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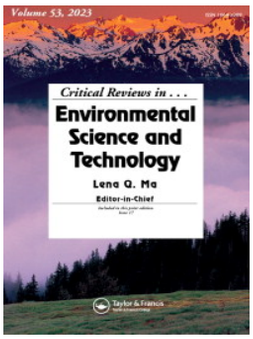

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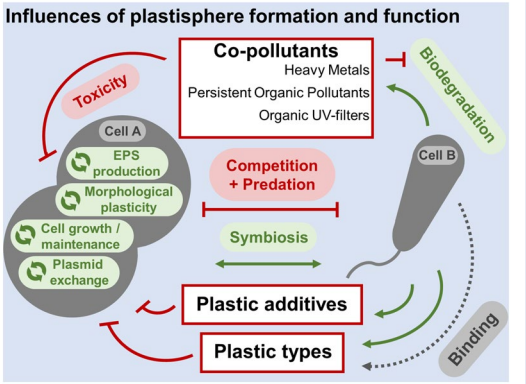
The primary molecular influences of marine plastisphere formation and function: Novel insights into organism -organism and -co-pollutant interactions

Charlotte E. Lee[a], Lauren F. Messer[a], Sophie I. Holland[b], Tony Gutierrez[b], Richard S. Quilliam[a] and Sabine Matallana-Surget[a]

[a]Division of Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, UK; [b]School of Engineering & Physical Sciences, Heriot-Watt University, Edinburgh, UK

ABSTRACT

Marine plastic pollution is rapidly colonized by a biofilm of microorganisms associated with the control of biogeochemical cycles, plastic biodegradation, and potentially pathogenic activities. An extensive number of studies have described the taxonomic composition of this biofilm, referred to as the 'plastisphere', and previous reviews have reported on the influence of location, plastic type, and plastic-biodegradation ability on plastisphere formation. However, few studies have investigated the metabolic activity of this complex biofilm and how microbial pathogenicity and bioremediation could be regulated in this ecosystem. In this review, we highlight the understudied molecular and abiotic factors influencing plastisphere formation and microbial functioning beyond taxonomic description. In this context, we critically discuss the impacts of (i) organism-organism interaction, (ii) microbial cell wall composition, and (iii) commonly encountered plastic-bound co-pollutants (heavy metals, persistent organic pollutants, UV filters). For the first time, we review the anticipated impact of lipophilic organic UV-filters – found in plastic additives and sunscreens – on the plastisphere due to their reported affinity for plastics, persistence, and co-location at high concentrations in touristic coastal environments. Herein, we integrate the findings of 34 global studies exploring plastisphere composition, 35 studies quantifying co-pollutant concentrations, and draw upon 52 studies of cell -cell and -substrate interaction to deduce the inferred, yet still unknown, metabolic interactions within this niche. Finally, we provide novel future directions for the advancement of functional plastisphere research applying advanced molecular tools to new, and appropriate research questions.



HIGHLIGHTS

- Data was compiled from 97 plastispheres across 34 different studies and an additional 87 studies relating to the impacts of plastisphere components on microbial species.
- The biotic and abiotic factors influencing microbial adhesion to different plastic polymers, including cell wall composition, and plastisphere location are considered.

CONTACT Sabine Matallana-Surget sabine.matallanasurget@stir.ac.uk Division of Biological and Environmental Sciences, Faculty of Natural Sciences, University of Stirling, Stirling, UK.

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- The impacts of heavy metals and organic co-pollutants – and for the first time, organic UV-filters – on plastisphere formation and function are reviewed and discussed.
- A change in direction from novel research questions to the use of state-of-the-art methodologies are recommended for the advancement of functional plastisphere research.

KEYWORDS Bacterial metabolism; marine pollution; microbial ecotoxicology; plastic biodegradation; plastic colonization; plastisphere dynamics

HANDLING EDITORS Jörg Rinklebe and Lena Q. Ma

1. Introduction

Throughout the last six decades, plastic has accumulated in the world's oceans to now represent more than 80% of all marine litter (Gewert et al., 2015; Ostle et al., 2019). Leaching from maritime activity, wastewater treatment plants (WWTP) and other municipal effluents (Mammo et al., 2020; Murphy et al., 2016), plastics have become one of the largest man-made threats to ocean life. The fragmentation of plastic also releases 1.15–2.41 Mt of microplastics (<5 mm size) into the world's seas and oceans each year (Eriksen et al., 2014), which is projected to persist in the marine environment for centuries (Worm et al., 2017). These plastics and microplastics contain synthetic additives, and can further aggregate anthropogenic leachate such as persistent organic pollutants (POPs) and heavy metals (Wang et al., 2020), which are environmentally stable from years to decades (Semones et al., 2017). As plastics are highly persistent and only removed through sedimentation or photodegradation (Gewert et al., 2015; Summers et al., 2018), the accumulation of these marine contaminants on plastic increases their persistence and dispersal throughout the ocean (Amelia et al., 2021; Brennecke et al., 2016). Microplastics can then bioaccumulate throughout the food chain (Cverenkárová et al., 2021), introducing potential chemical hazards to all other organisms (Amelia et al., 2021; Mammo et al., 2020).

In the ocean, plastics are exposed to ultraviolet-radiation (UV-R), temperature fluctuations, and ocean hydrodynamics (Gewert et al., 2015). This can induce the formation of reactive oxygen species (ROS) (Zhu et al., 2019), the release of chemical additives—namely plasticizers (Focardi et al., 2022; Peijnenburg, 2008)—and increase plastic charge and porosity (Wang et al., 2020). This abiotic plastic weathering is facilitated by the formation of biofilms (Hossain et al., 2019), termed 'plastispheres' (Zettler et al., 2013), which specifically and rapidly adhere to the surface of plastics (Latva et al., 2022). However, the impact of the anthropogenic chemicals which aggregate in and around the plastic-bound biofilm (Amelia et al., 2021) on the well-studied formation (Rogers et al., 2020), and composition (Amaral-Zettler, 2022; Wright et al., 2021) of the plastisphere, as well as its capacity for plastic biodegradation (Jacquin et al., 2019; Wright et al., 2020), and pathogenicity (Amelia et al., 2021; Wright et al., 2020; 2021) has not been reviewed. Mammo and coworkers (2020) and Amaral-Zettler (2022) have discussed the role of co-pollutants in the development of antibiotic resistance in pathogens, however this is not the only process which may be impacted by chemical-microorganism interactions. The activity of pathogens may also be inhibited by co-pollutants, while plastic-biodegrading organisms, or microorganisms important to biogeochemical cycling may also be affected (Falkowski et al., 2008; Fernández-Juárez et al., 2021; Focardi et al., 2022; Santo et al., 2013). Other aspects of the plastisphere, including the chemical composition of the plastic (Frère et al., 2018; Miao et al., 2020; Wright et al., 2021; Zhang et al., 2022), and organism-organism interactions within the biofilm (Anand et al., 2013; Pollet et al., 2018) may also impact these microorganisms and their metabolic processes. Greater exploration of these complex interactions is therefore required to understand the impact of plastisphere colonization on microbial metabolism.

In this review, we outline the selection pressures within the marine plastisphere and use studies examining the impact of plastisphere-related factors on single-organisms to synthesize how they may impact plastisphere metabolism. We elaborate on the role of location and plastic type in selecting for the early plastisphere's primary microorganisms; topics presented within previous reviews (Amaral-Zettler, 2022; Jacquin et al., 2019; Mammo et al., 2020; Rogers et al., 2020; Wright et al., 2020). For the first time, we also introduce organism-organism and organism-co-pollutant interaction as other essential parameters that are fundamental to the formation and functioning of the plastisphere. The impacts of chemical and heavy metal pollutants on the plastisphere have also gained little attention (Amelia et al., 2021; Jacquin et al., 2019; Rogers et al., 2020), and is therefore a major focus of this review. Lipophilic contaminants such as the organic ultraviolet (UV)-filters used in plastics and personal care products (Díaz-Cruz et al., 2008; Semones et al., 2017) have a greater capacity than most POPs to bind to plastic and impact the plastisphere. These organic UV-filters also accumulate in marine coastal environments (Díaz-Cruz et al., 2008) due to the increasing number of tourists in densely populated coasts (Amelia et al., 2021; Lozano et al., 2020), and are therefore discussed in this review as co-pollutants of critical importance for plastisphere research. For the first time, this review discusses the core molecular interactions which must be considered when studying plastisphere formation, metabolism, and related processes, and provides instructions for future research in the field.

