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Current Research on Microbe-Plastic Interactions in the Marine Environment

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Abstract

The microbial colonisers of plastics – the 'plastisphere' – can affect all interactions that plastics have with their surrounding environments. While only specifically characterised within the last 10 years, at the beginning of 2021 there were 140 primary research and 65 review articles that investigate at least one aspect of the plastisphere. We gathered information on the locations and methodologies used by each of the primary research articles, highlighting several aspects of plastisphere research that remain understudied: (i) the non-bacterial plastisphere constituents; (ii) the mechanisms used to degrade plastics by marine isolates or communities; (iii) the capacity for plastisphere members to be pathogenic or carry antimicrobial resistance genes; and (iv) meta-OMIC characterisations of the plastisphere. We have also summarised the topics covered by the existing plastisphere review articles, identifying areas that have received less attention to date – most of which are in line with the areas that have fewer primary research articles. Therefore, in addition to providing an overview of some fundamental topics such as biodegradation and community assembly, we discuss the importance of eukaryotes in shaping the plastisphere, potential pathogens carried by plastics and the impact of the plastisphere on plastic transport and biogeochemical cycling. Finally, we summarise the future directions suggested by the reviews that we have evaluated and suggest other key research questions.

Keywords

Plastisphere; Plastic biofilms; Microbial communities; Marine plastic pollution; Plastic biodegradation

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1. Introduction

The quantity of plastic pollution entering the oceans annually is increasing year-on-year [1], but the ultimate fate and durability of plastics in the oceans are unknown [2]. With some studies suggesting a persistence of hundreds of years [3] or fragmentation rates of only 1-5% per year [4], this has led us to look towards microbes for a solution to this problem. When plastics enter the environment, they are rapidly covered by organic matter, known as the ecocorona [5], and are colonised by microbes within minutes [6]. These plastic-colonising microbes – bacteria, fungi and single-celled eukaryotes as well as macro and other organisms – are collectively termed the 'plastisphere' [7]. While marine plastics have long been observed to have a colonising biofilm (*e.g.*, Carpenter & Smith, 1972 [8]), the first specific characterisation of the plastisphere was published by Zettler *et al.* in 2013 [7], following a call for research into microbial communities on plastics by Harrison *et al.* in 2011 [9]. Some earlier studies investigating biofilm formation in the marine environment did also include plastic materials (*e.g.*, [10]) or investigated the biomass colonising plastics in relation to plastic degradation (*e.g.*, [11]), but the specific focus on the taxonomic or functional characterisation of plastisphere communities has only been within the last approximately eight years. A literature search carried out on 4th January 2021 for the search terms "plastics plastisphere", "plastics microbial community", and "plastics microbial degradation" yielded a total of 1069 unique results. This was supplemented with our own literature collections and filtered manually to include only studies and reviews that fit the following criteria: (i) available online by the beginning of 2021; (ii) examined at least one aspect of the colonisation or degradation of surfaces in the marine environment; and (iii) the surfaces used included at least one recalcitrant, petrochemical plastic. This resulted in 140 primary research articles (Figs. 1 and 2 and Table S1) and 65 review articles (Fig. 3 and Table S2). Remarkably, 34 and 45% of the research articles and reviews, respectively, published to date were made available online in 2020.

1.1. Focus of plastisphere studies and methods used

Each of the 140 plastisphere primary research articles returned by our literature search was reviewed by one of the authors for details relating to the study topic, aims, experimental setup and methods used and key findings (Figs. 1 and 2; full details can be found in Table S1). To date, most plastisphere studies specifically focus (*i.e.*, "study topic"; Fig. 1) on the characterisation of the community structure of the colonising organisms (n=60), with a total of 46 or 77 studies (all study topics), that use microscopy to visualise these microbial colonisers or sequence at least one microbial community fraction, respectively. The majority of these use amplicon sequencing of marker genes (n=74) to characterise either the prokaryotes (n=61), the eukaryotes (n=4) or both (n=9). Only three studies returned by our literature search use metagenomic sequencing to characterise the plastisphere [12–14] (a fourth has since been published; Bhagwat *et al.* [15]) and one of these, Yang *et al.* [13], re-analyses data from Bryant *et al.* [12], meaning that there are currently only three metagenomic datasets. The remaining 80 studies were focussed on: (i) assessing the biodegradation of plastics by either communities or isolates (n=30), with a total of 36 studies including at least one measure of biodegradation, for example, weight loss, spectroscopy or microscopy; (ii) antimicrobial resistance (AMR), pathogenesis or harmful algal blooms (HAB; *n*=14), with a total of 20 studies including one measure of AMR or pathogenicity, for example, polymerase chain reaction (PCR) for virulence or AMR genes; (iii) vertical transport (*n*=9), with a total of 11 studies including some measure of vertical transport, for example, an assessment of plastic buoyancy before and after colonisation or an examination of plastic aggregation; or (iv) other (*n*=27), *i.e.*, they were focussed on another topic, such as assessing plastic concentrations in a given area but also included some information on or characterisation of the plastisphere. As we previously noted [16], there are relatively very few studies conducted in the Southern Hemisphere (*n*=16), only five of which use sequencing to characterise plastisphere communities, while there are a relatively large number of studies conducted around Europe (*n*=63), particularly in the North, Baltic and Mediterranean Seas.

1.2. Focus of plastisphere reviews and topics covered

Each of the 65 review articles returned by our literature search was examined by one of the authors for details on the focus of the review as well as the topics included (Fig. 3). Perhaps unsurprisingly, given that the first specific plastisphere characterisation was only published in 2013 [17], the first plastisphere-focussed review was published in 2015 [18]. All reviews published prior to 2015 were focussed on biodegradation (*n*=11) and the degradation of plastics by communities or consortia wasn't discussed in detail until 2017 [19]. In total, there are 16, 40, 9 and 3 reviews focussed on the plastisphere, plastic biodegradation, ecotoxicology of plastics or plastic-colonising pathogens, respectively. The first ecotoxicology of plastics review that discussed the plastisphere was published in 2017 [5], the first pathogen-focussed review was published in 2016 [20], and there are now 20 reviews that give an overview of the plastisphere while there are 50 that give an overview of plastic biodegradation. Interestingly, there are some research areas within both plastisphere and biodegradation topics that have received more attention than others. For example, while 15 reviews discuss microbial community assembly on plastics, only 6 discuss either horizontal or vertical transport that may be mediated or affected by the plastisphere and only 8 or 8 reviews discuss colonising pathogens and AMR or the methods used for plastisphere characterisation, respectively. Likewise, for degradation topics, 37 and 38 reviews discuss plastic degradation by isolates and the pathways or enzymes used for plastic degradation, respectively, but only one review discusses the rate at which degradation can occur, while 22, 18 and 11 reviews discuss factors that limit the degradation of plastics, the methods used to assess plastic degradation or plastic degradation by communities or consortia, respectively. There were intermediate numbers of reviews that included sections on the contaminants and additives of plastics (*n*=10) or plastic toxicity (*n*=19), while only four reviews discussed the role of plastics or plastic degradation in biogeochemical cycling.

In the following sections, we give an overview of current knowledge on the plastisphere. In some cases, we point the reader towards other reviews that have covered the topics in more detail. We summarise microbial community assemblages, the impact of eukaryotes on shaping the plastisphere, plastic biodegradation by marine microbes, microbial pathogens within the plastisphere and the combined effects of plastic pollution and plastisphere interactions on plastic transport and biogeochemical cycling. Finally, we summarise current knowledge, as well as the future directions suggested by the plastisphere reviews included here.

