and PP (Bhaduri et al., 2008). Notably, they reported improved degradation rates with supplementation of native carbon sources such as cellulose and lignin, which is in line with the improvements in degradation observed by Kay et al. More recent literature describes efforts to characterize enzymes from microbes which have shown degradation of target plastics. For example, Hu et al. described cloning a cutinase gene from *Fusarium solani* into *Pichia pastoris* to degrade polybutylene succinate in 2016 (Hu et al., 2016). In the same year, Yoshida et al. identified polyethylene terephthalate esterase (PETase) and monohydroxyethyl terephthalate hydrolases (MHETase) enzymes in *Ideonella sakaiensis* (Yoshida et al., 2016). Since then, there have numerous reports characterizing these enzymes, including detailed descriptions of their reaction mechanisms (Jerves et al., 2021).

Two themes relevant to utilization of plastic degradation activity emerge in the literature we reviewed. First, as is expected based on the fact that man-made polymers tend to persist in the environment, the timeframe for observable degradation is on the order of tens of days or weeks, with the exception of the Pantelic et al. study. These degradation rates, summarized in Table 1, are consistent regardless of polymer type and microbial host. However, substrate pre-treatment is a critical aspect in the observed degradation rate of plastics (Yasin et al., 2022), and this may account for the relatively high consumption rate observed by Pantelic et al. Pre-treatment approaches were heterogeneous across the literature we reviewed. Despite the various pre-treatment methodologies of these studies, the fastest reported degradation rates are at least an order of magnitude lower than those of native carbon sources in industrial settings, which are on the order of hours.

Table 1
Summary of historical characterization of plastic-degrading microbes and communities, excluding literature characterizing polyethylene terephthalate degradation. N.R. – not reported.

Year	Organism(s)	Substrate(s)	Degradation Rate (wt%)	Reference
1976	*Pseudomonas* sp	Polyvinyl alcohol	N.R.	Watanabe et al. (1976)
1991	*Corynbacterium* sp *Pseudomonas aeruginosa*	Polyurethane	100% in 12 weeks (with supplement)	Kay et al. (1991)
1999	*Pseudomonas chlororaphis*	Polyurethane	N.R.	Howard et al. (1999)
2005	*Brevibacillus borstelensis*	Polyurethane	11% in 30 days	Hadad et al. (2005)
2007	*Bacillus cereus*	Nylon-6 Nylon-6,6	2% in 3 months 7% in 3 months	Sudhakar et al. (2007)
2019	*Pseudomonas citronellolis* *Bacillus flexus*	Polyvinyl chloride	19% in 30 days	Giacomucci et al. (2019)
2021	*Lysinibacillus* sp JJYO216	Polyethylene Polypropylene	4% in 26 days 9% in 26 days	Jeon et al. (2021)
2021	*Pseudoxanthomonas* sp strain NyZ600	Bisphenol-A polycarbonate	N.R.	Yue et al. (2021)
2022	*Brevibacillus brevis*	Nylon-6,6	22% in 35 days	Tiwari et al. (2022)
2022	*Bacillus* spp *Micrococcus* spp	Polyvinyl chloride	90% in 6 months	Yadav et al. (2022)
2023	*Brevibacillus brevis*	Polyethylene	19.8% in 35 days	Tiwari et al. (2023)
2023	Uncharacterized consortium	Polyvinyl chloride	6% in 30 days	Xu et al. (2023)
2023	*Acinetobacter guillouiae*	Polyethylene	6% in 28 days	Kim et al. (2023)
2024	*Streptomyces* sp PU10	Polyurethane	96% in 48 h	Statista Research Department (2024)
2024	*Bacillus* sp YXP1	Polyurethane	42.1% in 30 days	Ji et al. (2024)

