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Critical Review

Gross Negligence: Impacts of Microplastics and Plastic Leachates on Phytoplankton Community and Ecosystem Dynamics

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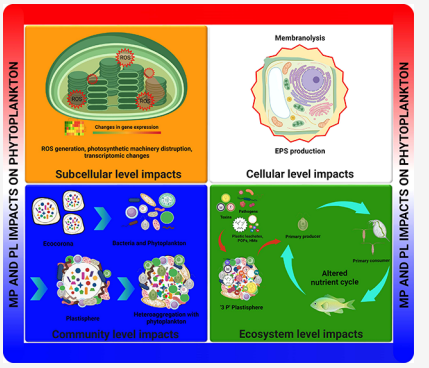
ABSTRACT: Plastic debris is an established environmental menace affecting aquatic systems globally. Recently, microplastics (MP) and plastic leachates (PL) have been detected in vital human organs, the vascular system, and *in vitro* animal studies positing severe health hazards. MP and PL have been found in every conceivable aquatic ecosystem—from open oceans and deep sea floors to supposedly pristine glacier lakes and snow covered mountain catchment sites. Many studies have documented the MP and PL impacts on a variety of aquatic organisms, whereby some exclusively focus on aquatic microorganisms. Yet, the specific MP and PL impacts on primary producers have not been systematically analyzed. Therefore, this review focuses on the threats posed by MP, PL, and associated chemicals on phytoplankton, their comprehensive impacts at organismal, community, and ecosystem scales, and their endogenous amelioration. Studies on MP- and PL-impacted individual phytoplankton species reveal the production of reactive oxygen species, lipid peroxidation, physical damage of thylakoids, and other physiological and metabolic changes, followed by homo- and heteroaggregations, ultimately eventuating in decreased photosynthesis and primary productivity. Likewise, analyses of the microbial community in the plastisphere show a radically different profile compared to the surrounding planktonic diversity. The plastisphere also enriches multidrug-resistant bacteria, cyanotoxins, and pollutants, accelerating microbial succession, changing the microbiome, and thus, affecting phytoplankton diversity and evolution. These impacts on cellular and community scales manifest in changed ecosystem dynamics with widespread bottom-up and top-down effects on aquatic biodiversity and food web interactions. These adverse effects—through altered nutrient cycling—have "knock-on" impacts on biogeochemical cycles and greenhouse gases. Consequently, these impacts affect provisioning and regulating ecosystem services. Our citation network analyses (CNA) further demonstrate dire effects of MP and PL on all trophic levels, thereby unsettling ecosystem stability and services. CNA points to several emerging nodes indicating combined toxicity of MP, PL, and their associated hazards on phytoplankton. Taken together, our study shows that ecotoxicity of plastic particles and their leachates have placed primary producers and some aquatic ecosystems in peril.



KEYWORDS: *Plastics, Ecotoxicology, Ecocorona, Plastisphere, Primary Producers, Algae, Cyanobacteria, Aquatic Ecosystems, Pathogens, Pollutants, Cyanotoxins*

1. INTRODUCTION

Plastics have become an indispensable part of human life and society with a logarithmic increase in production and consumption since the 1950s.[1] This logarithmic increase coupled with mismanagement of plastic waste due to the lack of consideration of the environmental impacts have created a humongous environmental hazard threatening entire ecosystems and all life forms today.[2] Plastics are classified based on their sources, monomers, polarities, and applications into different types. Polyethylene (PE), polyethylene terephthalate (PET), polypropylene (PP), polystyrene (PS), and polyvinyl chloride (PVC) are the most common types of polymers used in our daily life.[3,4] Globally, the amount of these anthropogenic polymers in landfills and the environment is ∼6300 million metric tons (MMT), and it is predicted to increase to ∼12,000 MMT by 2050.[5−7] Out of the total plastics produced globally, >40% are only used for short periods, often one month or less.[5,8,9] With the current rate of manufacture and disposal, plastic litter will increase 10-fold over the next 10 years, not accounting for COVID-19-induced single-use plastics disposal recently, and further exacerbate adverse impacts on environmental and human health.[6,10−12] In addition, the threats posed by emerging, omnipresent plastic hazards such as MP and PL are manifold and not yet completely understood.[13−17] This menace is particularly disconcerting in the great plastic patches in both