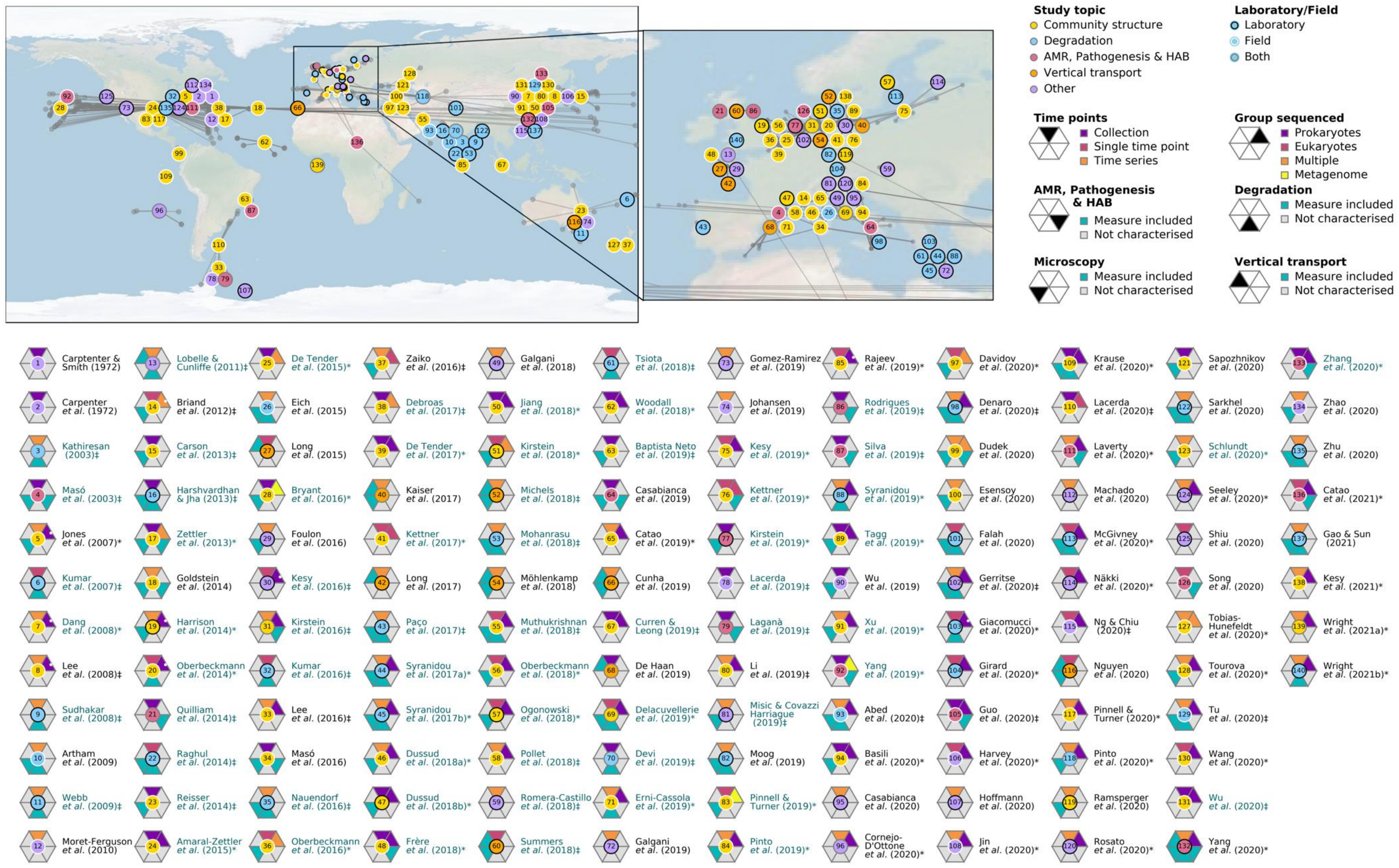


Figure 1. An overview of the sampling locations and methodologies used by all primary research articles that our literature search and subsequent filtering returned [4,6–8,10–

[14,16,21–150]. All sampling locations are marked by grey points with lines linking them to the numbered study that they were from (top; coloured by the topic that the study is focussed on, with black, white and grey edge colours being for studies carried out in the laboratory, field or both, respectively) with each study being represented by a hexagon (bottom) with six triangles summarising the experimental methodology used (legend top right). Note that white points within the "Group sequenced" triangle indicate that this sequencing was not high throughput, *e.g.,* by Denaturing Gradient Gel Electrophoresis (DGGE) or Terminal Restriction Fragment Length Polymorphism (T-RFLP). Study names shown in green were included in our previous review [151]. Asterisks after the study name denote that sequencing data are accessible, while ‡ denotes that data are not accessible. For example, 132. Yang *et al.* (2020) [56] was a laboratory study focussed on AMR, pathogenesis & HAB that employed a time series for sampling, used amplicon sequencing of the prokaryotes (16S rRNA gene) to characterise the microbial community (and made sequencing data accessible) and included measures of AMR, pathogenesis & HAB, degradation and microscopy, but did not include any measures of vertical transport. A table with full summaries (an extension of the table included in our previous review [151]) of the aims and experimental setup, polymer type, control substrate, community, degradation and aggregation/sinking determination methods and key findings for each study is in Table S1.

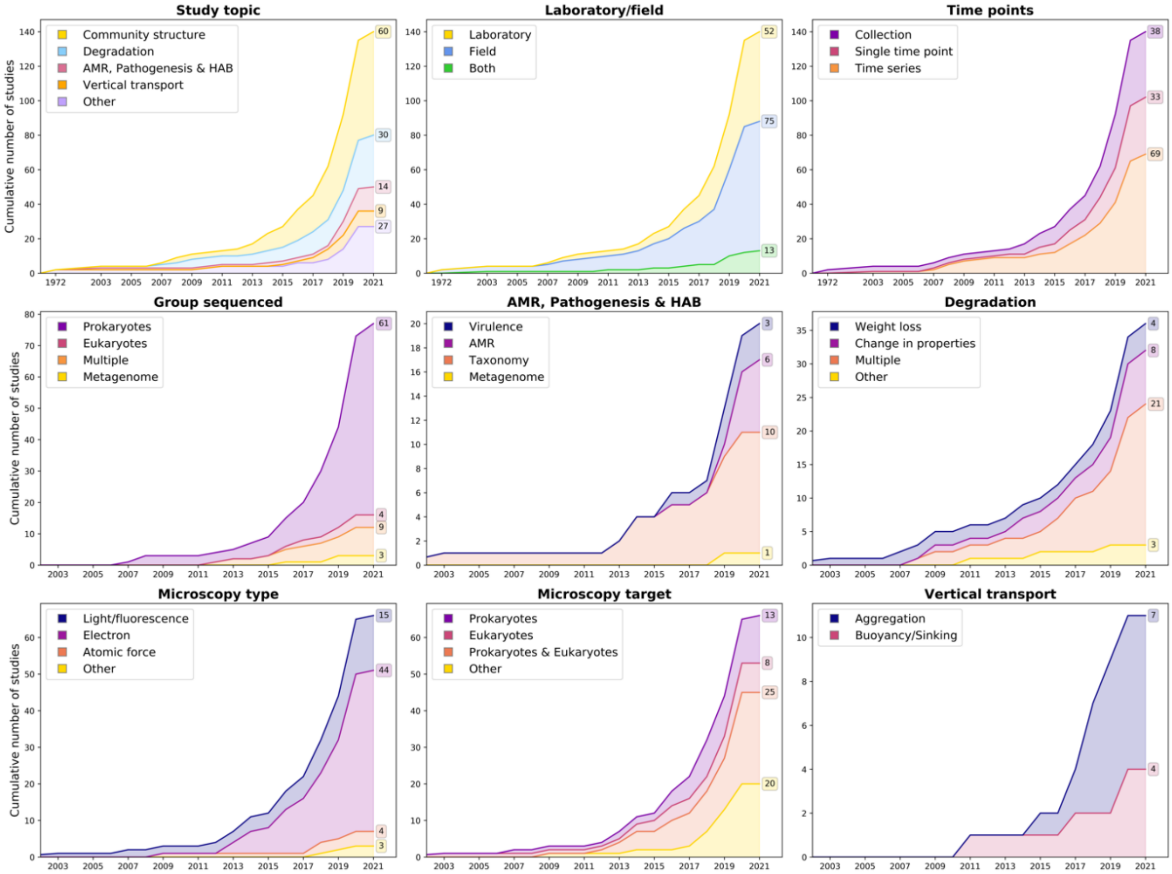
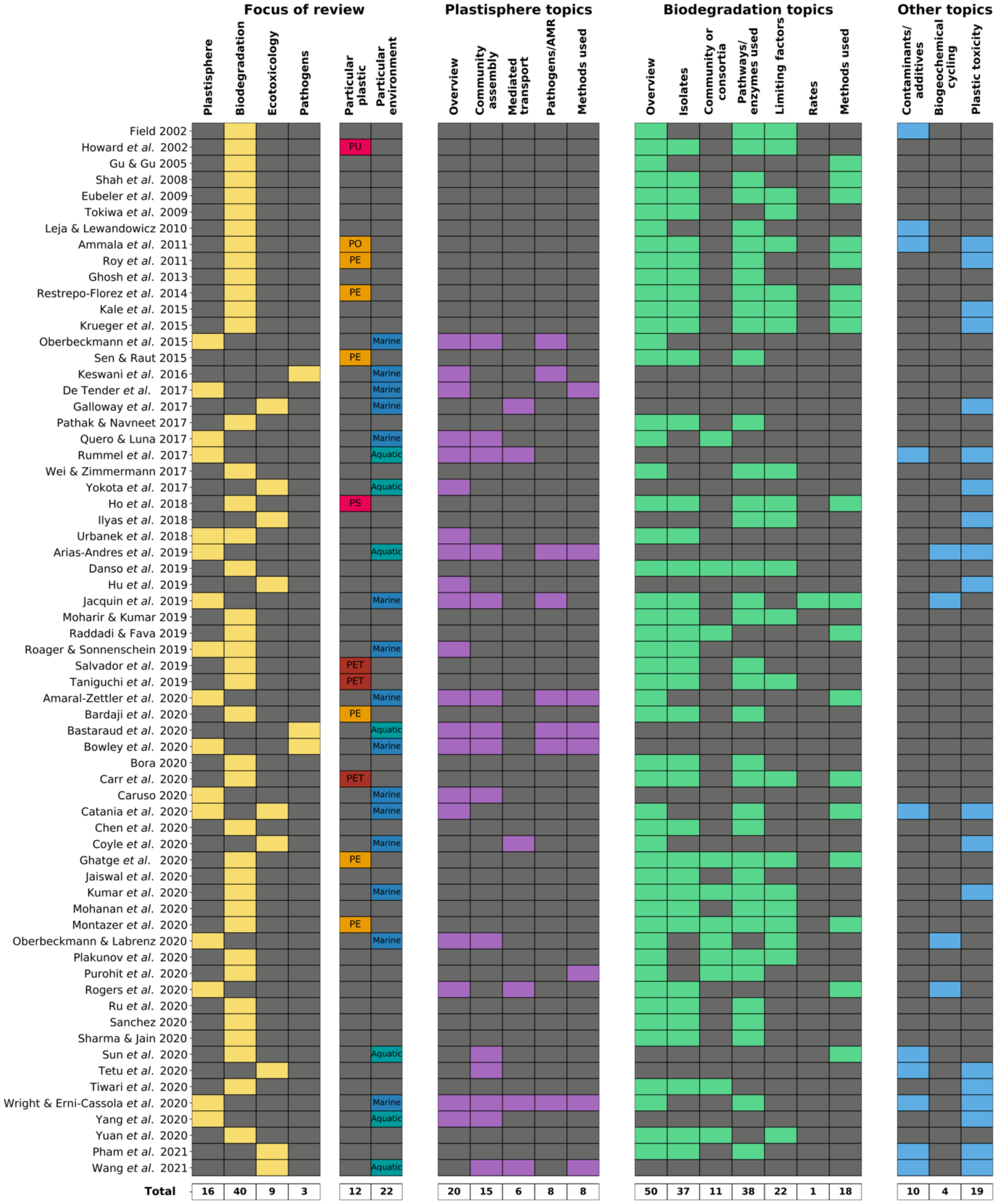