Second, despite these observed low degradation rates, there has clearly been a greater focus on finding new organisms and activities for plastic degradation than there has been for improving rates of known degradation activities. This is true even for polymers for which degradation activity had previously been established. For example, in our review, PE degradation was independently reported four times, with no improvement in degradation rate over time. The only apparent exception to this trend is PETases and MHETases, which have been extensively engineered since their discovery (Son et al., 2019). It is possible that these - and PET degradation more generally - have been subject to improvement efforts because the entire PET degradation pathway was characterized upon its discovery. In contrast, degradation pathways the other plastics described here have yet to be fully characterized. This may be due to the inherent difficulties of characterizing pathways distributed across community members, or it may be due to the fact that many plastic degrading microbes are not well characterized in general, so further investigation is challenging. Regardless, the lack of pathway characterization may limit metabolic engineering approaches to degradation improvement. Similarly, many of the plastic degrading strains identified here are non-model organisms, and as such there may be insufficient tools for their engineering.

These, and other challenges must be addressed in order for the degradation half of the degradation-upcycling loop to be made feasible by microbial processes. Uncovering the underlying pathways for plastic consumption will accelerate this work, as exemplified by the improvements in PETase activity that have been achieved. However, a promising complementary path forward, as demonstrated by Kay et al., is to engineer co-consumption of plastics alongside a more favourable carbon source, or other supportive media components (Kay et al., 1991). We provide an example of how such an approach could be useful in Section 3 of this paper.

1.2. Upcycling

The lack of characterization of degradation pathways for most plastics has also limited research characterizing possible upcycling routes for the products of these pathways. In contrast, the breakdown of PET – achievable by both chemical and biochemical methods – is well characterized and known to yield ethylene glycol (EG) and terephthalic acid (TA) (Tournier et al., 2020). These are high potential, next-generation feedstocks for metabolic engineering (Ma et al., 2021). Importantly, EG passively diffuses into cells and its consumption is therefore not subject to regulation by catabolite repression (Pandit et al., 2017; Tiso et al., 2021). In contrast, cellular import of TA may require pH values below those which are physiologically compatible, so expression of a tripartite tricarboxylate transporter (TTT) or a major facilitator superfamily (MFS) transporter, which must both be engineered to avoid repression, may be used for TA uptake (Pardo et al., 2020). EG is assimilated into central carbon metabolism (CCM) through conversion to glycerate, while TA enters CCM through conversion to β-ketoadipyl-CoA (Tiso et al., 2021; Boronat et al., 1983).

Flux may be rerouted from these assimilation pathways to produce value-added products, and the choice of product to target is critical for determining scale-up potential. This is, in turn, critical for establishing realistic microbial routes for circularizing the plastic economy. Though the inputs and outputs, and up- and downstream processing steps for each individual process must be considered individually to evaluate their economic feasibility, many bioprocesses have common core elements that constrain their economics. Thus, for a wide range of bioprocesses and bio-based products, viability of industrial scale-up is more likely if process productivity is at least 3 g/L/h, yields of ~80% of the theoretical maximum can be achieved, and titers of ~50 g/L can be achieved for products with prices near $1.00/lb (Dien, 2013). These benchmarks are not definitive: for example, lower values may be permissible for more valuable products, such as fine chemicals and

pharmaceuticals. However, we will use them here as a point of reference to evaluate the EG and TA valorization pathways in the literature we review. A summary of this review is presented in Table 2.

The earliest success of these works – and still one of the most notable results – involved screening both laboratory microbe strains and soil microorganisms that could grow on EG or propylene glycol as the sole carbon source and naturally produce glycolic acid (GA) (Kataoka et al., 2001). The yeast strain *Pichia naganishii AKU 4267* and the soil fungus *Rhodotorula* sp. *3Pr-126* were both demonstrated to accumulate GA from EG to high titer (105, 110 g/L) at approximately 80% of the theoretical yield of 1.2 g/g (Kataoka et al., 2001; Pandit et al., 2021). However, productivities were orders of magnitude lower than the industrial benchmark in both cases. Improving rates in these natural over-producers may be challenging because the synthetic and systems biology tools available for them are not as extensive as those for other industrially relevant organisms.