2. Influences of plastisphere formation

2.1. Plastisphere location

The world's oceans, though interconnected, are biogeochemically defined by broad variations in nutrient and light availability, temperature, pressure, salinity (Coons et al., 2021; Scales et al., 2021), and even pollution (Section 4.2; 4.3; 4.4). This creates many distinct niches within the water column to which each microbial species must adapt by the constitutive expression of traits increasing their survival (Barton et al., 2013; Nguyen et al., 2021). This cultivates unique communities at each location specifically adapted to their associated biogeochemical pressures (Barton et al., 2013). As a result, once plastic is introduced into a particular region, only the microorganisms suited to that region can bind to it (Coons et al., 2021; Scales et al., 2021). The current consensus is that this initial binding is indiscriminate, so members of the plastisphere will largely reflect the community composition of this region (Amaral-Zettler, 2022; Wright et al., 2020). In most marine regions, the SAR11 clade (Alphaproteobacteria) dominates the pelagic microbial community, while *Prochlorococcus, Synechococcus* (Cyanobacteria) (Bolaños et al., 2021), *Rhodobacteraceae* (Alphaproteobacteria), *Flavobacteria* (Bacteroidetes), and other Alphaproteobacteria, Bacteroidetes, and Gammaproteobacteria are also regarded dominant classes (Frère et al., 2018; Kirstein et al., 2018; Scales et al., 2021). However, only biofilm-forming (Section 2.3) species able to withstand the plastisphere's competition (Section 2.4) and co-pollutant toxicity (Section 4) will be enriched in the plastisphere. *Rhodobacteraceae* and *Flavobacteria* are still dominant on plastic in many locations, though *Prochlorococcus, Synechococcus,* and the SAR11 clade, along with many other SAR and OM1 clades are not (Bryant et al., 2016; Frère et al., 2018). The dominant bacteria in these biofilms are instead a mix of the other less-dominant classes found in those regions (Bryant et al., 2016; De Tender et al., 2015; Frère et al., 2018; Kirstein et al., 2018; Scales et al., 2021).

We compiled data from 97 plastispheres across 34 different studies which investigated plastisphere composition after a plastic's long or short exposure to endemic seawater communities (Figure 1). These studies show that Gammaproteobacteria, Alphaproteobacteria, and Bacteroidetes are the most dominant bacterial classes on plastic regardless of location (Figure 1). Warmer climates (Figure 1c-f), however, produce more heterogeneous plastispheres than temperate climates (Figure 1a-b; 1 g-h) due to the high species richness (Amaral-Zettler et al., 2015) and

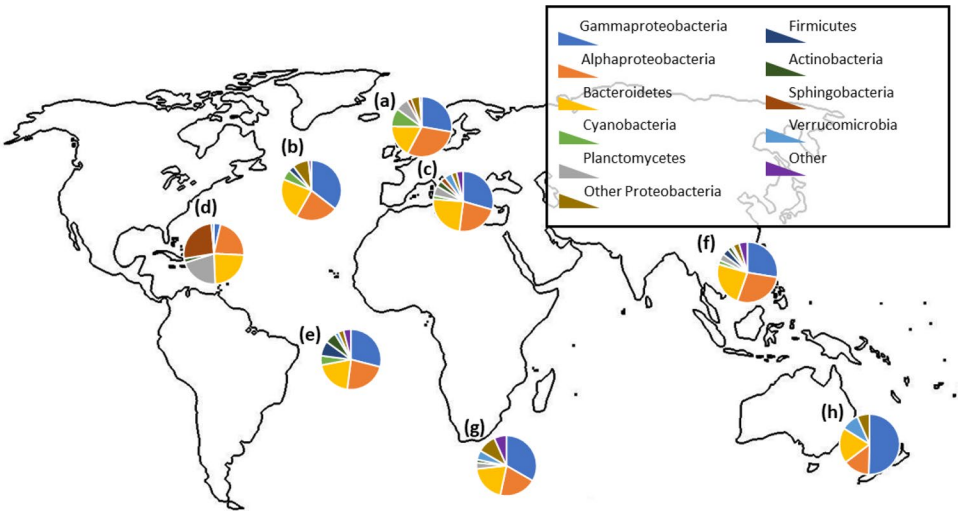

Figure 1. Bacterial classes present on plastics in different ocean regions.
Data was collected from 34 studies of plastisphere composition. With the exception of Scales and coworkers' (2021), and Coons and coworkers' (2021) studies, the community on one plastic type at one time point was considered a single plastisphere. In the aforementioned studies, data provided for bacterial abundances were given per location, so each location was also considered a 'plastisphere' here. Within the 34 studies, a total of 97 plastispheres were used to build pie charts: 13 **(a)**, 10 **(b)**, 18 **(c)**, 16 **(d)**, 7 **(e)**, 22 **(f)**, 4 **(g)**, and 7 **(h)**. Each lineage within each plastisphere was rated via a five-point scoring system: 10 for the most abundant, 8 for the 2nd, 6 for the 3rd, 4 for the 4th, and 2 for the 5th most abundant. To provide the final data for the pie charts, scores from all represented lineages were then totaled for each location. Microorganisms representing 6th most abundant communities or fewer were omitted, and total scores ranged from 0 to 184 per bacterial class per location. All charts presented here contain data retrieved from a mix of coastal, beach, and oligotrophic locations (Supplementary Table1).

accelerated microbial growth (Schlundt et al., 2020) in those climates. Indeed, 13.9% – 49.3% of these plastispheres represent microbial classes rarely observed in cooler climates (i.e., Actinobacteria, Sphingobacteria) (Figure 1c-f).

Coons and coworkers (2021) studied this effect across four global regions, finding biogeographical location to impact plastisphere community composition more than any other factor. In another cross-hemisphere study of three distinct global regions, consistencies were identified between plastispheres of each location, though phylogenies were mostly distinct (Scales et al., 2021). Amaral-Zettler and coworkers (2021) also examined plastic debris across four locations in the Mediterranean Sea, noting a gradual succession of plastisphere communities between regions. A greater distinction may be seen between plastispheres originating from different non-marine sources (i.e., soils, freshwater, wastewater) (Delacuvellerie et al., 2022; Rogers et al., 2020), though this has not been studied in depth. The marine plastisphere is also occupied by archaea, algae, fungi, and protozoa (Bryant et al., 2016; Kirstein et al., 2018; Zettler et al., 2013). The distribution of these additional kingdoms is also impacted by biogeography (Barton et al., 2013), meaning their abundance and taxonomic diversity would also depend on location. Early plastic colonization is therefore highly opportunistic, reliant on the present microbial communities capable of exploiting this niche (Section 2.3; Oberbeckmann et al., 2014) which is dependent on the region's temperature, salinity, and even co-pollutant concentrations (Section 4.2; 4.3; 4.4).

2.2. Plastic type

All plastics consist of hydrocarbon chains, some of which contain aromatic benzene rings (polystyrene, polyethylene terephthalate: PET), methyl groups (polyethylene, polyamide, PET, polypropylene), or other functional groups (e.g. carbonyls, ketones, esters) (Crawford & Quinn, 2017). These groups increase polymer branching which separate the hydrocarbon chains within the polymer matrix, therefore producing either aliphatic (loosely packed) (e.g. polyethylene and