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Atlantic and Pacific Oceans and the highly polluted coastal zones across the world.[18−21]

Processes such as photodegradation, biological degradation, chemical degradation, and physical fragmentation lead to reduced plastic particle sizes over time.[7] Based on their sizes, fragments formed via these processes have been classified as macroplastics (>20 mm diameter), mesoplastics (5−20 mm), MP (microplastics, < 5 mm) and nanoplastics (<1000 nm).[22,23] During weathering processes, along with fragmentation, chemicals weakly bound to the polymers are also leached to the surrounding media.[24−26] Ecotoxicity of MP has been studied in numerous model organisms, while such studies on PL are still limited.[26−29] MP and PL have been demonstrated to be cytotoxic, neurotoxic, teratogenic, and genotoxic.[26−31] In aquatic systems, the majority of these ecotoxicity studies have focused on fishes, small crustaceans, mollusks, and other macroorganisms, and only recently a few studies focusing on MP and PL impacts on phytoplankton have emerged.[30] Although studies predominantly on marine ecosystems are increasing, studies on freshwater ecosystems, especially lentic and at field level are rare.[30,32,33] Microbial colonization on plastics surfaces has been first reported as early as 1972 by Carpenter and his colleagues from waters of the southern New England coast.[34] Until recently, our understanding of the microbial community structure on aggregates, especially on MP associated with natural organic matter, termed as "Ecocorona", and their leachates was quite limited.[14,35] However, recently, the impacts of MP and PL on the microbial community structure and functions have been frequently studied.[32,36−38]

A huge leap in this field was initiated by Zettler and colleagues[39] who demonstrated and characterized through present-day omics methodologies the large scale presence of microbial communities on various plastic fragments across the North Atlantic Ocean, and termed these man-made niches as the "plastisphere". Subsequently, the plastisphere has been established in every major aquatic system—lentic, lotic, estuarine, and marine—and its impacts on natural aquatic ecosystems have been frequently reviewed in recent times.[40−42] From the human health perspective, MP have been documented in sewage, food, drinking water, and human organs,[15,16,43,44] whereby the formation of the plastisphere alters microbial communities in sewage, as in natural environments.[38,45−47] The plastisphere, in fact, constitutes hotspots of antibiotic-resistant bacteria.[45,46] Thus, reviews of MP and PL impacts on microbial communities are emerging, yet, their impacts on primary producers remain largely neglected in marine and freshwater ecosystems and have not been exclusively reviewed.

To close this important gap, our review sets a particular focus on the presently tangible and intangible impacts of MP and PL on phytoplankton and thereby on aquatic ecosystems. Studied phytoplankton communities comprise the major photosynthetic groups, as well as key players driving food web dynamics. Therefore, this review also focuses on MP and PL impacts at the organismal scale. To this end, the MP and PL impacts on the morphology, physiology, metabolism, and overall cellular status of these major groups and the key players are reviewed. Concurrently, several studies show that MP- and PL-induced effects on individual organisms and communities have profound impacts at the ecosystem level, recently summarized by Prinz and Korez.[48] Our review also points to the major challenges in the field, and by using citation network analyses (CNA), it visualizes developing research networks and recent advancements in the field.

2. PHYTOPLANKTON GROWTH AND METABOLISM DRASTICALLY ALTER DUE TO MP AND PL

Studies on MP and PL impacts on phytoplankton at organismal level have primarily relied on experimental data in the lab, and very few studies have been conducted at mesocosm scale or at *in situ* environmental conditions. Therefore, limitations associated with laboratory studies have been acknowledged here, and methods and deficiencies in MP and PL sampling, preparation, characterization have been summarized in the Supporting Information (SI S1 and S2).