More recently, *Gluconobacter oxydans* was used to produce GA from EG, with titer and productivity improvements over time (Kim et al., 2021a, 2021b). Other model organisms engineered to use EG include the more industrially relevant species *Yarrowia lipolytica* and *Pseudomonas putida*. For example, *Y. lipolytica* was used to produce GA from EG, with yield, but not productivity, reaching the industrial benchmark (Carniel

Table 2
Summary of recent progress in upcycling polyethylene terephthalate hydrolysates. Productivity and yield values determined from reported data.

Year	Organism	Substrate	Product	Product Category	Productivity (g/Lh)	Yield (g/g)	Titer (g/L)	Co-Culture?	Reference
2001	*Pichia naganishii* AKU 4267	Ethylene glycol	Glycolic acid	Commodity	0.88	0.95	105	No	Kataoka et al. (2001)
2001	*Rhodotorula* sp 3Pr-216	Ethylene glycol	Glycolic acid	Commodity	0.92	0.99	110	No	Kataoka et al. (2001)
2008	*Pseudomonas putida* G016, G019	Terephthalic acid	Polyhydroxyalkanoate	Biopolymer	0.0084	0.060	0.25	No	Kenny et al. (2008)
2012	*Pseudomonas putida* G016	Terephthalic acid, glycerol	Polyhydroxyalkanoates	Biopolymer	0.11	0.12	5.3	No	Kenny et al. (2012)
2018	*Pseudomonas putida* KT2440	Ethylene glycol	Polyhydroxyalkanoates	Biopolymer	0.0052	0.06	0.37	No	Franden et al. (2018)
2019	*Escherichia coli*	Terephthalic acid	Protocatechuic acid	Specialty	0.14	0.76	0.43	No	H. et al. (2019)
2019	*Escherichia coli*	Terephthalic acid	Gallic acid	Specialty	0.018	0.48	0.22	Yes	H. et al. (2019)
2019	*Escherichia coli*	Terephthalic acid	Pyrogallol	Specialty	0.023	0.25	0.14	Yes	H. et al. (2019)
2019	*Escherichia coli*	Terephthalic acid	Muconic acid	Biopolymer	0.064	0.73	0.38	Yes	H. et al. (2019)
2019	*Escherichia coli*	Terephthalic acid	Vannilic acid	Flavouring	0.000047	0.0061	0.0034	Yes	H. et al. (2019)
2019	*Gluconobacter oxydans*	Ethylene glycol	Glycolic acid	Commodity	0.067	1.2	0.76	No	H. et al. (2019)
2020	*Escherichia coli*	Terephthalic acid	2-pyrone-4,6-dicarboxylic acid	Biopolymer	0.086	1	0.52	Yes	Kang et al. (2020)
2021	*Escherichia coli*	Terephthalic acid	Protochatechuic acid	Specialty	0.14	0.84	3.8	No	Kim et al. (2021a)
2021	*Gluconobacter oxydans*	Ethylene glycol	Glycolic acid	Commodity	1.5	1	31	No	Kim et al. (2021a)
2021	*Pseudomonas umsongensis*	Ethylene glycol, Terephthalic acid	Polyhydroxyalkanoate	Biopolymer	0.0065	0.014	0.15	No	Tiso et al. (2021)
2021	*Pseudomonas umsongensis*	Ethylene glycol, Terephthalic acid	Hydroxyalkanoyloxy-alkanoate	Surfactant	0.005	0.01	0.03	No	Tiso et al. (2021)
2021	*Escherichia coli*	Terephthalic acid	Vanillin	Flavouring	0.005	0.79	0.12	No	Sadler and Wallace (2021)
2021	*Pseudomonas putida* KT2440	Bis(2-hydroxyethyl) terephthalate	Beta-ketoadipate	Biopolymer	0.16	0.48	15	No	Werner et al. (2021)
2021	*Escherichia coli*	Terephthalic acid	Catechol	Specialty	0.055	0.66	0.66	No	Kim et al. (2021b)
2021	*Pseudomonas stutzeri*	Ethylene glycol, Terephthalic acid	Polyhydroxybutyrate	Biopolymer	0.0023	0.025	0.2	Yes	Liu et al. (2021)
2021	*Escherichia coli*	Ethylene glycol	Glycolic acid	Commodity	0.1	0.8	10	No	Pandit et al. (2021)
2022	*Pseudomons putida* KT2440	Ethylene glycol, Terephthalic acid	Muconic acid	Biopolymer	0.077	0.5	5.7	No	Liu et al. (2022)
2023	*Rhodococcus jotii* strain PET	Ethylene glycol, Terephthalic acid	Lycopene	Specialty	0.00002	0.00012	0.0012	No	Diao et al. (2023)
2023	*Escherichia coli*	Ethylene glycol	Mevalonic acid	Specialty	0.035	0.052	1.6	No	Wagner et al. (2023)
2023	*Escherichia coli*	Terephthalic acid	Beta-ketoadipic acid	Biopolymer	0.091	0.93	2.2	No	You et al. (2023)
2023	*Yarrowia lipolytica*	Ethylene glycol	Glycolic acid	Commodity	0.46	0.96	33	No	Carniel et al. (2023)
2023	*Escherichia coli*	Ethylene glycol	L-tyrosine	Protein	0.021	0.2	2	No	Panda et al. (2023)
2023	*Escherichia coli*	Ethylene glycol	L-phenylalanine	Protein	0.016	0.15	1.5	No	Panda et al. (2023)
2023	*Escherichia coli*	Ethylene glycol	p-Coumaric acid	Specialty	0.01	0.1	1	No	Panda et al. (2023)
2023	*Pseudomonas putida*	Ethylene glycol, Terephthalic acid	Polyhydroxyalkanoate	Biopolymer	0.0065	0.028	0.39	Yes	Bao et al. (2023)
2023	*Pseudomonas putida*	Ethylene glycol, Terephthalic acid	Muconic acid	Biopolymer	0.03	0.14	1.8	Yes	Bao et al. (2023)
2023	*Escherichia coli*	Terephthalic acid	Adipic acid	Biopolymer	0.0048	0.69	0.12	Yes	Valenzuela-Ortega et al. (2023)
2023	*Pseudomonas putida* KT2440	Ethylene glycol, Terephthalic acid	Polyhydroxyalkanoate	Biopolymer	0.026	0.08	1.9	Yes	Liu et al. (2023)
2023	*Escherichia coli*	Glycoaldehyde	2,4-dihydroxybutyric acid	Biopolymer	0.042	0.26	1	No	Frazao et al. (2023)
2023	*Escherichia coli*	Ethylene glycol	2,4-dihydroxybutyric acid	Biopolymer	0.017	0.041	0.8	No	Frazao et al. (2023)
2024	*Pseudomonas putida* KT2440	Ethylene glycol, Terephthalic acid	Polyhydroxybutyrate	Biopolymer	0.0071	0.037	0.17	No	Manoli et al. (2024)