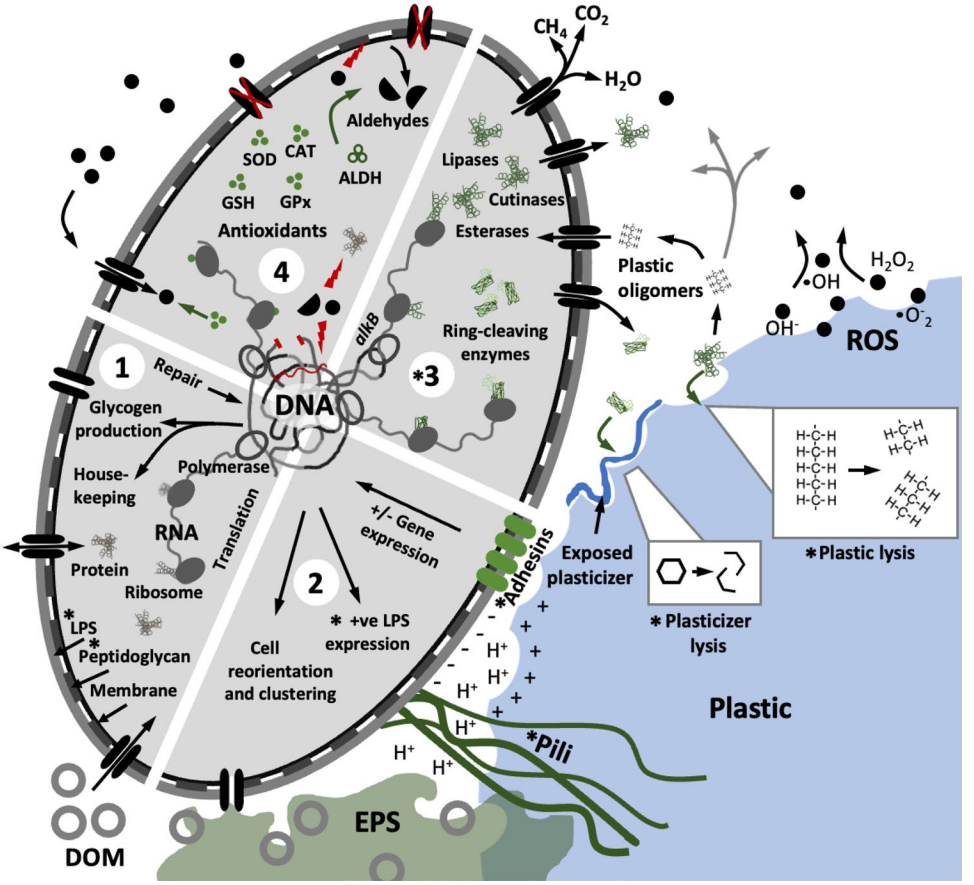

Figure 2. Inferred molecular interactions between marine microorganisms and plastics.
1 Neutral interaction: Homeostatic bacteria. **2 Adhesion:** Bacteria are drawn toward plastic through electrostatic interaction. Gene expression then shifts so they can adhere to the plastic using pili, adhesins, and by secreting EPS, and orientate themselves within the establishing biofilm. **3 Biodegradation:** Ring-cleaving enzymes are expressed which liberate plasticizers from the plastic, making it more susceptible to depolymerization via the enzymatic action of lipases, cutinases, and esterases. The resultant plastic oligomers and DOM-like plasticizers are released from the plastic allowing this and other bacteria to utilize them as a carbon source. CH_4, CO_2 and H_2O are also released as a biproduct. **4 Toxicity:** ROS released from plastic weathering react with the cell membrane (releasing aldehydes), proteins (resulting in their misfolding), and DNA (causing mutations and double-strand breaks). Aldehydes also damage DNA and proteins. Cells produce antioxidants and ALDHs to mitigate this damage, which diverts energy away from maintaining homeostasis and normal cell functioning.
The mechanisms depicted herein are synthesized from the literature and demonstrated for a Gram-negative bacterium, although the concept applies to other microorganisms. Processes and structures unique to bacteria marked with a '*'. Green – Molecules involved in cell response to binding Red - Disruption to cell; MP - Microplastic; DOM - Dissolved organic matter; ROS - Reactive oxygen species; LPS - Lipopolysaccharide; EPS – Exopolymeric substance; CAT - Catalase; SOD - Superoxide dismutase; GSH - Glutathione; GPx - Glutathione peroxidase; ALDH - Aldehyde dehydrogenase; alkB - Alkane hydroxylase gene.

polypropylene), or crystalline (tightly packed) plastics (e.g. polystyrene and polyvinyl chloride: PVC) (Crawford & Quinn, 2017). Within minutes of immersion in seawater, dissolved organic matter (DOM) and abiotic nanoparticles (i.e., trace metals) collect on the surface of submerged materials (Lorite et al., 2011). Marine microorganisms are then drawn to their surface through hydrophilic interaction, electrostatic interaction, or Van der Waals force, facilitated by functional groups expressed in the ecocorona (Figure 2; Lorite et al., 2011; Tuson & Weibel, 2013). Plastic charge, crystallinity, hydrophobicity, buoyancy, and surface roughness are therefore often used to explain differences in plastisphere diversity (Chao & Zhang, 2011; Kirstein et al., 2018; Tobias-Hünefeldt et al., 2021).

Frère and coworkers (2018), and Miao and coworkers (2020) found that polystyrene and PVC -bound communities were significantly different from aliphatic communities. Zhang and coworkers (2022) found microbial diversity to vary between all tested plastic types. A meta-analysis of extant plastisphere studies (Wright et al., 2021) also revealed that aliphatic plastic attracts

different microorganisms to other plastics, likely due to the varied, sometimes aromatic functional groups that these other polymers contain (Crawford & Quinn, 2017). Chemical additives also vary between plastic types (Section 4; Bakir et al., 2014; Birnsteil et al., 2022), further contributing to the differences observed between plastispheres (Frère et al., 2018; Miao et al., 2020). However, the influence of plastic-type on microbial community formation appears less significant than the influence of location (Coons et al., 2021; Scales et al., 2021), and location-dependent factors such as salinity (Delacuvellerie et al., 2022). The surface chemistry of different plastics also converges after biofilm formation, accounting for the overlap in biofilm diversity observed in the latter stages of plastisphere development (Kirstein et al., 2018; Woodall et al., 2018). This reduces the role that plastic type may have in late plastisphere colonization, though early biofilm formation is still dependent on the chemical composition of the base substrate (Kirstein et al., 2018; Tobias-Hünefeldt et al., 2021; Zhang et al., 2022), which can vary between plastics (Crawford & Quinn, 2017). Plastic type may not influence plastisphere formation as much as location, though it is still important for our understanding of why the plastisphere's microorganisms are there, and thus requires further investigation.

2.3. Attachment strategy

Microorganisms anchor themselves to substrates, including plastic, to form a biofilm which provides protection from environmental stressors, nutrient limitation, and predation (Scherwass et al., 2016). This ability of microorganisms to bind to plastic is a potential selection pressure of the early plastisphere, as only a limited number of microbial species express morphologies suited to substrate binding. *Hyphomonas*, for example, are often found in the plastisphere (Oberbeckmann et al., 2014; Zettler et al., 2013), possibly due to their uncommon expression of prosthecae, which are used for substrate binding (Zettler et al., 2013). Quorum-sensing as performed by some *Rhodobacteraceae*—the most abundant Alphaproteobacteria in the plastisphere (Bryant et al., 2016; Delacuvellerie et al., 2022; Zettler et al., 2013)—may also allow for better navigation to and throughout the plastisphere, allowing these lineages to more rapidly colonize and persist. Negatively-charged lipopolysaccharide (LPS) or capsular colonic acid expressed by Gram-negative bacteria also strengthens a bacterium's ionic, hydrogen, and covalent-bond interactions with plastic, and thus their final attachment (Chao & Zhang, 2011). For example, *Sphingomonas,* an Alphaproteobacteria (Dussud et al., 2018; Scales et al., 2021; Zettler et al., 2013) expresses Glycosphingolipids (Wedeking & van Echten-Deckert, 2007), a more negatively charged alternative to LPS, possibly contributing to its abundance in the plastisphere (Dussud et al., 2018; Scales et al., 2021; Zettler et al., 2013). No study has directly explored the impact of cell wall composition on plastisphere adhesion, though inferences can be made of the plastisphere's most effective adhesion strategies based on its most common microorganisms, and the strategies they use.

In the plastisphere, one of the dominant prokaryotic classes, Gammaproteobacteria is represented by species of *Alteromonadales, Pseudomonadales*, *Vibrionales*, and *Oceanospirillales* (Delacuvellerie et al., 2019; Dussud et al., 2018; Wright et al., 2021). All Gammaproteobacteria are Gram-negative, meaning they express LPS, facilitating their attachment to plastic (Chao & Zhang, 2011), while *Pseudomonadales* and *Vibrionales* also express type IV pili (Tfp), which can anchor them to the debris (Figure 2.2; Pelicic, 2019). The Gram-negative Planctomycetes and Cyanobacteria, mixed-Gram Firmicutes, and Gram-positive Actinobacteria also bind frequently, which in the case of Actinobacteria, may be due to the production of sprawling filamentous structures specifically for substrate binding (Figure 1; Pelicic, 2019). Despite being less abundant than Proteobacteria and Bacteroidetes, these are some of the most active microorganisms in the plastisphere, particularly Cyanobacteria (Delacuvellerie et al., 2022; Oberbeckmann et al., 2021), which secrete EPS for protection and microbial aggregation (Figure 2.2; Lagarde et al., 2016; Scherwass et al., 2016; Schlundt et al., 2020). Arthropods, sponges, cnidaria, nematodes, and a

range of protists, also significantly contribute to plastisphere diversity (Bryant et al., 2016; Kirstein et al., 2018; Zettler et al., 2013). However, it is not known how many present eukaryotes, such as the protozoan *Radiolaria*, bind to plastic (Zettler et al., 2013). Archaea and fungi are also rarely observed (Amaral-Zettler et al., 2021; Latva et al., 2022; Woodall et al., 2018) considering their ability to bind to substrates using archaella and hyphae (Bryant et al., 2016; Kirstein et al., 2018; Pelicic, 2019). Cell morphology therefore seems to play a lesser role in plastisphere adhesion for eukaryotes and archaea compared to bacteria. It is important to note that bacteria are generally primary colonizers, while eukaryotes and archaea are secondary colonizers (Bryant et al., 2016; Pollet et al., 2018). It is therefore likely that cell structure, alongside location, impacts the constitution of the early prokaryotic plastisphere more than the developed plastisphere.

2.4. Organism-organism interaction

In the environment, a combination of top-down and bottom-up selection pressures shape the composition of biofilm communities (Tobias-Hünefeldt et al., 2021). The number of grazers and pathogens which negatively impact bacterial populations (Moresco et al., 2021; Zettler et al., 2013) may therefore be depleted in the plastisphere through the joint secretion of toxins and EPS by bacteria and algae (Buchan et al., 2014; Scherwass et al., 2016). *Pseudoalteromonas* sp. also produce metalloproteases that specifically target peptidoglycan, and consequentially, Gram-positive bacteria (Tang et al., 2020). Gram-positive Actinobacteria then produce antibiotic enzymes (Jackson et al., 2018) which are likely used to compete with and protect against Gram-negative bacteria. This enzyme production, if widespread, may contribute to the lower abundance of Gram-positive bacteria in early plastispheres (Figure 3; Wright et al., 2021). However, there is no direct evidence of these enzymes within the plastisphere (Delacuvellerie