Figure 2. Cumulative number of plastisphere primary research articles published per year relating to different study topics (as in Fig. 1). Note that: (i) *x*- and *y*-scales vary between panels; (ii) 'AMR' within the AMR, Pathogenesis and HAB panel includes both studies where AMR genes are detected by PCR and studies that have tested susceptibility to antibiotics; (iii) 'Changes in properties' in the Degradation panel includes methods such as Raman or Fourier-Transform Infrared (FTIR) spectroscopy, contact angle measurements (hydrophobicity) and testing for changes in tensile strength or crystallinity; (iv) in the Microscopy type panel, where a study has used multiple types of microscopy, only the method with the highest resolution is listed; and (v) 'Other' in the Microscopy target panel means that the microscopy was not aimed at looking at the colonising taxa (and in most of these cases, biofilms were removed prior to visualisation), and was usually aimed at looking for signs of degradation or fragmentation.



	Focus of review						Plastisphere topics					Biodegradation topics							Other topics		
	Plastisphere	Biodegradation	Ecotoxicology	Pathogens	Particular plastic	Particular environment	Overview	Community assembly	Mediated transport	Pathogens/AMR	Methods used	Overview	Isolates	Community or consortia	Pathways/ enzymes used	Limiting factors	Rates	Methods used	Contaminants/ additives	Biogeochemical cycling	Plastic toxicity
Field 2002		■										■			■	■			■		
Howard *et al*. 2002		■			PU							■	■		■	■					
Gu & Gu 2005		■										■						■			
Shah *et al*. 2008		■										■	■		■			■			
Eubeler *et al*. 2009		■										■	■		■	■		■			
Tokiwa *et al*. 2009		■										■	■			■					
Leja & Lewandowicz 2010		■										■			■				■		
Ammala *et al*. 2011		■			PO							■	■		■	■		■	■		■
Roy *et al*. 2011		■			PE							■	■		■			■			■
Ghosh *et al*. 2013		■										■	■		■						
Restrepo-Florez *et al*. 2014		■			PE							■	■		■	■		■			
Kale *et al*. 2015		■										■	■		■	■		■			■
Krueger *et al*. 2015		■										■	■		■	■		■			■
Oberbeckmann *et al*. 2015	■					Marine	■	■		■		■									
Sen & Raut 2015		■			PE							■	■		■						
Keswani *et al*. 2016				■		Marine	■			■											
De Tender *et al*. 2017	■					Marine	■				■										
Galloway *et al*. 2017			■			Marine			■												■
Pathak & Navneet 2017		■										■	■		■						
Quero & Luna 2017	■					Marine	■	■				■		■							
Rummel *et al*. 2017	■					Aquatic	■	■	■										■		■
Wei & Zimmermann 2017		■										■			■	■					
Yokota *et al*. 2017			■			Aquatic	■														■
Ho *et al*. 2018		■			PS							■	■		■	■		■			
Ilyas *et al*. 2018			■												■	■					■
Urbanek *et al*. 2018	■	■					■					■	■								
Arias-Andres *et al*. 2019	■					Aquatic	■	■		■	■									■	■
Danso *et al*. 2019		■										■	■	■	■	■					
Hu *et al*. 2019			■				■														■
Jacquin *et al*. 2019	■					Marine	■	■		■		■	■		■		■	■		■	
Moharir & Kumar 2019		■										■	■		■	■					
Raddadi & Fava 2019		■										■	■	■				■			
Roager & Sonnenschein 2019	■	■				Marine	■					■	■								
Salvador *et al*. 2019		■			PET							■	■		■						
Taniguchi *et al*. 2019		■			PET							■	■		■	■					
Amaral-Zettler *et al*. 2020	■					Marine	■	■		■	■	■						■			
Bardaji *et al*. 2020		■			PE							■	■		■						
Bastaraud *et al*. 2020				■		Aquatic	■	■		■	■										
Bowley *et al*. 2020	■			■		Marine	■	■		■	■										
Bora 2020		■										■	■		■						
Carr *et al*. 2020		■			PET							■	■		■	■		■			
Caruso 2020	■					Marine	■	■													
Catania *et al*. 2020	■		■			Marine	■					■			■			■	■		■
Chen *et al*. 2020		■										■	■		■						
Coyle *et al*. 2020			■			Marine			■			■									■
Ghatge *et al*. 2020		■			PE							■	■	■	■	■		■			
Jaiswal *et al*. 2020		■										■	■		■						
Kumar *et al*. 2020		■				Marine						■	■	■	■	■					■
Mohanan *et al*. 2020		■										■	■		■	■					
Montazer *et al*. 2020		■			PE							■	■	■	■	■		■			
Oberbeckmann & Labrenz 2020	■					Marine	■	■				■		■		■				■	
Plakunov *et al*. 2020		■										■		■	■	■					
Purohit *et al*. 2020		■									■	■		■	■						
Rogers *et al*. 2020	■						■		■			■	■					■		■	
Ru *et al*. 2020		■										■	■		■						
Sanchez 2020		■										■	■		■						
Sharma & Jain 2020		■										■	■		■						
Sun *et al*. 2020		■				Aquatic		■										■	■		
Tetu *et al*. 2020			■					■											■		■
Tiwari *et al*. 2020		■										■	■	■							■
Wright & Erni-Cassola *et al*. 2020	■					Marine	■	■	■	■	■	■			■				■		■
Yang *et al*. 2020	■					Aquatic	■	■													■
Yuan *et al*. 2020		■										■	■	■		■					
Pham *et al*. 2021			■									■	■		■				■		■
Wang *et al*. 2021			■			Aquatic		■	■		■								■		■
Total	16	40	9	3	12	22	20	15	6	8	8	50	37	11	38	22	1	18	10	4	19

Figure 3. The focus and topics covered of all plastisphere reviews that our literature search and subsequent filtering returned [5,18–20,151–211]. The focus of the review is the over-arching topic that the review addresses, with aquatic referring to both marine and freshwater environments, while plastisphere topics, biodegradation topics and other topics are whether each review has a full, titled section on that theme. Where cells are coloured, these topics are present within the review. Abbreviations are shown where reviews are focussed on a single plastic type: PU (polyurethane), PO (polyolefins), PE (polyethylene), PS (polystyrene) and PET (polyethylene terephthalate). Full details of the topics in each review, as well as the future directions suggested and conclusions drawn by each study are in Table S2.

2. The plastisphere as a microbial biofilm on plastics

The microbial communities on plastics are typically dominated by Proteobacteria (~70% relative abundance), Bacteroidetes (~10%) and Cyanobacteria (~20%). There are usually not large differences in alpha diversity indices between plastics, control marine biofilms and planktonic samples, although some control marine biofilms have been found to have larger proportions of Bacteroidetes (~20%) and Planctomycetes (~5%), while planktonic samples have a larger proportion of Verrucomicrobia (~5%) [16]. Surprisingly, while our previous review found that just 19 of the 66 studies included a control biofilm surface [151], there are only an additional 13 studies with a control biofilm surface in the studies evaluated here (*i.e.*, 32 of 140 studies; Table S1). There are a number of factors that influence plastisphere formation and composition – most of which would apply to any aquatic biofilm – which we discuss in this section.