et al., 2023). EG conversion to GA is a popular target for metabolic engineers because the pathway is simple, requiring only two well-characterized steps (Boronat et al., 1983), and GA is a commodity chemical with broad industrial relevance. However, the first EG-derived, fermentation-based GA product is now on the market (Web, 2022). Therefore, academic research to transform EG to GA may no longer be a critical priority; rather, finding novel products that can be made from EG may be more useful.

In contrast, TA valorization strategies are much more heterogeneous because its biochemistry is more complex. For example, *Escherichia coli* was used to convert TA to protocatechuic acid, gallic acid, pyrogallol, muconic acid, and vanillic acid in a single fermentation. Of these, only vanillic acid had a yield below 0.1 g/g, demonstrating potential for continued work toward generating these products using this platform strain (Kim et al., 2021a). The same group that achieved this also improved production of protocatechuic acid – and its derivative catechol – from TA using *E. coli* (Kim et al., 2021a, 2021b). Work to produce biopolymer precursors and biopolymers from TA using *P. putida* is also ongoing. For example, promising results have been achieved for β-ketoadipate and muconic acid production as feedstocks for chemical polymerization (Werner et al., 2021; Liu et al., 2022). These should motivate future work, but at present the productivities, yields, and titers presented in these studies are a fraction of the industrial benchmarks we introduced earlier in this section (Table 2).