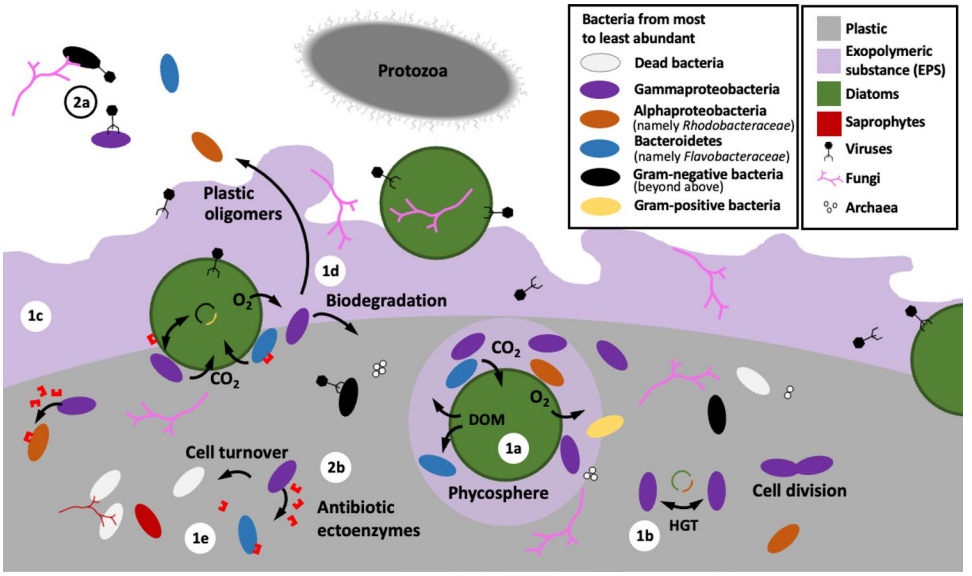

Figure 3. Predicted organism-organism interactions within the marine plastisphere.
The plastisphere is a diverse microbial community, primarily consisting of bacteria, then diatoms, fungi, and Archaea. Eukaryotes other than diatoms and fungi are also noted as plastisphere constituents, but are not included here.
1 Symbiosis: a Bacteria are often found within the phycosphere, allowing bacteria and diatoms to cooperate by exchanging essential supplies and **b** genetic material (via HGT). **c** Both also benefit from their mutual production of EPS which may trap and remove grazers (protozoa) and parasitic organisms (viruses and fungi) from the plastisphere. **d** Oligomers produced by plastic degradation, and **e** the dead microorganisms produced by the biofilm's high cell turnover also fuel heterotrophic, and saprophytic growth inside and outside the plastisphere. **2 Competition: a** Parasitism by viruses and fungi may occur within the plastisphere. **b** To reduce resource competition, bacteria can release antibiotics, lysing nearby cells, increasing the amount of nutrients (in the form of lysate) available, and reducing the number of other microorganisms competing for the same resource.
DOM - Dissolved organic matter; HGT - Horizontal gene transfer. Estimates for most abundant bacteria from (Supplementary Table1).

et al., 2022; Oberbeckmann et al., 2021) despite their common use in bacteria (Figure 3.2b; Anand et al., 2013; Ma et al., 2014). Many of the most abundant bacteria have also been found to be dormant on plastic (Delacuvellerie et al., 2022; Oberbeckmann et al., 2021), suggesting that this antagonism would not be a selection pressure in these plastispheres.

Regardless of their activity, microorganisms constitutively express negatively charged and adhesive proteins (Figure 2.2; Chao & Zhang, 2011; Hossain et al., 2019) such as those which allow Bacteroidetes, Actinobacteria, and Alphaproteobacteria to attach to plastic (Section 2.3; Dussud et al., 2018; Pelicic, 2019; Mammo et al., 2020). Attracted by bacterial hydrophilicity (Buchan et al., 2014; Delacuvellerie et al., 2019; Lorite et al., 2011), diatoms are drawn to the plastisphere during early stages of microbial succession (Figure 3; Schlundt et al., 2020). All diatoms accommodate an associated phycosphere in which bacteria (namely *Rhodobacteraceae* and *Flavobacteria* species) assemble for mutual gain (Buchan et al., 2014). Members of these phycospheres are then immobilized against stress through the exchange of dissolved organic carbon (DOC) and horizontal gene transfer (Figure 3.1a; 1b; You et al., 2021). This may explain why *Rhodobacteraceae* and *Flavobacteria* are two of the three most well represented (Delacuvellerie et al., 2019), metabolically active (Delacuvellerie et al., 2022) bacterial lineages in the plastisphere (Figure 3), although no published work has so far characterized active symbiotic interactions within the plastisphere. Diatom abundance remains consistent as the plastisphere population stabilizes (Cheng et al., 2021; Kirstein et al., 2018; Oberbeckmann et al., 2014; Zettler et al., 2013), also supporting the notion that the plastisphere biofilm is an inclusive community (Pollet et al., 2018).

By examining the understood interactions between species found in the plastisphere, we can therefore predict that the presence and abundance of species during early succession will impact that of the latter species (Datta et al., 2016; Lorite et al., 2011; Schlundt et al., 2020) as in other communities. This concept of inclusion versus inhibition is commonly used when exploring selection pressures of newly created niches. However, this is not explored in the study of plastisphere progression and may be one of the reasons for plastisphere variation between locations.

3. Plastisphere function

3.1. Plastic biodegradation

The discovery of microorganisms able to utilize plastic polymers as a source of carbon is still ongoing, though this research has already identified plastic-biodegrading species in many global ecosystems, including the ocean (Delacuvellerie et al., 2019; Wright et al., 2021; Yoshida et al., 2016). To biodegrade plastic, aromatic plasticizers (e.g. phthalates) stabilizing the polymer matrix (Peijnenburg, 2008), are first removed by physical weathering (Gewert et al., 2015), or through the specialized bacterial expression of ring-cleaving enzymes, such as homogentisate 1, dioxygenase (Figure 2.3; Cao et al., 2015; Bryant et al., 2016). By oxidizing and hydrolyzing plastic's chemical chains using lipases, esterases, and cutinases, plastic-degrading bacteria then depolymerize the plastic surface into oligomers (Figure 2.3; Danso et al., 2019); a process also performed by some fungi and archaea (Pramila & Ramesh, 2011; Zhao et al., 2020). With no shortage of water or oxygen to fuel these processes in the ocean, considerable concentrations of CO_2, H_2O, N_2 and CH_4 are produced by the plastic-utilising microorganisms, alongside the hydrocarbon oligomers (Figure 2.3; Royer et al., 2018). Many of these hydrocarbon oligomers are further broken down within the plastisphere, or are directly transported into the cell with the aid of biosurfactants (Ghosh et al., 2019). The remaining hydrocarbons are then captured in the water column, namely by Alphaproteobacteria which use esterases and hydrolases to liberate carbon-rich monomers (Figure 3.1d; Meyer-Cifuentes et al., 2020). This process continues until the plastic ceases to be a viable energy source; up to six months on polystyrene (Syranidou et al., 2017).

The polymers polyethylene, PET, and polystyrene can support several species of fungi (Pramila & Ramesh, 2011) and bacteria (Delacuvellerie et al., 2019) that express enzymes associated with this specialized metabolism. *Rhodococcus ruber* from marine sites, and *Pseudomonas spp.* from soil biodegrade polyethylene by expressing laccase and alkane hydroxylase to liberate small chain hydrocarbons (Santo et al., 2013; Yoon et al., 2012). The freshwater Actinobacterium *Arthrobacter sp. KI72* expresses hydrolases and oxidoreductases associated with polyamide metabolism (Takehara et al., 2018). *Ideonella sakaiensis* from sediments and the fungus *Humicola insolens* both secrete cutinases associated with PET depolymerization (Ronkvist et al., 2009; Yoshida et al., 2016). The *Oceanospirillales, Alcanivorax borkumensis* forms thick, uniform colonies on polyethylene after two months (Delacuvellerie et al., 2019). And in the marine environment, *Thioclava dalianensis,* and *Bacillus aquimaris* express hydrolases, oxidoreductases, and other uncharacterized enzymes associated with PET depolymerization (Wright et al., 2021). Capable of accessing these secure carbon stores, such bacteria are likely to outcompete others on their respective plastics, particularly during early plastisphere succession (Dussud et al., 2018). This may explain why microbial diversity has been found to differ on plastics compared to organic substrates (Miao et al., 2019; Tobias-Hünefeldt et al., 2021; Zhang et al., 2022). Although conflicting results from Kirstein and coworkers (2018), and Woodall and coworkers (2018) reported no effect of substrate type on microbial diversity. It is also unlikely that plastic biodegradation significantly influences plastisphere formation as metabolism is reduced upon binding to plastic (Miao et al., 2020; Murínová & Dercová, 2014). In fact, in the first studies of plastisphere protein expression, no plastic-biodegrading microorganisms or metabolic biproducts of degradation have so far been found associated with an active plastisphere (Delacuvellerie et al., 2022; Oberbeckmann et al., 2021). It is therefore suggested that when metabolically active, early colonizers instead use DOM (Birnstiel et al., 2022; Datta et al., 2016) or photosynthesis (Bryant et al., 2016; Delacuvellerie et al., 2022; Schlundt et al., 2020; Tobias-Hünefeldt et al., 2021; Wright et al., 2021) for growth, while latter colonizers, including saprophytes (Figure 3.1e), use cell detritus (Datta et al., 2016; Tobias-Hünefeldt et al., 2021). Factors other than a microorganism's use of plastic polymers (*Section 2; 4*) must also impact the presence and activity of each microbial species in the plastisphere. As a valuable route for pollutant bioremediation, this should be considered in ongoing study of the plastisphere and plastic biodegradation.