When plastics (or any surface) first enter the environment, they are rapidly covered by organic material and contaminants – the ecocorona [5] – which facilitates microbial colonisation by reducing the hydrophobicity of the surface [151]. These microbial communities are initially composed of fast-growing organisms that are good at colonising surfaces. If the surface is degradable, then these first colonisers are gradually replaced by organisms capable of degrading the surface, which will eventually be replaced by cheaters or cross-feeders – organisms that are not capable of degrading the surface but are able to use the sub-products of degradation [212]. Our current understanding of these successional states on plastics is complicated by the long-time scales favoured by many plastics studies (in our recent meta-analysis, the mean incubation time for all samples was 100 days [16]). A relatively low proportion of studies to date include characterisation of the eukaryotic or other non-bacterial plastisphere constituents, and we therefore focus on prokaryotes here and discuss eukaryotes separately in the following section. While in our previous review (Wright and Erni-Cassola *et al.* [151]) we reported that only 21 out of 66 studies reviewed included a time series – only 6 of which also sequenced part of the microbial community [151] – there are now 69 studies (of 140) that include a time series, 32 of which also sequence part of the microbial community (Figs. 1 and 2).

Whilst results fluctuate depending on the individual study, when looking at coarse time scales, current research suggests that the Alphaproteobacteria are generally more abundant at early (below one week) than late (above one week) time points, while the opposite is true for the Gammaproteobacteria, Bacteroidetes and Actinobacteria [16]. However, only 15 of the time series studies include these early time points, with only two studies including sequencing of the microbial community before one day of incubation, Lee *et al.* (2008) and Kesy *et al.* (2021) [32,61]. Interestingly, Lee *et al.* [32] found that, at the earliest time points (3 or 9 h incubation), the Gammaproteobacteria dominate, while their results from 24 or 36 h of incubation were consistent with that suggested above where the Alphaproteobacteria dominate. The other study including time points of less than one day, Kesy *et al.* [61], only reported on the *Vibrio* genus (Gammaproteobacteria), and while they did find colonisation by *Vibrio* spp. by 1 h of incubation, further studies (or re-analysis of the data obtained by Kesy *et al.*) are needed to confirm the findings of Lee *et al.* in different settings.

The composition of macro-molecules likely drives colonisation in the first few minutes of incubation [213–216], but – as for other substrates – much of the variation in plastisphere composition is driven by stochasticity [217] as well as environmental variables [16,178,194]. Studies examining which factors have the largest influence on plastisphere composition find that environmental variables such as light availability, salinity and geographical region as well as experimental variables such as DNA extraction method or primer pair used for sequencing have the largest impact on plastisphere composition [16,105,135,194]. Plastic type has also been found to have an impact on plastisphere composition, and some of the discriminating taxa between different plastic types have been suggested to play a role in plastic degradation [16,128,135], although the extent to which this may occur needs further verification (see below for discussion on this). A preference for a surface-attached rather than planktonic lifestyle is likely also a larger driver of plastisphere composition than plastic type and while many studies have simply compared the plastisphere with the free-living planktonic community (Table S1; *n*=23), some studies also include controls of either an inert surface (such as glass, ceramic or shells; *n*=28) or particle-associated seawater or sediment communities (*n*=19; Table S1).

Our knowledge of the functional potential as well as the functional capacity of the plastisphere is currently very limited, although the abilities of plastisphere isolates have been more comprehensively tested. There are just three metagenomic datasets available [12,14,15] as well as several studies that measure one or several aspects of plastisphere function (discussed further below), *e.g.,* alkane degradation [93,94,111], antimicrobial resistance [26,33,49,56,130,218] or pathogenesis [80,114,138]. The metagenomic datasets, collected by Bryant *et al.* [12], Pinnell and Turner [14] and Bhagwat *et al.* [15], were from plastics collected from the Northern Pacific Gyre, incubated in coastal Gulf of Mexico sediments or incubated in an Australian estuary, respectively. While Pinnell and Turner and Bhagwat *et al.* included both control biofilm samples (either ceramic or wood, respectively) and a biodegradable polyester (either polyhydroxyalkanoate [PHA] or polycaprolactone [PCL], respectively), Bryant *et al.* compared the plastisphere only with planktonic samples. It is likely for this reason that while Bryant *et al.* found that functions including nitrogen fixation, chemotaxis, type IV and VI secretion systems and xenobiotics degradation were significantly enriched on plastics (polyethylene [PE] and polypropylene [PP]), Pinnell and Turner found that recalcitrant plastic biofilms (polyethylene terephthalate [PET]) were not distinguishable from control biofilms (ceramic; although biodegradable plastic biofilms were) and Bhagwat *et al.* did not find significant functional differences between any material types (PCL, PP, polystyrene [PS], polyvinyl chloride [PVC] and wood). It is therefore important that we continue to design experiments that test whether the functional capacity of plastic biofilms differs from that of other biofilms rather than planktonic samples.

3. Importance of eukaryotes in shaping the Plastisphere

Despite almost 10 years of Plastisphere research, the eukaryotic community fraction has consistently received far less scientific attention compared with prokaryotes (Figs. 1 and 2; [151,178,219]). Among the studies included in our literature review, 77 papers characterised plastisphere communities using PCR-based methods, and only 16 of these included a eukaryotic fraction. The highest number of publications per year, so far, was reached for both the prokaryotic and the eukaryotic fractions in 2020. Surprisingly, while there were 29 studies that included the prokaryotes published during 2020 (up from 14 published in 2019), there were only four that included the eukaryotic fraction, although this was still an increase on the three studies published in 2019 (two of which were metagenomes that did not comment on the eukaryotes). Similarly, the representation of eukaryotes in review papers has been modest: we did not include eukaryotes as a category in Figure 3 because none of the review papers in Table S2 contained sections that matched with our inclusion criteria (*i.e.*, section heading with one of the keywords: eukaryote, diatom, dinoflagellate, microalgae, protist). Three degradation themed reviews in total, however, did have at least one section dedicated to fungi [160,193,199]. Furthermore, out of the 65 publications included on our list of plastisphere reviews (Table S2) only one was focussed on eukaryotes, reviewing the potential of fungi to degrade petrochemical plastics [199]. The low inclusion rate of eukaryotes in plastisphere research, however, does not correlate with their prevalence or ecological importance in these biofilms: metagenomic investigations in the North Pacific Gyre revealed that 40–99% of reads from each of the 12 samples analysed were identified as eukaryotic sequences [12]. Due to the highly variable rRNA gene copy number in eukaryotes [178,220] the number of reads usually does not directly correspond to the number of actual individuals [178], however, these findings still highlight the significant contribution of eukaryotes to the overall community composition of the plastisphere [178].

Most plastisphere metabarcoding studies have targeted the overall eukaryotic fraction using the 18S rRNA gene as a marker [7,31,50,85,86,88,90,100,127,148,150], but some have focussed particularly on the fungal plastisphere fraction [31,90], in some cases employing fungal-specific ITS [148] or ITS2 [31,87] marker genes. Additional markers for marine microalgae (*tufA*) and metazoans (COI) have also been included on one occasion [148]. Taxa including (but not limited to) members of the diatoms, dinoflagellates, ciliates, fungi, brown, green and red algae, as well as a range of metazoan taxa are often reported as the dominant eukaryotes in the plastisphere (*e.g.*, [7,12,85,86,88,100,127,148,150]; see also the review by Rogers *et al.* [197]). Indeed, diatoms are consistently described as an abundant and diverse group of colonisers on plastics, particularly during the early stages of biofilm formation [8,22,67,73,85,148,178], while macro- and microscopic forms of metazoan taxa (*e.g.,* bryozoans, crustaceans, molluscs, anthozoans, sponges, nematodes and annelids) often also make up a major proportion of the eukaryotic communities [12,85,86,100,127] likely, at least in part, because of their multicellular nature [127,178]. Apart from PCR-based methods, eukaryotic plastisphere members have been described in several publications using microscopy techniques [22,41,44,67,69,73,76,89,113,131] (Fig. 2). These techniques, however, are not high throughput and do not usually provide sufficient coverage or taxonomic resolution for estimation of the whole microbial community [161]. They can, however, be useful for revealing structural and spatial details unattainable via sequencing approaches [148,161], particularly when used in combination with phylogenetic labelling with fluorescent probes [46,161].

Eukaryotic micro-organisms play several important roles in community regulation, dynamics and functioning in marine biofilms, ranging from photosynthesis and primary production (*e.g.*, diatoms [7]) to predation (*e.g.*, predatory ciliates [7,88,127] and amoebae [150]), parasitism (*e.g.*, parasitic dinoflagellates and fungi [127]) and other symbiotic interactions (*e.g.*, ectosymbiotic bacteria on ciliates [7,127] or coral-symbiont dinoflagellates [12]) (see review by Amaral-Zettler *et al.* [178]). Several studies have also reported that certain fungal taxa are able to degrade plastics, however only three of these strains are marine (*Zalerion maritimum* [92], *Aspergillus tubingensis* and *A. flavus* [221]; reviewed by Rogers *et al.* [197] and Sanchez [199]). Nevertheless, the search for marine plastic degraders has prompted a special interest in fungi and, in recent years, the fungal fraction of the plastisphere – which has been found to comprise approximately 2.8–3% of the overall eukaryote sequences in field and lab incubations in Baltic (along an estuarine continuum) and North Sea waters, respectively [90,100] – has been specifically targeted by at least four studies [31,87,90,148].