Nearly all of the studies we analyzed used two-stage fermentation to achieve measurable conversion of either EG or TA, likely because neither feedstock alone can support significant biomass productivity. In these two-phase strategies, biomass was first accumulated using a high-yield carbon source (typically glucose), then a production phase was initiated to convert the PET hydrolysates into target products. In one study, cells were fed glycerol – another next-generation feedstock – and TA in a two-stage bioprocess for polyhydroxyalkanoate (PHA) production. The results of feeding carbon sources at different points in the process were compared, revealing that the most productive and highest-yield fermentation resulted from feeding glycerol during both phases, while only feeding TA for the production phase (Kenny et al., 2012). This suggested that there was some inhibitory effect of exposure to TA; future work should examine this effect further to narrow the scope of possible hosts for valorization.

More recent work on PHA production has taken an approach opposite to the two-phase fermentation strategy by coupling growth and PHA production, which are natively decoupled, in an engineered overproducing *P. putida* strain capable of consuming TA and TA-derived feedstocks (Manoli et al., 2024). The authors of this work showed that, for PHA production, coupling can increase productivity and substrate utilization and decrease the formation of unwanted by-products. Impressively, their strain was able to co-consume EG and TA from PET hydrolysates directly to produce PHA, albeit at a relatively low rate of 20 mM hydrolysate consumed after 50 h.

Based on our review, the most common microbial hosts used for upcycling PET hydrolysates are the model organisms *E. coli* and *P. putida*. Although other organisms have shown better natural assimilation of these feedstocks, the use of model organisms may be favourable because the extensive synthetic biology and modelling tools available for them can be leveraged to engineer higher overproduction of value-added compounds. Many of the studies we examined used co-cultures – of different strains or species – to compartmentalize sections of the assimilation and production pathways and thus reduce the metabolic burden on individual community members (Kim et al., 2021a; Bao et al., 2023; Kang et al., 2020; Liu et al., 2021, 2023; Valenzuela-Ortega et al., 2023). This strategy typically resulted in increased productivity and/or yield, suggesting that the metabolic burden of valorization pathways - especially for TA - may be an inherent challenge. We also found significantly more literature characterizing EG valorization. However, TA was used for a wider range of products, as EG was primarily used to produce GA or PHA.

Although there are a few promising PET upcycling routes that could impact a number of sectors, almost all products in the literature we examined have yet to be produced at levels that meet the industrial benchmarks. The exception to this trend is GA, for which production from EG has met (Kataoka et al., 2001; Carniel et al., 2023) or exceeded benchmarks (Kim et al., 2021b) in multiple studies; as such, it is no surprise that the EG-to-GA bioprocess has been successfully commercialized. High yields have been achieved for other products, but productivity is still orders of magnitude lower than the industrial benchmark. Such low productivities will undoubtedly continue to limit industrial feasibility for both EG and TA valorization bioprocesses. We therefore suggest that it is critical for future work to focus on increasing transformation rates to enable scale-up. Indeed, in the studies we examined, two-stage fermentation, which is generally a favourable strategy for maximizing productivity (Venayak et al., 2015), was still insufficient to overcome low utilization rates. Other, likely novel, metabolic and/or process engineering strategies may be essential to meet industrial benchmarks.