3.2. Pathogens in the plastisphere

Horizontal gene transfer (HGT) is the exchange of genetic information between microorganisms for the benefit of the recipient, and often the entire microbial community (Falkowski et al., 2008). In the plastisphere, this increases the resistance of all microorganisms capable of HGT to stressors, including antibiotics (Yang et al., 2019; You et al., 2021). Potentially pathogenic bacteria have been of particular interest concerning the development of this antibiotic resistance (Metcalf et al., 2022; Radisic et al., 2020; Silva et al., 2019; Yang et al., 2019; You et al., 2021). For example, *Vibrionaceae* can dominate a marine plastisphere (Delacuvellerie et al., 2022; Dussud et al., 2018), including *V. cholerae* (Silva et al., 2019), *V. parahaemolyticus* (Kirstein et al., 2018), *V. anguillarum* (Dussud et al., 2018), and *V. vulnificus* (Metcalf et al., 2022) which are often associated with water-borne diseases (Silva et al., 2019). As antibiotic resistance is promoted on the surface of plastic (Metcalf et al., 2022; Radisic et al., 2020; Yang et al., 2019), the virulence of these potentially pathogenic bacteria may also be increased. Concerningly, microplastics facilitate the transport of pathogenic bacteria throughout the water column and up the food chain once consumed by marine organisms (Mammo et al., 2020; Miller et al., 2020), and are therefore considered a significant risk to public health (Amelia et al., 2021). However, the virulence of these bacteria on plastic has not yet been confirmed (Delacuvellerie et al., 2022; Oberbeckmann et al., 2021), and needs to be further investigated.

4. Influence of ROS and co-pollutants

4.1. Plastic toxicity

Plasticizers, other POPs, and heavy metals induce toxicity in marine species by infiltrating essential tissues and disrupting cell homeostasis (Davarpanah & Guilhermino, 2019; Harmon, 2015; Qiao et al., 2019). Upon ocean weathering and photodegradation, the plastic itself also induces stress through the formation of polymer radicals, leading to carbon-chain scission and the production of ROS (Rabek, 1990). Due to their lack of tissue barriers, microorganisms in the plastisphere are directly exposed to the ROS that plastics produce (Zhu et al., 2019), making them more likely than larger organisms to be negatively impacted by oxidative stress (Figure 2.4; Figure 4.3).

Plastic-induced oxidative stress affects microbial metabolism and physiology in a plastic- and species- specific manner (Figure 2.4; Figure 4.3). For instance, exposure to plastic reduces nitrogen cycling and cellular rearrangement in *Halomonas alkaliphila* (Sun et al., 2018), and impairs

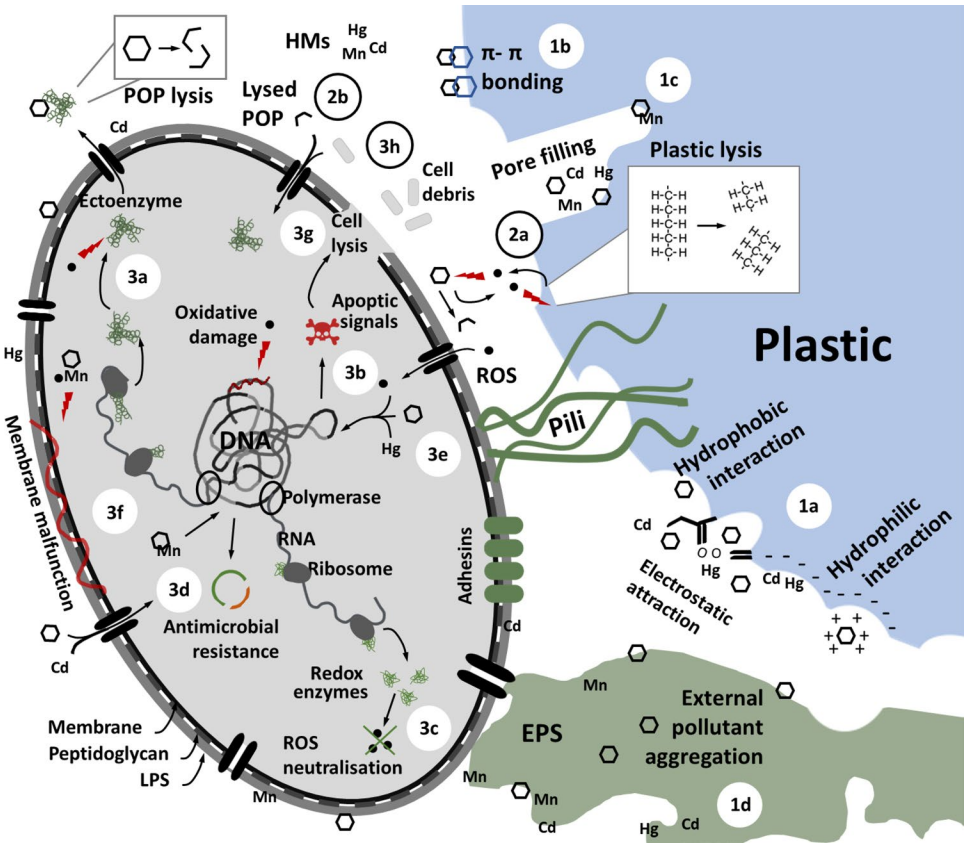

Figure 4. Deduced molecular interactions between microorganisms and plastic's co-pollutants.
1 Binding: Pollutants are first attracted to the plastisphere through **a** hydrophilic interaction, hydrophobic interaction, electrostatic attraction, and **b** π-π bonding. **c** These are then retained in plastic pores, **d** and in secreted EPS, keeping most pollutants from entering the cell.
2 POP Lysis: a The ROS released from pollutants expedites the POP and plastic degradation driven by microorganisms (Figure 2), **b** which can fuel much cell growth. **3 Stress:** ROS also
a disrupts protein synthesis, **b** and induces apoptosis. In response to this persistent exposure to POPs and HMs, microorganisms will **c** produce antioxidants, and develop a resistance to this stress, **d** also propagating antimicrobial resistance. Persistent stress, and **e** direct exposure to certain POPs and HMs will ultimately lead to **f** structural deformation and **g** cell death.
h However, this ROS-induced cell turnover increases saprophytic cell growth in the plastisphere.
Processes are assumed from literature review involving studies of ecotoxicology, bioremediation, and biofilm function. Branched oxygenated structures on plastic - Cationic exchange sites (i.e. carboxyl groups); ϟ - oxidative damage; POP - Persistent organic pollutant; HMs - Heavy metals (Hg, Cd, and Mn used to represent the group); EPS – Exopolymeric substances; ROS - Reactive oxygen species; LPS – Lipopolysaccharide. Regular cellular processes are highlighted in green; pollutant-induced cellular damage and disruption is highlighted in red.

membrane function, photosynthesis, and DNA integrity in the marine diatom *Phaeodactylum tricornutum* (Sendra et al., 2019). Polyethylene and polypropylene ROS increase EPS production and expression of apoptotic markers in the freshwater algae *Chlamydomonas reinhardtii* (Lagarde et al., 2016), and polystyrene impairs membrane integrity, and promotes microcystin toxin production in the freshwater cyanobacterium *Microcystis aeruginosa* (Feng et al., 2020). However, 200 mg/L of polystyrene increases the growth of *Clostridiaceae*, *Geobacteraceae*, *Dethiosulfovibrionaceae*, *Desulfobulbaceae,* and *Anaerolineaceae,* while decreasing the growth of *Cloacamonaceae*, *Porphyromonadaceae*, *Gracilibacteraceae*, and other *Anaerolineaceae* (Fu et al., 2018). *Phaeodactylum tricornutum* is also unaffected by 500 mg/L of polyethylene (Niu et al., 2021), which is 10x the plastic toxicity threshold in other algal species (Sjollema et al., 2016; Zhang et al., 2017). These studies suggest that plastic type may influence plastisphere composition (Section 2.2). However, as extant plastic toxicity has exclusively been explored in model bacteria, the wider implications of plastic-induced ROS on the plastisphere remain unknown. Metabolomics, proteomics, or specialized redox (reduction and oxidation) assays would reveal if microorganisms of the plastisphere experience oxidative stress and reduced functionality after binding (Section 5.2).

4.2. Heavy metals

Plastics, unlike other materials found in the ocean, are a source of heavy metals and anthropogenic chemicals, as well as a substrate on which they can aggregate (Amelia et al., 2021; Birnstiel et al., 2022; Crawford & Quinn, 2017; Wang et al., 2020). These pollutants are therefore likely to be a far more effective and persistent vector for pollutant transport than any other marine debris (Amelia et al., 2021; Brennecke et al., 2016; Mato et al., 2001; Worm et al., 2017). The plastic degradation performed in part by bacteria also exposes O_2 functional groups (Figure 4.1a; Liu et al., 2019), cationic exchange sites (Figure 4.1a; Syranidou et al., 2017), and increases plastic porosity (Figure 4.1c; Zettler et al., 2013). DOM produced in the biofilm then further increases electron abundance, and consequently site polarity (Brennecke et al., 2016; Turner & Holmes, 2015), attracting more pollutants and microorganisms to the plastisphere.

As cationic substances, heavy metals bind with greatest affinity to polar plastics (e.g. PVC) through electrostatic attraction (Figure 4.1a; Brennecke et al., 2016), although are found on a range of plastics, particularly after ocean weathering (Gao et al., 2019; Holmes et al., 2012; Turner & Holmes, 2015). Fe^{2+} is the most common of these metals in the water column, and when attached to plastics, which also accumulate Al, Mn, Zn, Pb, Cu, Cr, Ni, Co, Cd, Hg, Ag, and As (Table 1). Once bound, the production of ROS from plastic and heavy metals can oxidize co-pollutants (Figure 4.2; Barboza et al., 2018), and cause oxidative stress in affected organisms (Figure 4.3; Qiao et al., 2019).