Perhaps the most interesting aspect about eukaryotes in the plastisphere, however, is their potential to shape the composition of the prokaryotic community inhabiting the biofilm through eukaryote–prokaryote interactions and close associations [12,46,85,127,150], some of which are known to be species-specific [222,223]. Bacteria can benefit from phytoplankton by gaining access to their cell exudates that provide a source of carbon, energy and nutrients [46,127,224,225], as well as oxygen produced *via* photosynthesis (reviewed by Stocker and Seymour [226]). Bacteria are often observed either colonising (see review by Amin *et al.* [225]) or living in close proximity [46,227] to phytoplankton cells, where they may end up as a result of random encounters or active chemotaxis towards the variety of chemical cues originating from the micro-environment surrounding individual phytoplankton cells – the 'phycosphere' (reviewed by Stocker and Seymour and Seymour *et al.* [226,228]). Similar associations, particularly between diatoms and bacteria, have been observed in biofilms on plastics incubated in coastal waters of the Atlantic Ocean and Wadden Sea *via* microscopy [46], but also by inference from sequencing data from samples incubated in the North Sea [85]. A co-occurrence network analysis conducted on samples incubated at five locations along a river–Baltic Sea continuum in North-East Germany further suggested that prokaryotic community dynamics on plastic substrates (PE and PS) were largely driven by interactions with the eukaryotic community fraction. Wood substrates, on the other hand, were mainly characterised by connections between bacteria [127], probably because bacteria were able to use the wood as a carbon source [50] while inert plastics often support carbon-producing phototrophic communities [12,50]. In addition to plastic surfaces and diatoms, prokaryotes can also attach to and interact with a variety of other eukaryotic organisms [12], such as encrusting bryozoans [12,46] or ciliates [7]. Interestingly, diatom-associated bacterial groups have often been found dominating bacterial communities on marine biofilms, including those on plastics [16,46,85].

Dudek *et al.* [150] reported that in their time series investigations in the Caribbean Sea, eukaryotes – diatoms in particular – were observed to exhibit substrate specificity between the different plastic types incubated, in contrast to prokaryotes. This observation was supported by earlier findings by Eich *et al.* [76] where diatom communities differed between PE and a starch-based biodegradable plastic. Phytoplankton are known to produce hydrocarbon compounds, both aliphatic and aromatic, and/or adsorb them from the surrounding seawater, thereby accumulating these compounds in the phycosphere [224]. The potential ramifications of these hydrocarbons for degradation assessments are discussed further below, but further investigations are needed that experimentally address the dynamics of eukaryote–prokaryote interactions in the plastisphere and differentiate them from microbe–plastic interactions (see Bryant *et al.*[12]). Schlundt *et al.* [46] recently conducted the first study that incorporates analysis of the spatial structure and eukaryote–prokaryote interactions in the plastisphere by combining phylogenetic labelling (Combinatorial Labelling And Spectral Imaging – Fluorescence In Situ Hybridization [CLASI-FISH]) with confocal microscopy, as recommended earlier by Oberbeckmann *et al.* [85]. We hope that more studies like this will follow in the future, ideally in combination with high-throughput sequencing of all community fractions, elucidating the real drivers behind plastisphere community composition.

4. Plastic degradation

Biodegradation refers to the breakdown of organic chemicals by the action of living organisms (*i.e.,* biotic degradation), usually carried out through enzymatic catalysis [229]. However, this process in nature is never isolated from the action of abiotic factors. Hence, biodegradation can be understood as a chemical breakdown of organic molecules by the synergetic contribution of biotic and abiotic factors [230]. There are several key stages in the biodegradation of polymeric hydrocarbons: (i) biodeterioration – a decline in physicochemical properties mediated by microbial activity on the surface of the polymer [230]; (ii) biofragmentation – a lytic process reducing polymer molecular weight [230] ; (iii) assimilation – integration of atoms resulting from the fragmentation process into biomass [230], in this case carbon uptake; and (iv) mineralisation – the process of carbon uptake and complete transformation into biomass, CO_2/H_2O in oxic environments and $CO_2/CH_4/H_2O$ in anoxic environments [151,210]. While assimilation and mineralisation are the most significant biological factors, abiotic factors also play a role in biodegradation. The abiotic degradation of polymers produces weathered materials by the action of either temperature, light, gases, mechanical forces, water or a combination of these factors [231]. Depending on the type of weathering, polymers' modifications can take place through different routes. For instance, sunlight can influence the weathering of polymers by the action of ultraviolet (UV) (*i.e.*, photooxidation; UV-A ~295-315 nm and UV-B ~315-400 nm) radiation and by heating (*i.e.,* thermooxidation) which is mediated by the visible section of sunlight (400-760 nm) and infrared radiation (760-2500 nm) [210]. The oxidation of polymers can be observed by the formation of different chemical groups, such as ketones, carboxylic acid, and esters [232]. The biological degradation of chemicals is an intricate process in which the abiotic contribution is essential as the initial step of the degradation of many recalcitrant polymers [233], which we focus on here.

Physicochemical properties inherent to the polymers impact the (bio)degradability of a specific material [234]. Among these properties, molecular weight, glass transition temperature, hydrophilic/hydrophobic behaviour and crystallinity are relevant features to look at when determining biodegradability [152,234]. For instance, highly crystalline polymers have shown to be resistant to biodegradation compared with polymers with more amorphous regions – irregular polymer structures that are more susceptible to microbial/enzymatic attack [157,235]. Furthermore, the chemical structure of the polymer itself can indicate how prone to degradation a polymer may be. For instance, polyesters such as PET and PCL contain functional ester groups that serve as susceptible points for the catalytic action of enzymes with esterase activity [236]. On the other hand, polymers with no evident functional groups are less susceptible to enzymatic attack (*i.e.*, more recalcitrant polymers); some examples are typical olefins such as PE and PP. Expectedly, for the potential degradation of polyolefins, it seems essential to have abiotic pre-oxidation, introducing weak points for enzymatic attack; functional groups. This oxidation will generate degradation products of lower molecular weight that can be taken up by cells and metabolised (*i.e.*, mineralised), completing the degradation process [233,237]. Overall, biodegradation requires: (i) the presence of microbes able to access, uptake and mineralise the substrate, (ii) appropriate environmental conditions (*e.g.,* temperature, salinity, pH) to propitiate microbial development and (iii) the polymer must be susceptible to enzymatic degradation.

Microbes' potential ability to degrade plastics seems to be well distributed across a wide range of taxa. Furthermore, the majority of putative degraders reported in degradation studies were found in soil (27.8%), followed by plastic waste dumping sites (9.6%) and finally compost (5.3%) [238]. Interestingly, the isolation and characterisation of aquatic plastic degraders are less frequent [239], which is probably related to the extra challenge that aquatic environments, such as the oceans, represent (*e.g.,* low nutrient concentration and temperature) compared with soil and compost. In soil and compost, high nutrient availability, humidity and temperature are often conditions in which microorganisms thrive, positively impacting any potential biodegradation processes [240]. As previously explained, functional groups within a polymer (*e.g.,* ester carbonyls and ketones) will serve as a target for the enzymatic breakdown of the polymer. In this regard, lipases and esterases have been connected to the degradation of polyesters such as PET, initially in the terrestrial environment [170,241] but now also in the marine environment (Table S3 [62,63]). Conversely to polyester degradation, the identification of enzymes related to the degradation of polyolefins has been more challenging. So far, we do not think there is sufficient evidence to determine whether this is an active process (*i.e.,* polymer break down mediated by enzymes) or only a passive uptake of the released carbon from the process of weathering. However, the degradation of plastics has been repeatedly linked to hydrocarbon degradation, particularly alkane degradation, due to their chemical semblance to polyolefins – inert carbon-based backbone chains [242,243]. Thus, several marine studies have targeted alkane degradation genes, especially the alkane monooxygenase *alk*B (Table S3 [93,94,111]).

To date, there is not a unified fashion to determine plastic degradation in the literature [244]. On the contrary, there are different methods to determine degradation, with the most commonly applied being mass loss, spectroscopic profiles (addition and removal of functional groups) and scanning electron microscopy (SEM; Fig. 2 and Table S3; for more related techniques see Chamas *et al.* [245]). Though these techniques on their own are not enough to properly screen for biodegradation, a combination of these can provide a better idea of the potential of putative plastic degraders. Some other more informative but less frequently applied methods involve tracking the incorporation of isotopically labelled carbon – monitoring the integration of ^{13}C-labelled carbon into biological structures and monitoring CO_2 evolution [197]. Using a combination of methods to evaluate plastic degradation is especially relevant when the degradation rate is minimal or when plastics contain a high concentration of plasticisers (*e.g.,* PVC contains around 30-80% plasticisers by weight [246]).