1.3. Co-consumption as a novel approach

To overcome some of the current limitations of PET upcycling, model-informed co-consumption strategies should be considered more broadly. Manoli et al. (Manoli et al., 2024) engineered co-consumption of TA and EG specifically to couple PHA production to growth, demonstrating increased PHA accumulation to 46% of dry cell mass compared to 7.09% in the wild type *P. putida* as a result. Their approach provides an interesting template which we believe could be tailored to a wide range of products because of specific favourable properties of both EG and TA. As substrates, these can both be co-consumed with various more traditional carbon sources, including next-generation feedstocks such as waste- or algae-derived glycerol (Chilakamarry et al., 2021), or acetate derived from CO_2 reduction (Crandall et al., 2023). Additionally, protein burden notwithstanding, both have assimilation pathways which are at least cofactor-neutral, with the EG consumption pathway actually favourably generating two units of NADH per molecule assimilated (Boronat et al., 1983). This makes it ideal for coupling to some biosynthetic pathways, such as fatty acid production, as these require net energy input.

As an illustrative example of this principle, we considered the co-consumption of EG with three more traditional carbon sources - glucose, glycerol, and acetate - in *E. coli* using flux balance analysis (FBA). We chose butyrate as an example value-added product in part because it has a well-characterized pathway that has been used in *E. coli* previously (Wang et al., 2019), but more critically because this pathway requires net energy input in the form of NADH. Thus, an additional source of reducing power to recycle NAD + to NADH could be useful to drive flux toward butyrate production. *Any* pathway requiring NADH could similarly benefit from co-consumption with EG; butyrate is just a straightforward example of this principle. A schematic of the butyrate pathway in relation to both CCM and the ethylene glycol assimilation pathway is shown in Fig. 2A. The first two steps of EG assimilation require NAD+ and produce NADH, which is in turn required for two steps of the butyrate production pathway. This yields a direct material and energetic coupling between EG in and butyrate out, with the co-consumed carbon source supporting growth via CCM.

We generated production envelopes for all three co-consumption strategies using the *E. coli* iAF1260 genome-scale metabolic model (Feist et al., 2007) augmented with reactions required for EG assimilation as previously reported (Pandit et al., 2021). Based on unpublished data, we set the EG uptake rate to 3 mmol/gCDW/h, with all other uptake rates set to their default values in the model. In Fig. 2B, we show that for all three carbon sources, co-consumption with EG can significantly increase butyrate production for all growth rates (top row). For example, at the best operating point in cells fed glucose and EG, a production rate of ~3 mmol butyrate/gCDW/h is predicted, compared to