Microorganisms are exposed to a greater concentration of heavy metals in the plastisphere than in the water column, so are more likely to experience heavy metal toxicity (Figure 4.3). Ag, Cu, and As display bactericidal properties (Hansen et al., 2013; Lozano et al., 2014; Morones et al., 2005) and have been found on plastic (Qiao et al., 2019; Yang et al., 2019). Cu (5 µg/L) precipitates glutathione peroxidase and catalase expression—indicators of oxidative stress—in the microalgal species *Rhodomonas salina* (Hansen et al., 2013; Lozano et al., 2014). In *Escherichia coli,* Ag elicits a severe disruption of intracellular protein transportation, resulting in membrane destabilization and adenosine triphosphate depletion, ultimately causing cell death (Lok et al., 2006). The interaction between heavy metals and plastic also exacerbates Cu toxicity in *Chlorella vulgaris* (Fu et al., 2019), and Au toxicity in *Tetraselmis chuii* (Davarpanah & Guilhermino, 2019). However, heavy metals can also accelerate plastic biodegradation (Santo et al., 2013) and increase microbial resistance to other pollutants, such as antibiotics in the plastisphere (Section 3.2; Poole, 2017; Yang et al., 2019). Heavy metals may therefore regulate many metabolic processes within the plastisphere, and require further exploration.

Table 1. Heavy metal concentrations on natural substrates and plastics (ppm).

	Fe	Al	Mn	Zn	Pb	Cu	Cr	Ni	Co	Cd	Hg	Ag	As
SSW	[a]94	[a]62.8	[a]2.02	[a]0.15	[a]$3.2x10^{-2}$	[b]0.123	[a]1.93	[a]0.71	[b]$5x10^{-3}$	[b]$5x10^{-4}$	[b]$7.7x10^{-4}$	[a]$1.7x10^{-4}$	[a]$1.28x10^{-2}$
	[b]0.34	–	[b]0.29	[b]$5.7x10^{-2}$	[b]$5x10^{-3}$	[a]0.102	[b]$2.1x10^{-2}$	[b]$6.8x10^{-2}$	[c]$2.3x10^{-6}$	[a]$1.1x10^{-4}$	[a]$1.9x10^{-4}$	[e]$3.56x10^{-5}$	[d]$5.7x10^{-3}$
	[c]$2x10^{-5}$	–	[d]$3.5x10^{-3}$	[d]$6x10^{-3}$	[d]$8.2x10^{-5}$	[d]$7.6x10^{-3}$	[d]$1.2x10^{-3}$	[c]$4.13x10^{-4}$	–	[d]$3.8x10^{-4}$	–	–	[b]$3.9x10^{-3}$
	–	–	[c]$4.6x10^{-5}$	[c]$3.14x10^{-4}$	[c]$9x10^{-6}$	[c]$1.5x10^{-4}$	–	–	–	[c]$7x10–^{5}$	–	–	
Plastic	[f]97.8	[f]55.8	[d]31.252	[f]2.68	[d]1.318	[f]0.44	[f]237	[f]131	[f]107	[f]1.65	[g]$<3x10^{-4}$	[g]$<3x10^{-4}$	[d]$3.7x10^{-2}$
	[g]34.4	[g]7.43	[f]20.5	[d]$1.4x10^{-2}$	[f]1.02	[d]0.223	[d]$8.4x10^{-2}$	[g]$2.9x10^{-2}$	[g]$1.3x10^{-2}$	[d]$2.3x10^{-2}$	–	–	–
	–	–	[g]0.712	–	[g]0.11	[g]$4.7x10^{-2}$	[g]$4.25x10^{-2}$	–	–	[g]$5x10–^{3}$	–	–	–

Data collected from **a** sediment in Puerto Rico (Whitall et al., 2014), **b** seawater in Danube Delta (Gheorghe et al., 2017), **c** seawater in Ross sea (Gerringa et al., 2020), **d** seawater, and pristine plastics in China coast (Gao et al., 2019), **e** seawater in Ottowa (Dressler et al., 2001) **f, g** pristine polyethylene and beached plastic in the UK (Holmes et al., 2012; Turner & Holmes, 2015). Data from f and g namely from heavy metals attached to beached plastics, as they presented greatest concentrations.

Shaded regions express an increase in heavy metal concentration on plastics compared to sediment. SSW - sand and seawater; Fe – Iron; Al – Aluminum; Mn – Manganese; Zn – Zinc; Pb – Lead; Cu – Copper; Cr – Chromium; Ni – Nickel; Co – Cobalt; Cd – Cadmium; Hg – Mercury; Ag – Silver; As – Arsenic.

4.3. Persistent organic pollutants

Persistent organic pollutants (POPs) are utilitarian chemical products (Harmon, 2015), turned pollutants after leaching into the ocean (Figure 5a). These POPs can be additives—core structural elements of plastics (Crawford & Quinn, 2017)—leached after photodegradation (Birnstiel et al., 2022; Focardi et al., 2022), or superficially attached to plastics from another source (Figure 5b; Wang et al., 2020). Non-polar pollutants, such as polycyclic aromatic hydrocarbons (PAHs), mainly attach to plastics through hydrophobic interaction (Figure 4.1a; Hirai et al., 2011). Aromatic pollutants, with a foundation of benzene rings, attach through π–π interaction, connecting to the benzene rings in plastics such as polystyrene and PET (Figure 4.1b; Crawford & Quinn, 2017), while polar plastics (i.e., polyamide and PVC), are bound through electrostatic interaction, hydrogen interaction or hydrophilic interaction (Figure 4.1a; Crawford & Quinn, 2017; Liu et al., 2019; Wang et al., 2020).

Many POPs attach through a combination of the above, although non-polar, or hydrophobic interaction, particularly with polyethylene and polypropylene, represents one of the strongest of all interfaces (Teuten et al., 2007; Wang et al., 2020). However, hydrophobic PAHs such as phenanthrene are only found on plastics at concentrations reaching 16.4 mg/kg (Figure 5b). Conversely, phthalates and polychlorinated biphenyls (PCBs), which bind *via* π–π interaction, reach 84.6 mg/kg and 18.6 mg/kg on plastic surfaces respectively (Figure 5b). Pollutants binding through both of the aforementioned mechanisms, such as the aromatic, hydrophobic dichlorodiphenyltrichloroethane (DDT) have the greatest binding coefficients [96,900 K_d] (Bakir et al.,

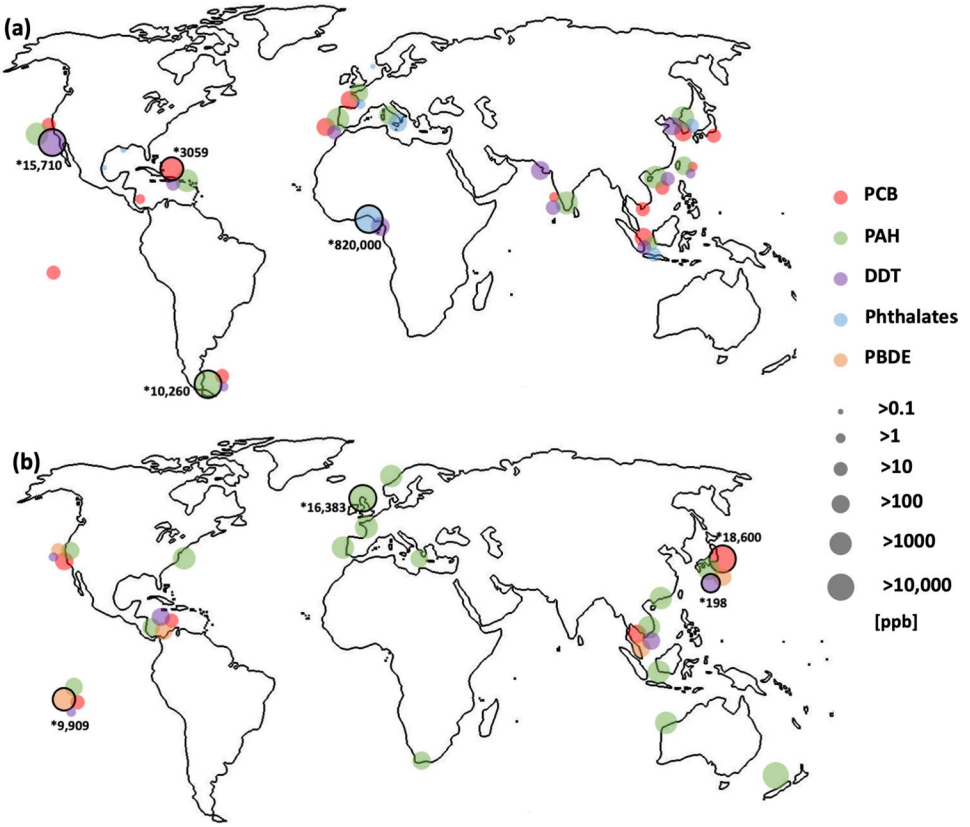

Figure 5. Global distribution of persistent organic pollutants.
Persistent organic pollutants have been detected in the ocean **(a)** and bound to plastics **(b)**.
*(circled)- Highest recorded value for each persistent organic pollutant (POP); ppb - parts per billion; PCB - polychlorinated biphenyl; PAH - polycyclic aromatic hydrocarbon; DDT - dichlorodiphenyltrichloroethane; PBDE - polybrominated diphenyl ethers.
POP data: Supplementary Table 2.