At the cellular level, impacts of MP on photosynthetic microorganisms tend to vary between studies, which are typically conducted at the laboratory scale. Among the basic impacts, growth and thus productivity are obvious parameters to be considered. A meta-analysis on the impact of MP and nanoplastics on standard growth measurements of various algae included several studies between 2010 and 2020.[49] In total, MP and nanoplastics from five polymers and 16 algal species were studied with a size range of particles ranging from 0.04−3000 μm. The meta-analysis revealed limited generalized trends across polymers and study algae, primarily because different studies have used different conditions, polymers, test organisms, durations of exposure, particle sizes, and thus different leachates and additives, eliciting diverse and highly variable impacts.[49] Therefore, we discuss each study and its respective findings separately. For instance, impact on algal growth is due to several reasons. One visible MP impact on phytoplankton is light shading during close contact with MP, which can prevent absorption of light energy and thereby directly affects photosynthetic rate and nutrient assimilation. One of the earliest studies[50] shows that high numbers of PS beads have negative impacts on photosynthesis and algal cell growth by light shading, which can also block cellular gas exchange. However, light shading through close contact may not manifest severely in environmental conditions, unlike in laboratory experiments. Additionally, charge neutralization of negatively charged algae by positively charged beads is another major reason for decreased zeta potential and agglomeration.[50] More recent findings on the impact of PS MP on cyanobacteria reveal strikingly similar patterns to the earlier study, i.e., charge neutralization and decreased photosynthetic efficiency.[51] Likewise, in the bloom-forming cyanobacteria, *Microcystis aeruginosa*, MP of PVC, PS, and PE have adverse effects on its growth by eliciting oxidative stress and disrupting cell membrane integrity.[52] Interestingly, toxin production by *M. aeruginosa* was also enhanced in the presence of MP,[52] which could be related to the fact that cyanobacteria may mitigate MP-induced oxidative stress by toxin production.[53,54] Furthermore, another study[55] has conclusively proved that the same MP also act as vehicles for Microcystin-LR and Microcystin-LF, increasing their lethality and demonstrating MP as potential vehicles for toxins.[56] On the other hand, MP can also have positive effects on cyanobacterial growth at environmental and higher MP concentrations, suggesting increased dissolved inorganic nitrogen levels in MP-treated samples.[32,57] In contrast, organic additives have a highly significant negative impact on the growth of cyanobacteria.[57] The authors claim that MP decrease the uptake of phosphorus by the diazotrophic cyanobacterium, *Halothece* sp., possibly due to adsorption of phosphate ions to the MP. Surprisingly, the same study did not find any significant effects of MP on nitrogen fixation and assimilation in *Halothece* sp., but speculates that the combined impacts of MP and PL may

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significantly alter nitrogen fixation in the environment as cyanobacterial growth is positively impacted by MP, but inhibited by PL.[57]

For green algae, impacts at the cellular level has been documented for both freshwater and marine organisms. When the freshwater green alga, *Chlorella pyrenoidosa*, was exposed to PS fragments of various sizes, there were observed adverse effects, especially the inhibition ratio varied with particle size.[58] Subcellular impacts such as plasmolysis and vacuolation were also observed in this study.[58] The predominant impacts such as cell structure alteration and oxidative stress are patently identical to impacts observed in cyanobacteria.[52] Furthermore, the study shows that algal stress responses are growth phase dependent, with algae homoaggregation, algae-MP heteroaggregation, and return to cell structure normalcy in the stationary phase. These findings are complemented by other studies on *Chlorella* and cyanobacteria.[50−52] The model green alga, *Chlamydomonas reinhardtii*, formed heteroaggregates composed of microalgae, MP, and extracellular polysaccharides (EPS).[59] The role of algal EPS is significant not only for the formation of heteroaggregates but also for the resultant vertical transport of aggregates and their constituents from the water surface to the sediment.[60] Another significant development with respect to EPS is the change in metabolic activity within *C. reinhardtii*; in particular, ca. 700-fold increases in the expression levels of genes involved in the biosyntheses of xylose and galactose, which are constituents of the EPS, have been recorded.[59] This MP-induced carbohydrate-rich EPS secretion by algae may select for different microbial communities in the phycosphere compared to their planktonic counterparts.[38,61] Emerging studies on defense mechanisms of MP-impacted phytoplankton are given in Section 4.4.