Even though plasticisers are chemically complex structures, they are degradable molecules with several described degradation pathways [247]. Furthermore, the hydrocarbons produced by phytoplankton (described above) may provide sustenance for hydrocarbon-degrading bacteria when other sources of hydrocarbons are scarce (see Gutierrez 2018 [224] for further discussion), and it has been suggested that diatoms could attract and concentrate hydrocarbon degraders in the plastisphere [150]. It is therefore necessary to rule out any preliminary 'positive' results of biodegradation studies that may be attributed to the potential underlying degradation of plasticisers or phytoplankton-produced hydrocarbons as additional carbon sources – possibly more readily available for microbes to degrade than the plastics themselves. Performing comprehensive studies that monitor the integration of labelled carbon into biomass and characterise the spatial structure of the plastisphere will allow us to go beyond just noting the presence of taxa of interest and will hopefully shed light on potentially conflicting speculations that higher abundances of hydrocarbonoclastic members could be: (i) degrading the plastics [119,121]; (ii) due to UV-induced leaching of degradation products [135]; or (iii) whether these are in response to phototrophs [150].

5. Potential pathogens

After the description of the plastisphere by Zettler *et al.* [7], increasing attention has been directed toward identifying and understanding of the potential role of the microbial community drifting along with plastic material in several environments (*e.g.*, oceans, rivers and wastewater). Apart from describing the microbial community on plastic marine debris, Zettler *et al.* also noted the presence of a *Vibrio* OTU (Operational Taxonomic Unit). Although the pathogenicity of this OTU could not be determined, this has sparked multiple enquiries surrounding the concept of 'harm' relating to plastics, a concept that can potentially have several derivatives. In this sense, the occurrence of potentially pathogenic taxa on plastics has been extensively reviewed [20,57,181], and several investigations have reported examples of these microorganisms. These are usually referred to as 'potential' pathogens (Table S4), with findings being especially dominated by microorganisms related to *Escherichia coli*, *Vibrio* spp. and occasionally to dinoflagellates such as *Alexandrium* spp. However, it is essential to highlight that the actual pathogenicity of these microorganisms is not usually assessed, and their classification as pathogens is frequently attributed indirectly by mere taxonomic association (Fig. 2). For instance, *Vibrio* strains are frequently found on marine plastic debris and are automatically associated with the pathogenic members of the genus [248]. Here we give an overview of the genetic material associated with the pathogenic process and antimicrobial resistance in prokaryotes as well as the potential mode of pathogenicity, or toxicity, for micro-eukaryotes.

To gain insight into the harm posed by potentially pathogenic prokaryotic taxa colonising plastic debris, it is useful to look at the primary examples of potential pathogens such as *E. coli* and *Vibrio* spp., both found on these materials [138]. Even though there are many examples of pathogenic *E. coli* and *Vibrio* spp. associated with human disease [248,249], not all strains are necessarily pathogenic [250–253]. Thus, it is necessary to have substantial evidence to catalogue a particular strain as a pathogen. In this context, several pathogenic or virulence factors are usually used as markers for pathogenicity. For instance, the encoding of adherence factors, toxins, type III and IV secretion systems, among others, are typically targeted as genetic features encoded by pathogenicity islands [254,255]. Of equal importance, pathogenic microorganisms are defined by the presence of a susceptible host – an organism vulnerable to the infection process. The existence of a susceptible host will enable a pathogen to successfully display different infectious traits, determined by genes associated with pathogenicity (*i.e.,* pathogenic factors), which establish the type and infectious impact on the host – human or not [256]. However, despite the relevance of identifying pathogenicity islands and the set of pathogenic factors encoded by these distinct genomic regions, such characterisation of microbial isolates retrieved from plastic debris or metagenomic analysis targeting these genetic elements are not frequently performed. One example is the investigation carried out by Silva *et al.* [138], where it was possible to detect several virulence genes from different *E. coli* and *Vibrio* spp. isolates obtained from plastic debris. Similarly, Kirstein *et al.* [80] also tried to identify virulence-related genes in *Vibrio* spp. isolates retrieved from marine plastics, but none of their isolates encoded any of the targeted virulence genes (Tables S4 and S5).

As noted above, microorganisms' capacity to produce infectious disease relies on the expression of virulence factors. In this context, the host is compelled to retaliate against the intrusion of potentially harmful microbes. When the natural immune response is insufficient, the application of antibiotics may diminish and terminate the infectious process of virulent microbes. Unfortunately, microbes have also evolved several strategies to elude antibiotics' effect, a capacity provided by various antibiotic resistance genes (ARGs). The spread of antibiotic-resistant bacteria is considered a matter of global concern [257]. ARGs in virulent microbes can complicate infections, potentially leading to fatal results; it is estimated that annually in the U.S.A., more than 35,000 people die as a consequence of the more than 2.8 million antibiotic resistant infections [258]. Furthermore, it is expected that antimicrobial resistant diseases could push 24 million people into extreme poverty by 2030 and reach a staggering 10 million deaths per year by 2050 [257]. Therefore, the elucidation of such resistance genes and the physio-pathological activity of microorganisms carrying ARGs have been extensively studied [259,260]. This also includes several investigations trying to determine the potential for plastics to harbour microbes containing such genetic elements. Some prevalent ARGs on plastics are tetracycline (*tet*) and sulfonamide (*sul*) resistance genes, together with macrolide-lincosamide-streptogramin (MLS) and multidrug resistance genes; these last two examples especially have been detected by metagenomic analyses (Table S4). Interestingly, extended-spectrum beta-lactamases (ESBLs) are not frequently identified on plastics despite their widespread global distribution [49,261,262].

Alongside potentially pathogenic bacteria, plastics have also been reported to host potentially pathogenic or HAB-forming microeukaryotes (see Audrezet *et al.* 2021 [263]; Table S4); these taxa include members of toxin-producing dinoflagellates (*e.g.,* the genera *Alexandrium* [7,114,131,150], *Amphidinium* [150], *Coolia* [131], *Heterocapsa* [127], *Ostreopsis* [114,131], *Pfiesteria* [127] and *Prorocentrum* [83,150]) and diatoms (*Pseudo-nitzschia* [114]) as well as other protists that comprise potential seagrass (*Labyrinthulaceae* sp(p). [150,264]) and coral (*Halofolliculina* sp. [69]) pathogens. As with the potential pathogenicity of plastic-associated bacteria, the hypothetical threats from these micro-eukaryotic rafters are mostly just noted but are rarely tested in any experimental manner, and the harmfulness of micro-eukaryotes may not always be easily determined by amplicon sequencing or taxonomic approaches alone. For example, the toxin production (or lack thereof) of dinoflagellates from the genus *Alexandrium*, responsible for causing Paralytic Shellfish Poisoning in humans, varies considerably in both quantity as well as quality between – and even within – species, and can also be affected by a number of factors related to growth cycle phase and environmental conditions (reviewed by Murray *et al.* [265]). Likewise, several ecological and environmental factors are likely to regulate their bloom-forming potential in marine waters [265]. To our knowledge, the only marine plastic related study that took this a step further and quantitatively characterised the toxin-production profiles of harmful dinoflagellates (*Alexandrium pacificum*) isolated from marine plastic debris was that of Casabianca *et al.* [114], who found that all of the 10 dinoflagellate strains produced four or more of the 12 Paralytic Shellfish Toxins tested. They further hypothesised that marine plastic debris could accumulate these toxins and aid their transfer through the food web [114].

Overall, the analysis of plastic samples collected from different environments reveals that potentially virulent – or harmful – microbes and ARGs are present within the plastisphere (Tables S4 and S5).

Caution is suggested when analysing and interpreting results because of both the uncertainty in determining whether plastisphere microbes are pathogenic and the issues related to transport and plastic residence times, discussed below. However, more robust evidence is necessary when suggesting the presence of pathogens on plastic debris.

6. Effects of microbe-plastic interactions on plastic buoyancy and transport

As discussed in the previous sections, marine plastics serve as vectors for a plethora of rafting organisms, including microbes, such as bacteria and microalgae, as well as macro-colonisers (reviewed by Barnes [266] and Kiessling *et al.* [267]). While many of the taxa found colonising plastics may already be present in the areas in which the plastics are found, there are concerns about members of the plastisphere related to two key themes: the transport of non-indigenous taxa and the transport of pathogenic or harmful taxa, *i.e.*, horizontal transport [20,71,80,137]. Even though in many cases naturally occurrent substrates (*e.g.,* wood, leaves and rocks) are also able to concentrate high abundances and diversity of potential pathogens [49,138,142], plastics are light-weight and highly resistant to both biotic and abiotic degradation (as discussed above). This means that – whereas naturally occurring organic materials such as wood, leaves or other biogenic substrates will be eventually degraded [268] – plastics can be easily transported in the environment, from one ecosystem to another. This can occur via rivers [269], currents [270,271] and winds [272,273] as well as rain [274], snowfall [275] and melting sea ice [276,277] and is often referred to as a dynamic process: stranded plastic particles – potentially colonised by resident microbiota – can be subsequently washed back into the water flow and transported downstream or back out to sea. This extended life afloat enables plastic debris to be transported across long distances [278–280], sometimes crossing oceans between continents [281,282], reaching remote islands [266,283] and other locations that may host vulnerable ecosystems (*e.g.,* [284–286]).