2014), meaning that they have a great capacity to accumulate on plastics. DDT is therefore found on plastic at concentrations ranging from 0.2 mg/kg (Hirai et al., 2011) to 1600 mg/kg (Logan, 2012). The variation in POP concentrations observed here may be due to environmental concentrations (Figure 5a) or sampling strategy.

Hydrocarbonoclastic microorganisms which can metabolize POPs, such as some Euryarchaeota and Proteobacteria, represent up to 34.4% of the plastisphere (Wang & Fingas, 2003). By expressing hydroxylases capable of breaking the benzene rings within pesticides, PCBs and PAHs (Cao et al., 2015; Uhlik et al., 2009), they can use POPs as carbon and energy sources (Figure 2.3). *Oceaniserpentilla sp.* and *Celeribacter indicus* are the most common species responsible for this (Cao et al., 2015; Syranidou et al., 2017; Wright et al., 2021), though other bacteria can also perform this function (Mak & Gu, 2021), as demonstrated by Birnstiel and coworkers (2022), who showed a positive correlation between the release of additives from low-density polyethylene and bacterial growth. This abundance of POPs in the plastisphere may therefore prevent plastic biodegradation in providing a more accessible source of carbon for these communities. However, no study has so far characterized the activity of the plastisphere relating to POP degradation, or which specific additives may be used as a source of carbon.

Rosato et al. (2020) demonstrated that a singular POP is not sufficient to influence the community composition of the plastisphere, but the inclusion of multiple additives, such as those used to produce color, may influence microbial abundance and diversity. When studying the colonization of yellow, blue, and transparent plastics, Wen et al. (2020) found a significantly greater abundance of *Aquabacterium sp.* on blue polyethylene plastics than any other color. De Tender and coworkers (2015) also noted the selective growth of *Mycobacterium frederiksbergense* on only blue and yellow patches of plastic, and not any other color, attributing this selection to the presence of anthracene in only these tested plastics. It is therefore probable that these additives will impact the colonization of the plastisphere; selecting for specialized hydrocarbonoclastic organisms, and selecting against microorganisms affected by POP toxicity.

The electron transfer between plastic and POPs also propagates the release of free radicals from plastic (Zhu et al., 2019). These free radicals can then react with POPs to form chemical subspecies with higher toxicity (Figure 4.2; Lai et al., 2020), increasing oxidative stress in the plastisphere. This increases cell death, and thus the accumulation of biomass within the plastisphere, also drawing saprophytes to the biofilm, attracted by the abundance of dead microorganisms (Figure 3.1e; Figure 4.3h; Tarafdar et al., 2022). POPs can also be antimicrobial in application, as in the case of triclosan, which is more toxic when bound to plastics (Syberg et al., 2017). In a study of autotrophic (*Halothece sp.* and *Fischerella muscicola*) and heterotrophic (*Cobetia sp., Marinobacterium litorale* and *Pseudomonas azotifigens*) bacteria, the inclusion of additives—particularly Fluoranthene (a PAH) and dioctyl-phthalate—significantly reduced growth of all microorganisms on plastic, apart from *P. azotifigens* (Fernández-Juárez et al., 2021). By binding directly to cell walls of plastisphere microorganisms (Murínová & Dercová, 2014), pollutant toxicity may be amplified by POP and ROS proximity (Figure 2.4; Figure 4.3). Archaea (Urakawa et al., 2012), single-celled photosynthetic algae (Peijnenburg, 2008), and members of the ubiquitous SAR supergroup (Focardi et al., 2022), as well as other photosynthetic eukaryotes and prokaryotes are particularly sensitive to this POP toxicity. The bacterium *Vibrio fischeri*, and the protozoa *Tetrahymena pyriformis* also experience acute toxicity (LC_{50}) when exposed to 11–23 mg/L and 7 mg/L of phthalate respectively (Peijnenburg, 2008). This species-specific response to pollutant exposure may be explained by differences in cell morphology (Section 2.3; Murínová & Dercová, 2014), though the physiological and functional mechanisms underpinning these taxonomic differences require further investigation. Nonetheless, it is evident that microbial response to POP exposure is POP-dependent, and microorganism-dependent. POPs may therefore facilitate (Birnstiel et al., 2022) or inhibit (Fernández-Juárez et al., 2021) processes such as bioremediation and biogeochemical cycling in the marine plastisphere.

4.4. Organic UV-filters

Organic UV-filters are compounds used to protect against UV-A (320–400 nm) and UV-B (290–320 nm) radiation (Díaz-Cruz et al., 2008). As a component of plastics and personal care products (PCPs), including sunscreens (Díaz-Cruz et al., 2008; Semones et al., 2017), organic UV-filters have become a rising contaminant in municipal effluents, with up to 223 µg/L released in UK effluents alone (Kasprzyk-Hordern et al., 2009). PCPs, unlike many POP sources, are used by a majority of the general public (Díaz-Cruz et al., 2008), making these organic UV-filters ubiquitous throughout the ocean (Figure 6), and highly concentrated at the coast when applied before bathing (Lozano et al., 2020). The organic UV-filter Benzophenone-3 (BP3), also known as oxybenzone, is used in many PCPs, and reaches concentrations of 1.395 mg/L in coastal regions (Downs et al., 2016). While other PCP-sourced organic UV-filters including octocrylene, 4-methylbenzylidene camphor (4-MBC), and ethylhexyl methoxycinnamate (EHMC), reach up to 7.301 µg/L, 1.043 µg/L, and >4 µg/L respectively (Figure 6). Significantly, organic UV-filters remain chemically stable in the environment for >2.4 years (Semones et al., 2017), and sorb to plastics with a coefficient of up to 53,200 K_d (4-methylbenzylidene) (Wu et al., 2016). PCP-sourced organic UV-filters also bind most strongly [$LogK_d \leq 4.58$] to the ocean's most abundant plastics, polyethylene and polystyrene (Miao et al., 2020; Teuten et al., 2007; Wang et al., 2018), which in combination with those leached from the plastic, means many UV-filters are likely present in the plastisphere (Figure 4).

BP3 is the lowest molecular weight [228.243 g/mol] UV-filter (Brooke et al., 2008), and as such, has the greatest capacity to surpass the lipid bilayer of cell membranes and disrupt life in the plastisphere. In algae, BP3 induces oxidative stress (Gao et al., 2013), cytotoxicity (Esperanza et al., 2019), as well as impaired metabolic functions (Thorel et al., 2020), and photosynthetic profiles (Gao et al., 2013). *Isochrysis galbana* growth is reduced after exposure to concentrations as low as 13.8 µg/L of BP3; the lowest threshold for damage of all UV-filters tested with this species (Giraldo et al., 2017; Paredes et al., 2014). While, in a study of 27 bacterial strains, only Gram-negative bacteria were affected by BP3 (Lozano et al., 2020). This was also observed by Liu et al. (2015), Mao et al. (2017), and Zhang et al. (2017). BP3 may therefore negatively

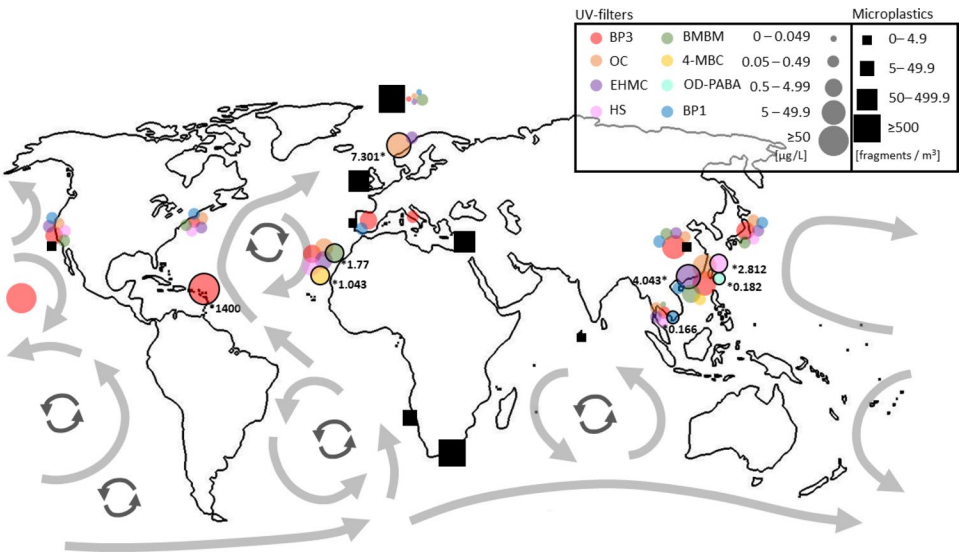

Figure 6. Global distribution of UV filters and microplastics.
Large grey arrows represent dominant ocean currents during northern hemisphere winter months and small cyclical arrows represent ocean gyres in which plastic accumulates, forming 'garbage patches'.
*(circled) - Highest recorded value for each UV-filter (µg/L); BP – benzophenone; EHMC- ethylhexyl methoxycinnamate; OC - octocrylene; 4-MBC - 4-methylbenzylcathinone; HS - homosalate; BMBM - butyl methoxydibenzoylmethane; OD-PABA - ethylhexyl dimethyl *p*-aminobenzoic acid.
UV-filter data: Supplementary Table 3; Plastics data: Mammo et al. (2020).

impact many of the plastisphere's most abundant bacteria (i.e., Proteobacteria) (Figure 3; Cheng et al., 2021; Dussud et al., 2018), or facilitate the growth of BP3-degrading bacteria (Fagervold et al., 2021). Concerningly, BP3 sorption is greatest on smaller plastics (Cui et al., 2022), which are more widely distributed than larger plastics (Amelia et al., 2021), equally increasing BP3 distribution and impact on plastisphere communities.