In the halophilic green alga, *Dunaliella salina*, cell and particle size ratio had a major influence on the cellular responses,[62] whereby larger-sized MP enhanced algal growth. However, the authors caution against smaller MP, which decreased growth, and their leached products were not quantified and tested individually.[62] In three marine diatoms, PVC MP resulted in adverse impacts such as physical damage and decreased photosynthetic efficiency.[63] Even the siliceous cell walls of diatoms seem to provide little resistance from physical damage caused by MP, yet, the severity of MP impact was dependent on microalgal species and MP dose.[63] Similarly, the adsorption of 1 μm-sized PVC spheres on the surface of the marine diatom, *Skeletonema costatum*, showed breakage of silicic thorns and wrapping of the caveola.[64] Another study found that PS microbeads decreased cellular esterase activities and the neutral lipid contents of marine diatoms, indicating MP-induced modulation of the diatom's energy metabolism.[65] Finally, impacts of PS spheres on an assortment of marine cyanobacteria, green algae, haptophyte, and diatoms indicate that size, morphology, and physiology of the tested algae determine the severity of impact on the algae and, in turn, their stress response.[66] Larger-sized algae aided to coaggregation, and smaller MP exerted higher toxicity on larger algae, skewing the MP−phytoplankton size−volume ratio presented by other studies[51,62,66,67] (Table 1).

Unlike MP, studies documenting PL toxicity on photosynthetic microorganisms present unequivocal adverse impacts of PL for at least one polymer tested in the studies (Table 2). PL have been reported to impact photosynthetic rate, oxygen production, and number of transcripts of major processes in the marine, highly abundant single-cell cyanobacterium *Prochlorococcus*.[26] Reduced expressions of genes involved in photosystem II, carbon fixation, metal transporters, and cell division after short-term exposures to HDPE and PVC leachates were observed. In fact, studies documented that PL extracted from nearly all polymers, except PET, result in decreased algal growth.[26,27,86,87] However, as PL constitute diverse groups of chemicals, the composition of leachate, exposure time, and extraction time as well as medium used for incubation play vital roles for the responses elicited in these studies. In the case of additives, e.g., heavy metals, the leachate was highly toxic for *M. aeruginosa*, and the observed toxicity increased in a dose-dependent manner with leachates from aged MP.[87] The impacts of Lead(II) chromate-pigmented PE on the study organism was found to be manifold and comprehensive as impacts of the polymer backbone can combine with those of the additives leached.[87] Likewise, toxic impacts of fluorescent additives leached from polyurethane sponge MP in simulated medium and natural waters on *Chlorella vulgaris* resulted in decreased growth at high PL concentrations. The analyzed PL comprised 3,3′-diaminobenzidine-like compounds which are toxic to aquatic organisms and commonly affect photosynthesis.[88] In addition, a combination of MP and their respective PL have a devastating effect on morphological and physiological characteristics of microalgae. Morphological changes in *C. pyrenoidosa* detected by TEM analysis revealed damage of the cytoderm and membranolysis when exposed to the plastic additive dibutyl phthalate. Furthermore, dibutyl phthalate exposure impaired the photosynthesis in *C. pyrenoidosa* leading to a decreased electron transport rate which in turn led to the accumulation of harmful reactive oxygen species (ROS). Subsequently, this resulted in lipid peroxidation in the cell membrane, preventing the protoplast from dividing.[58]