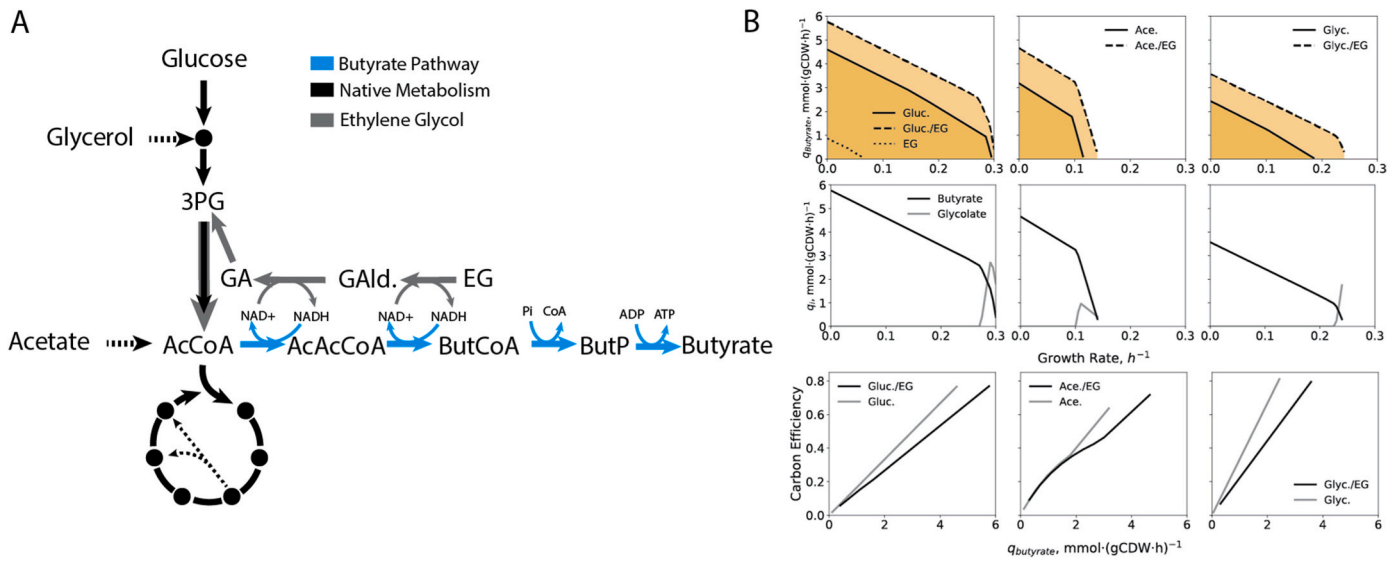

Fig. 2. Co-consumption of ethylene glycol and traditional carbon sources can boost productivity. **A.** Schematic of ethylene glycol (EG) assimilation and butyrate production coupling in a co-consuming strain. The EG assimilation pathway, in grey, transforms two molecules of NAD + to NADH, which are required in the butyrate production pathway, in blue. Central carbon metabolism, in black, is supported by the other carbon source - glucose, acetate, or glycerol here. Dashed lines indicate non-glucose entry points to metabolism, and corresponding active pathways. Some steps omitted to highlight critical metabolic nodes. EG - ethylene glycol; GAld - glycoaldehyde; GA - glycolic acid; 3 PG - 3-phosphoglycerate; AcCoA - acetyl-CoA; AcAcCoA - acetoacetyl-CoA; ButCoA butyryl-CoA; ButP - butyryl-phosphate. **B.** Predicted performance of co-consuming cells. Top row: production envelopes for glucose, glycerol, and acetate, respectively, for the single carbon source (sold line), co-consumption (dashed line), and EG-only (stippled line) scenarios. Note that the production envelope for the EG-only scenario is the same for all conditions, so it is only presented in the first panel. Middle row: butyrate (black line) and glycolate (grey line) production rates as a function of growth rate for the co-consumption scenario. Bottom row: carbon efficiency, defined as the ratio of carbon assimilated into butyrate to total carbon uptake as a function of butyrate production rate. For all three scenarios, with the grey line corresponding to the sole carbon source scenario and the black line corresponding to the mixotrophic scenario.

just ~1 mmol butyrate/gCDW/h for cells fed glucose alone. Despite this 3x increase, the best operating point growth rate for either scenario is similar, indicating that indeed the butyrate production flux is directly derived from the EG uptake flux. As a result, we predict that the best of both worlds is possible with co-consumption: cells can grow at a relatively high rate, while also producing at a high rate. This directly addresses the primary challenge of low upcycling productivity that we identified in our review of the microbial plastic degradation literature.

Though this effect is less prominent for glycerol and acetate, co-consumption significantly increases the predicted maximum possible growth rate in these scenarios. The increase is largest for glycerol, for which a maximum growth rate near 0.25/h is predicted for the co-consumption scenario compared to around 0.19/h on glycerol alone. This 31% increase represents significant potential for process intensity reduction in a hypothetical full-scale process making use of this co-consumption strategy. In all cases, "overflow" of EG metabolism resulting in GA production is predicted for unbalanced EG consumption at high growth rates (middle row). However, GA production drops to zero at the best operating point and for all growth rates lower than this for all three scenarios. Therefore, GA side production is not necessary in any of the co-consumption scenarios. The carbon efficiency, defined as the fraction of imported carbon molecules that are assimilated into butyrate, is lower for all production rates in all three scenarios (bottom row), because more carbon is necessarily required for the increased biomass production rate predicted in the co-consumption scenario. However, since co-consumption makes higher butyrate production rates possible, it enables similar carbon efficiency to the single carbon source case, but for higher butyrate production rates.