Several non-indigenous taxa have been documented in association with marine plastic debris (as recently reviewed by Audrezet *et al.* [263]), prompting concerns regarding the ecological impacts caused by the spread of potentially invasive species to new areas (*e.g.,* [284–286]). Caution regarding these potentially harmful rafters seems justified, especially as global warming may further support the spread of non-indigenous or harmful species to new areas, particularly in polar regions [27,266]. Moreover, recent research indicates that ecologically and economically important seagrass meadows [287–291] and other habitat-forming taxa, such as hard corals [290], can trap and accumulate microplastics, while potential seagrass [150] and coral [69] pathogens have been found on plastics and plastic debris has been associated with an increased likelihood of disease on coral reefs [292]. Other taxa that are not generally regarded as invasive, toxic or pathogenic as such, but that can cause nuisance *via* mucilage events, such as the diatom species *Ceratoneis closterium* [83] have also been reported as plastisphere members. Alongside the potential toxicity of the plastic polymer itself, or plastic additives and sorbed contaminants (as reviewed recently by Pham *et al.* [207]), plastics' potential to be considered harmful clearly also depends on the interaction with pathogens and non-native taxa present in the environment (see above), especially in polluted environments such as wastewater effluents and water bodies in the proximity of densely populated urbanised areas [180].

The role of biofouling has long been acknowledged as a factor affecting the buoyancy and potential sedimentation of marine plastics, *i.e.*, vertical transport. Observations of low-density plastics resting on the seafloor or buried in sediments have been reported since the mid-1970's [293–295]. Despite that most plastic debris found in the marine environment are less dense than seawater [295,296], recently these should-be-buoyant polymers have also been collected from the deeper layers of the water column [297–301], demonstrating the 'fallout' of plastics from surface waters [301]. Due to the rapid colonisation of marine plastics – including by calcareous animals and various types of algae that can cover the plastics with thick, filamentous growth [89,266,302,303] – the overall density of biofouled particles may exceed that of seawater, causing them to lose buoyancy and sink, as observed in field investigations [89,302,303]. Both experimental field studies and mathematical sinking models have found that biofouled plastics that sink to deeper layers of the water column can also undergo rapid de-fouling due to a number of factors [151,302]. This could potentially cause them to continue oscillating up and down in the water column as a result of recurring fouling and de-fouling events, thereby retaining the highest microplastic concentrations at mid-depths of the water body [304] (see Wright and Erni-Cassola *et al.* [151] for further discussion of this topic).

Among the relatively few field-based incubation studies [89,302,303] and other observations on the topic [293], buoyancy-loss and biofouling-induced sinking of plastics (≥ 1 mm) in the marine environment have been mainly associated with colonisation by macro-organisms, including calcareous mussels, barnacles and bryozoans [89,302,303]. It is therefore currently unclear whether natural microbial biofouling alone can cause individual, low-density microplastics to sink [89,151,303,305]. While some studies [89] have concluded that macro-organisms are likely necessary for the transport of buoyant plastics through the water column, others have noted that some macro-organisms (*e.g.*, barnacles) are unlikely to colonise sub-millimetre particles [306,307]. Assuming this statement can be extended to most macro-colonisers, the potential for vertical transport of individual sub-millimetre microplastic particles should depend mainly on microbial colonisation [89,151,303], although the incorporation of inorganic matter and detritus are likely to play a role as well [89,103,308]. A recent modelling study concluded that small (radius range 10 µm – 1 mm) spherical microplastics did not sink within 90 days in oligotrophic ocean waters, where algal growth is scarce [65]. To our knowledge, however, no studies have been published that experimentally investigated the effect of microbial biofouling on the buoyancy of individual, sub-millimetre low-density microplastics in either lab or field settings, likely due to the difficulties in the handling, recovery and analysis of small particles while retaining natural exposure conditions, as noted by several studies [50,52,89,305,309].

The effects of interactions between biogenic material (such as marine snow [310] and marine microalgae [77,91,103,116]) and very small, sub-millimetre microplastics (down to 2 μm) have in fact been investigated in a number of laboratory studies. These studies, however, have either focussed on heteroaggregation [38,77,91,103,116], rather than the colonisation of individual microplastic particles or polymers that are denser than seawater [38] (and would therefore readily sink in the marine environment even without biofouling). These studies have found that heteroaggregation can either increase or decrease the settling or rising velocity of microplastics or even change the direction of their movement altogether (*i.e.*, making buoyant polymers sink and non-buoyant polymers float/rise), depending on the polymer type and the composition of the heteroaggregates [38,77,91,103,116]. Biofilm coating has further been shown to promote aggregation between microplastics and natural particles [101], while field-collected marine aggregates have also been found to incorporate microplastics [118,311]. Despite a number of studies having been published on the sinking and rising behaviour of microplastics incorporated into heteroaggregates, the experimental data needed to enable comparisons between empirical data and mathematical model (*e.g.* [38,151,304,312–314]) predictions is lacking [151,314,315], specifically: (i) on the effects of microbial biofouling on the buoyancy of individual sub-millimetre microplastics; and (ii) on natural marine biofilm parameters, namely biofilm thickness and density [151]. Further impacts of microbial colonisation on the vertical transport of plastics are related to the ingestion of plastics by macro-organisms [5,316,317], although micro-eukaryotes, including marine dinoflagellates [91] and ciliates [318], have also been observed to ingest small microplastics, possibly making microplastics more bioavailable for marine organisms at higher trophic levels [318].

7. Effects of plastic pollution on biogeochemical cycling in the oceans

Despite being included in the call for research by Harrison *et al.* (2011) [9] 10 years ago, the potential impacts of plastic pollution and microbe-plastic interactions on ecologically critical biogeochemical processes have remained less discussed (Fig. 3) and largely understudied. This topic is beginning to gain more attention, with a number of studies published so far in 2021, including original research articles (*e.g.,* [319,320]) as well as reviews and other works that either focused solely on biogeochemical effects of marine microbe–plastic interactions [321] or included it as one of several topics (*e.g.,* [219,322,323]).

Although often referred to as ‘inert’ materials, plastics can release many chemical compounds [321,324]. This happens when immersed in seawater – particularly when exposed to solar irradiation – and the compounds range from additives [325,326], metals [324,326], greenhouse gases (*e.g.,* methane and ethylene [327]) and other degradation and weathering products [237] to pollutants adsorbed from the surrounding environment [328]. Depending on the integrity and chemical composition of the plastic, these leachates can either stimulate [59,108] or inhibit (*e.g.,* [59,324,329]) microbial activity. It has been estimated that dissolved organic carbon (DOC) leaching from marine plastics (*i.e.,* plastic leachates) can amount to up to 23,600 metric tons per year and, in areas with high levels of plastic pollution, could comprise as much as 10% of all DOC present in the marine surface microlayer [108]. Note that the term DOC is used

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by Romera-Castillo *et al.* [108] to include all potential leachates from plastics and has previously been defined as the organic carbon present in water after filtering out particles of approximately > 0.45 µm in size [330]. This definition is rather problematic given that nanoplastics (1-1000 nm [331]) could therefore be included within this and we therefore suggest that future research looks to make a distinction between the 'dissolved' organic carbon that is particulate and that which is in suspension. Nevertheless, this organic carbon is also available for microbial utilisation, enhancing the growth of heterotrophic marine microbes [59,108]. Since marine microbes play a crucial role in global biogeochemical processes, including carbon and nutrient cycling as well as oxygen production and climate regulation, while also forming the basis of marine food webs *via* primary production [332], the potential threat of plastic pollution disturbing these processes is not trivial.

The presence of microplastics has been shown to alter the composition of the overall pool of marine Dissolved Organic Matter (DOM) by accumulating light-absorbing and more recalcitrant forms of DOM (*i.e.,* Chromophoric DOM [CDOM]) as a result of increased microbial processes [98,321]. This accumulation of CDOM in surface waters, along with the potential shading effect due to the accumulation of buoyant plastics [309], could hamper light availability in deeper layers of the water column and have implications for phototrophic primary production as well as the overall marine carbon dynamics [98]. Microplastics can also stimulate microbial production of organic carbon and marine gel particles [123] which, alongside the demonstrated capacity of microplastics to agglomerate with and alter the sinking rates of natural marine aggregates [38,77,91,103,110,116] (as discussed above), may potentially affect the functioning of the marine biological pump [123,321]. Several studies have previously suggested that similar effects would be caused by any inert or inorganic particles [98,123,333], and this hypothesis was recently confirmed [320]. Boldrini *et al.* [320] compared the effects of PS microplastics to those of silica gel particles and found that the silica gel particles actually increased the production and transformation of CDOM by microbes even more than microplastics. Indeed, it has long been known that solid particles immersed in seawater adsorb and concentrate nutrients as well as organic matter on their surfaces, transforming them into 'hotspots' [12,98,123,309] of microbial activity [7,334,335]. This phenomenon has been shown to apply to plastics as well, demonstrated for example by higher bacterial activity on different polymer substrates (*i.e.,* PE, PE with pro-oxidant [OXO], thermally aged OXO [AA-OXO] and PHBV) compared with seawater [96] and by the ability of bacterial communities to remain viable over several months in cultures amended with PET particles, while similar cultures without PET soon died out [54,335]. Plastics, however, compared with other marine particles, pose a greater risk to marine ecosystems because they are a durable and mostly (at least initially [321]) buoyant anthropogenic pollutant. Furthermore, their abundance in the environment is only predicted to increase [1], thereby having the potential to considerably and irreversibly [336,337] increase the amount of particles affecting microbial activities in the (otherwise largely oligotrophic) oceans [12,98,105].