As opposed to BP3, octocrylene toxicity is limited by its high molecular weight [361.477 g/mol] relative to other UV-filters (Brooke et al., 2008). While growth of the prymnesiophyte *Isochrysis galbana* was impacted after chronic exposure to as little as 80 µg/L (Giraldo et al., 2017), only one of 27 Bacteria (*Arthrobacter aurescens*) was sensitive to 1 mg/L exposure (Lozano et al., 2020). As such, no study has yet demonstrated microbial toxicity to octocrylene at environmentally relevant concentrations.

Despite being less concentrated in the ocean (Figure 6), 4-MBC is a more toxic, and more adherent (53,200 K_d) organic UV-filter than BP3 (Gao et al., 2013; Wu et al., 2016). 4-MBC is therefore more likely to bind to the plastisphere and affect microbial activity once there. Upon direct exposure, this filter can impair the function of bacterial (Lai et al., 2020), algal (Paredes et al., 2014), and fungal (Schmitt et al., 2008) colonies. However, in the study of 27 marine bacterial isolates (Lozano et al., 2020), no species was affected by 4-MBC exposure. Regardless, it has been shown that upon chlorine-mediated photodegradation, 4-MBC toxicity toward *Vibrio fischeri* is increased 10-fold (Lai et al., 2020), meaning even low concentrations of 4-MBC may be toxic in the environment.

EHMC toxicity is also exacerbated by photo- and bio- degradation which produces additional toxic photoproducts (Butt & Christensen, 2000; Zhang et al., 2021). In the study by Lozano and coworkers (2020), EHMC affected the growth of the most bacterial species across three different phyla: Actinobacteria, Firmicutes, and Alphaproteobacteria (*Arthrobacter aurescens, Dietzia maris, Halobacillus dabanensis, Paenibacillus glucanolyticus,* and *Pelagibacterium halotolerans*), suggesting EHMC may pose a significant threat to a bacterial-dominated plastisphere. Growth of the algal species *Isochrysis galbana* is also inhibited by 74.73 µg/L of the accumulated UV-filter (Paredes et al., 2014). These findings suggest that EHMC sorption to plastic may significantly impact both Eukaryotic and prokaryotic members of the plastisphere and warrants further investigation.

It is evident that UV-filters have a strong affinity for the plastisphere, will impact microbial viability and activity, and often co-occur in high concentrations alongside plastic pollution. This must therefore be considered in future research of microbial associations with plastic.

5. Future research/recommendations

5.1. Plastispheres in the ocean

Plastisphere composition, and how it changes over space and time is pivotal to understanding which hazardous (*Section 3.2*), biogeochemical (Falkowski et al., 2008), or bioremediative (Section 3.1) processes may be facilitated in the plastisphere. Further study is therefore required to understand how location and plastic type determine the plastisphere's composition (Section 2.1; 2.2) and control the conditions which enrich its primary metabolic processes (Section 3; Barton et al., 2013; Nguyen et al., 2021). Each location, for example, will be a unique combination of temperature, salinity, oxygenation, and plant/animal diversity which will impact nutrient load and microbial diversity in each location, and should be further explored (Barton et al., 2013; Coons et al., 2021; Scales et al., 2021). It is also highly probable that the DOM which forms the conditioning film on plastics (Lorite et al., 2011)—potentially containing co-pollutants—will change between locations (Figure 5; Figure 6), thus impacting prokaryotic binding and metabolism in each region. Several more recent studies have also explored the plastisphere's non-prokaryotic community (Bryant et al., 2016; Latva et al., 2022; Oberbeckmann et al., 2014; Tobias-Hünefeldt et al., 2021). Continued, integrated study of these eukaryotic, fungal, and

archaeal species, and their viruses in the plastisphere may therefore reveal their prevalence and key metabolic processes (Section 5.2) in the next five years. Further study of plastic types would also confirm which factor—plastic type or location—is the prevailing influence of plastisphere formation. Current study of plastisphere location (Section 2.1), is not matched by present study of plastic type (Section 2.2), meaning location is currently presumed to be the prevailing influence of plastisphere formation (Coons et al., 2021; Delacuvellerie et al., 2022; Scales et al., 2021), though this may just be due to a lack of evidence regarding the impact of plastic polymers. The impacts of plastic pollution on planktonic microorganisms which do not bind to plastic (Bryant et al., 2016; Zhang et al., 2022), are also rarely considered when researching marine plastic debris. This is of particular concern due to the extreme shift in planktonic community composition observed after exposure to plastic leachates (Bakir et al., 2014; Birnstiel et al., 2022; Focardi et al., 2022). Further research must therefore be conducted in these areas, particularly focusing on the reasons behind location- and plastic- dependent plastisphere variation, and how leachates impact the surrounding seawater community.

5.2. Plastisphere function

As discussed in this review, plastisphere function encompasses the ability of microorganisms to metabolize abiotic elements of the plastisphere (*Section 3*), their cellular interaction with each other (Section 2.4), and effects of co-pollutants (Section 4.2; 4.3; 4.4). This can be studied using meta-omics; techniques that enable the elucidation of how plastisphere-driven processes are performed through community-level analyses. Progression onto this area of research has so far been limited by the novelty of plastisphere research (Zettler et al., 2013), and thus, the necessity to first characterize its members using 16S rRNA metabarcoding; a low resolution technique used to identify bacteria based on a variable region of the 16S rRNA gene (Delacuvellerie et al., 2022; Oberbeckmann et al., 2021; Pollet et al., 2018; Schlundt et al., 2020). This technique cannot distinguish between active, inactive, or dead cells (Li et al., 2017), meaning any assumptions made based on taxonomic markers are skewed by present dead and dormant bacteria (Tarafdar et al., 2022). However, many plastispheres have now been characterized using 16S rRNA metabarcoding (Dussud et al., 2018; Kirstein et al., 2018; Wright et al., 2021; Zettler et al., 2013), and the use of metagenomic sequencing (Bryant et al., 2016), has also allowed for more in-depth analyses of the plastisphere community. Now two studies have used metaproteomics to characterize the plastisphere's metabolic profile (Delacuvellerie et al., 2022; Oberbeckmann et al., 2021).

Metaproteomics enables researchers to identify the proteins expressed by a complex microbial community, revealing the most prevalent microbial processes at the time of sampling (Delacuvellerie et al., 2022; Matallana-Surget et al., 2018). When used alone, or in conjunction with other high-throughput methods such as metatranscriptomics and metabolomics (Wright et al., 2021; Zhao et al., 2020), these techniques can provide an accurate method for characterizing the plastisphere's active bacteria and their metabolism. Comparative metaproteomics could answer the questions: (i) What is the functioning of the plastisphere? (ii) Are the potential pathogens/plastic degraders metabolically active?

(iii) How do microorganisms metabolically respond to plastic co-pollutants?

A focus on these questions and the topics highlighted in Section 5.1 would reveal the risks that a dynamic plastisphere may pose (Amelia et al., 2021), and which microorganisms may be utilized to reduce the marine plastic pollution problem (Gewert et al., 2015; Wright et al., 2021).

Conclusion

In this review, we have examined studies of plastics, the plastisphere, and bacterial isolates to predict plastisphere activity and the factors that influence it in the ocean. For the first time, the effects of cell wall composition, organism-organism interaction, plastic-bound co-pollutants,

plastic type, and location on the formation and function of the marine plastisphere are considered. In doing so, we critically discuss the synergistic interactions between these factors and explore how they likely underpin the key microbial metabolic processes in this niche. Although location is currently considered to be one of the primary driving forces of plastisphere formation, in this review we articulate how the presence of specific microorganisms not only depends on their occurrence in the water column, but also on their cell wall composition and resulting compatibility with the plastic surface at the molecular level. Thus, cell wall composition, and the expression of adhesins, pili, genetic plasticity, and other traits of biofilm-forming bacteria, directly affect the resulting taxonomic diversity of the community, contributing to the metabolic profile of the biofilm. We discuss how cell wall composition also likely plays a role in a microorganism's response to potentially toxic sorbed co-pollutants and exposed additives, impacting their growth and ability to perform characteristic metabolic processes (i.e., biodegradation). The toxicity of organic UV-filters especially is of emerging concern considering their significant impact on microbial metabolism, affinity for plastic, and high concentrations in coastal environments. In this review, we therefore recommend further study of the abiotic factors associated with location (i.e., temperature), the forgotten organisms—beyond plastic-biodegraders and potential pathogens –, and the impact of plastic leachates on the plastisphere and the ocean. Most importantly, we strongly encourage a shift in plastisphere research away from taxonomic descriptions, and toward more advanced molecular techniques to allow for a greater mechanistic understanding of plastisphere development and function.

Disclosure statement

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ORCID

Sabine Matallana-Surget http://orcid.org/0000-0002-6023-3215

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