Importantly, this simple stoichiometric analysis does not consider the economics of such hypothetical coupled pathways. The addition of a second carbon source represents an additional operating cost that would scale with process volume. This additional cost could constrain scalability overall, despite the fact that co-consumption is likely to boost process productivity. However, this case study establishes a motivation for future technoeconomic assessment (TEA) of co-consumption processes because it establishes the baseline potential for this strategy to enable large scale valorization of PET-derived feedstocks. Mixotrophy could, in theory, support both high biomass productivity and high production rates for target chemical products. This is especially true for products of biosynthetic pathways, such as butyrate and biopolymers more generally, because these require net energy input and this can be derived from breakdown products of plastic. We showed that co-consumption with ethylene glycol is advantageous, but coupling to other plastic degradation products - whether derived from microbial degradation or from more traditional thermochemical means - could be readily considered in a similar way.

2. Discussion

Addressing the plastics end-of-life crisis will require significant technical development across a number of sectors, with corresponding policy support and appropriate incentives. Microbial degradation-upcycling routes will no doubt play a role in the broader movement toward a sustainable plastics future, but the exact way in which they will be leveraged depends on the constraints limiting their development and how quickly progress can be made toward alleviating these limitations. Our literature review suggests that constraints on microbial plastic degradation and upcycling are still actively being uncovered, and that heterogeneous progress currently limits application of microbial systems to the circularization of the plastic economy. In particular, work on the degradation half has been driven by novelty, rather than efficiency, and as such there has seemingly been near-zero improvements in degradation rates over to date. This is a major barrier to the usefulness of microbial degradation pathways for plastic upcycling, especially as competing thermochemical degradation technologies rapidly advance. In contrast, there has been significant development of plastic monomer upgrading pathways - to the point of commercialization of an EG upcycling process. However, progress to date has primarily been limited

to the valorization of PET monomers, with upgrading pathways for other plastic monomers lagging. The misalignment between research into degradation and upcycling pathways has undoubtedly limited the development of fully microbial degradation-upcycling loops, and will continue to do so. We suggest two possible routes to address this challenge.

First, work should be (re)focused on developing known plastic degradation pathways and processes instead of on uncovering new such activities for plastics for which degradation pathways are already known. While there are a multitude of man-made polymers for which degradation pathways must be found, PE, PP, PU, and PET make up the volume majority of all plastic streams (Stegmann et al., 2022). Investigation into known degradation activity for these plastics should therefore be a priority, with the approach that has been taken to improve PET degradation serving as a model for the other plastics in this list.

Second, tandem thermochemical-biological degradation-upcycling processes should be prioritized as a research focus. This approach has already proven promising for mixtures containing PET, PS, and high density PE (Sullivan et al., 2022), but there is potential for a wide spectrum of plastics to be upcycled this way via pyrolysis followed by gas fermentation, and/or by degradation of mixed plastics to monomers which can be upgraded via fermentation. Such work will require interdisciplinary cooperation to characterize and align the rates of thermochemical production of monomers and upcycling via fermentation.

For both proposed routes, co-consumption should be considered to support increased productivity to support rapid scaling. There is evidence from our literature review that co-consumption can dramatically improve degradation rates (from no degradation to 100% degradation (Kay et al., 1991)), and we have shown here that pairing EG, for example, with traditional carbon sources could significantly boost the synthesis rate of products of anabolic pathways, such as butyrate. However, full costing of such novel approaches must be performed via TEA to understand the cost-benefit trade-off arising from integrating a second carbon source into microbial processes for plastic breakdown product upcycling.

CRediT authorship contribution statement

Michael Weldon: Writing – original draft, Investigation, Data curation. **Sanniv Ganguly:** Writing – original draft, Data curation. **Christian Euler:** Writing – review & editing, Writing – original draft, Visualization, Investigation, Data curation, Conceptualization.

Declaration of competing interest

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

Data availability

No data was used for the research described in the article.

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