In addition to carbon cycling, some studies have demonstrated that microplastics can interfere with nitrogen cycling in marine sediments [47,338]. PVC microplastics were found to inhibit nitrification and

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denitrification in coastal salt marsh sediments in a microcosm study, while microparticles of polyurethane foam (PUF), polylactic acid (PLA) and PE enhanced these processes, although the effect of PE was not statistically significant [47]. Contrastingly, PE microbeads extracted from a cosmetic product were found to impair microbial ammonium removal *via* denitrification in intertidal sediment microcosms, leading to the accumulation of ammonium in the overlying water which could result in eutrophication and harmful algal bloom incidents in the natural environment [338]. It was suggested that residues of antimicrobial compounds in the cosmetic PE microbeads may have adversely affected the microbial communities responsible for ammonium removal [47,338], whereas the disruptions to nitrogen cycling in the PVC treatment were possibly caused by sulfide producing bacteria, whose significant enrichment in the PVC treatment was potentially linked to an unidentified additive, highlighting the importance of the chemical composition and additive content of plastics [47].

Marine plastics harbour microbial communities that are taxonomically [7,16] and functionally (*e.g.,* enrichment of genes coding for nitrogen fixation [12]; see also a freshwater study [309]) distinct from planktonic communities, and conservative estimates reveal that marine plastic biofilms comprise approximately 1% of the total biomass in the surface microlayer of the oceans [58]. As discussed above, it is unclear whether marine microbes biodegrade and utilise the recalcitrant polymer backbones for growth, although evidence for microbial mineralisation and assimilation of some plastics exists [62,63]. Concerns have, however, been raised regarding the ecological and biogeochemical impact of alterations to the overall marine microbiome as plastic surfaces provide new niches for and enrich taxa that would otherwise be scarce in abundance in the planktonic community fraction [12,58,105,194]. Further, high concentrations of plastic debris are accumulating in oligotrophic open ocean gyres [339–343], with unknown consequences to the functioning of these ecosystems [105,335]. Increased (heterotrophic) microbial activity is often coupled with increased oxygen consumption [309,344], which could potentially lead to oxygen depleted conditions in areas with high levels of plastic pollution, including the seafloor (*e.g.,* [30,270,309,345,346]). Moreover, the impacts of plastic pollution to primary production by microbial photoautotrophs in the marine environment need further clarifying as floating plastic debris has been described as hotspots for net autotrophic production [12], while adverse effects on these organisms have also been reported [165,324,329,347,348]. The plastisphere has also been found to contribute to greenhouse gas (CO_2 and N_2O) fluxes in the eastern South Pacific Ocean, albeit the contribution was rather small (less than 1% of the overall ocean contribution [147]). Experimental evidence also indicates that exposure to plastics and related leachates can negatively affect biocalcification by marine forams, resulting in possible impacts on oceanic carbon storage and consequently climate regulation [319].

8. Conclusions and future directions

We now have a wealth of information on the taxonomic composition of the prokaryotic (particularly bacterial) component of the plastisphere, and whilst we are not advocating for studies to stop characterising the prokaryotes, several other areas need further investigation. We have therefore brought together some of the key themes that came up in the conclusions and future directions suggested by many of the reviews returned by our literature search (Fig. 3), namely that future studies should:

(i) use multi-OMIC and interdisciplinary approaches to understand the role of the plastisphere in plastic biodegradation as well as in determining the mechanisms and pathways used for biodegradation [19,151,157,161,164,170,172,175,178,180,181,183,184,188,189,191,194,196,198–200,204–207];

(ii) examine the impacts of plastic waste in concert with other ecological threats, such as climate change and antibiotic resistance [5,169,181,184];

(iii) assess the consequences of the microbial communities on plastics on plastic toxicity and interactions with other organisms and their environments [5,18,151,163,169,180,181,197];

(iv) empirically investigate the ability of the potentially harmful microbes (including bacteria and micro-eukaryotes) already identified on plastics to induce infection or cause harm [151,172,180,181];

(v) use isotopically labelled plastics or other methods in order to more comprehensively and more easily confirm plastic degradation [177,188,193] alongside assessments of plastic degradation in the environment [18,19,155,157,172,174,206].

There are also suggestions by several studies to standardise methodologies in order to increase the ability to draw fair comparisons between different locations and environmental conditions [161,170,171,183,193,197,208,210]. Whilst we agree that standard methodologies or test substrates could be useful tools in order to compare the plastisphere on a global scale and could be incorporated with data collected for the Earth Microbiome Project [175,349,350], this must be balanced against the rapid development of new and better methodologies, alongside the fact that there are few universally agreed upon best practice methods for microbiome [351] or plastics research [161]. Furthermore, a standardised methodology is only useful if the authors of studies guarantee that their data is made available upon publication of their study. Even in 2020, 24% of published plastisphere studies that used next generation sequencing did not make their data accessible (Fig. 1). We therefore urge authors and reviewers to confirm that these data are made accessible at the time of publication, ensuring that these data may be used for other purposes, such as in other meta-analyses [16], the construction of databases containing known genes for plastic degradation [238,352], or for the mining of metagenomes for plastic degradation genes [353].

As discussed above, we are also currently lacking information on the non-bacterial plastisphere constituents; to our knowledge, there are currently no studies reporting on or investigating viruses in the plastisphere, and we have relatively little information on the eukaryotic plastisphere fraction (Fig. 2). We hope that with the decreasing cost and therefore increasing availability of metagenomic sequencing, this approach will be used more extensively, and future studies will therefore include information on all taxonomic groups. This will hopefully help to elucidate the role of eukaryotes in shaping the plastisphere. It is currently not clear whether it is 'cost efficient' for hydrocarbonoclastic taxa to degrade plastic polymers (if theoretically capable) when more accessible forms of hydrocarbons may be available from other biofilm members (*e.g.,* diatoms) [12,127]. Therefore, future research should aim to determine whether prokaryotic community composition differs if eukaryotes are excluded from the colonisation process [12]. There are further key research questions brought about by both: (a) the criticisms within the microplastic research field that many studies use unrealistically high particle concentrations (*e.g.*, [354–357]), while current levels of larger microplastics (>10 μm) are predicted to inflict little ecological harm on the marine environment from an ecotoxicological perspective [358,359]; and (b) the increasing number of studies examining the effects of plastics on biogeochemical cycling (discussed in the previous section). Specifically:

1. are current concentrations of plastics in the marine environment high enough to induce alterations to biogeochemical processes (either locally or globally)?
2. if not at the moment, will the situation change in the future if plastic pollution continues to increase as predicted [1]?
3. is there a critical threshold [336]?
4. similar to point (ii) above, will any impacts be amplified by combined effects caused by other environmental stressors, such as global warming or ocean acidification [27,286,319,321]?

One suggested solution to the problems caused by the environmental accumulation of traditional (*i.e.*, petrochemical) recalcitrant plastics is the use of biodegradable plastic types (*e.g.*, polylactic acid [PLA], polybutylene adipate terephthalate [PBAT], polybutylene succinate [PBS], PHA and PCL [360]). However, the risks and benefits of such replacement must be carefully weighed in light of microbial processes and biogeochemical cycling [14,360], particularly as high concentrations of bioplastics also have the potential to affect marine carbon, nitrogen and sulphur cycles [14,47]. Together with further implications to marine methanogenesis and cycling of natural PHAs [14], it seems that replacing traditional plastics with biodegradable ones could lead to an equally bad – or even worse – situation. Therefore, the most important ways of mitigating the effects of plastic pollution are to radically decrease the production and use of single-use plastics – degradable or not – and improve waste management practices globally.

Supplemental materials

All supplementary tables are on Figshare: doi.org/10.6084/m9.figshare.14096912

Table S1: Summary of all primary research articles reviewed. Includes references [4,6–8,10–14,16,21–150].

Table S2: Summary of all plastisphere review articles reviewed. Includes references [5,18–20,151–211].

Table S3: The methods used and degradation found by studies including a measurement of biodegradation. Includes references [4,11,21,23,24,30,35,43,45,52,56,59,62,63,65,68,70,72,76,81,84,92–94,102,104,111,119–122,134,139,144,149,361].

Table S4: Potential pathogens (prokaryotic and eukaryotic) found on plastics by the studies reviewed here. Includes references [7,13,26,33,49,56,57,60,69,71,80,83,97,114,127,130,131,137,138,150,362].

Table S5: Antibiotic resistance genes found on plastics in aquatic environments. Including references [13,26,142,218,362–365].

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