In another study on UV-weathered MP leachates, the leachates from electronic waste and a computer keyboard showed severe effects on growth and photosynthesis of the green alga *Scenedesmus vacuolatus*.[89] The results have huge implications for cell, community, and ecosystem health of primary producers as e-wastes are the fastest growing waste streams in the past decade.[90] The final disposal of as much as 70% of the e-wastes generated is unknown or unreported and may end up in water bodies to a large extent. Severe water contamination has been reported in several areas surrounding such e-waste dumpsites and recycling units.[90,91] The release of PL into the natural environment depends on several factors which are difficult or even impossible to study under laboratory conditions. Although agitation, UV exposure, and extraction medium have been frequently tested, a new study shows that other factors such as hydrostatic pressure also affect the leaching of additives.[92] It is pertinent to model the spatial distribution of the leachates in the water column. For example, increasing pressure together with increased plastics age prevents leaching of additives in the deep seas; therefore, PL should be more prevalent in surface waters.[92] Moreover, the influence of biological factors such as the roles of prokaryotic microbial communities in aiding the leaching process have been also demonstrated.[92] Based on the studies reviewed, we summarize that PL seem to have a relatively higher impact on primary microbial producers than MP, which may also be related to the broad spatial distribution of PL in the water column (Table 2).

While laboratory studies on MP and PL point to several threats faced by the primary producers, as discussed above, these studies are not without limitations. High concentrations of MP used in most studies, and difficulties in mimicking the

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Table 1. Summary of Observed Effects of MP on Various Phytoplankton Species in Laboratory Studies

Polymer	Size	Exposure time	Dosage	Phytoplankton species	Parameters studied	Toxicological effects	Ref
PS	1 μm	30 days	10−100 mg/L	*C. pyrenoidosa*	Growth, Photosynthetic efficiency	Growth inhibition observed, pyrenoid damage, distorted unclear thylakoids, and cell wall thickening were observed impacting photosynthetic efficiency	68
	2 μm	35 days	0.004 mg/L; 0.04 mg/L	*Chaetoceros neogracile, Heterocapsa triquetra,* and *Tisochrysis lutea*	Growth	No impact on growth, but aggregation observed	69
	2 μm	72 h	2.5 mg/L	*C. neogracile*	Growth, Chlorophyll *a* (Chl-*a*) fluorescence, Photosynthetic efficiency, Neutral lipid content, ROS, Esterase activity	Decrease in growth, no significant alterations in Chl-*a* content, decrease in neutral lipid content, no oxidative stress, decrease in esterase activity	65
	5 μm	96 h	1, 10, 20 mg/L	*S. costatum*	Growth	No adverse effects on growth	70
	5 μm	96 h	0.5−64 mg/L	*C. pyrenoidosa*	Growth	Size-dependent growth inhibition	58
	6 μm	72 h	25 and 250 mg/L	*Dunaliella tertiolecta* and *Thalassiosira pseudonana*	Growth, Photosynthetic efficiency	No toxicity on growth and photosynthesis	71
	74 μm	96 h	10−100 mg/L	*S. costatum*	Growth	Growth inhibition observed	72
	1 and 5 μm	7 days	5−200 mg/L	*C. reinhardtii*	Growth, Chl-*a* content, Superoxide dismutase (SOD) activity	Growth inhibition, reduced Chl-*a* content and enhanced SOD levels	73
	1 μm	8 days	10 mg/L	*Prorocentrum minimum, Karenia mikimotoi, Prorocentrum donghaiense, Prorocentrum micans, Alexandrium tamarense, Akashiwo sanguinea,* and *Heterosigma akashiwo*	Growth, Optimal photochemical efficiency (Fv/Fm), Chl-*a*, SOD activity, Cell morphology	Growth inhibition, reduction of Chl-*a* content in majority of the species, Fv/Fm showed species-specific effects, higher SOD levels, and impact on cell morphology	67
	0.1 and 2 μm	10 days	25, 50, and 75 μL/100 mL	*Tetraselmis suecica* and *Amphora subtropica*	Growth, Photosynthesis, Cell density	MP concentration of 75 μL/100 mL disrupted microalgal photosynthesis, reduced growth rate and cell density	74
		96 h	0, 5, 10, 20, 40, and 80 mg/L	*Chaetoceros meülleri*	Growth, Chl-*a*, Photosynthesis, Oxidative stress	Inhibited growth, dose-dependent effect on oxidative stress; there was no obvious decrease in Chl-*a* content	75
Plain PS: PS-NH_2	Plain PS (0.1, 0.5, 1, and 2 μm); PS-NH_2 (0.1 μm)	48−250 h	250 mg/L	*Scenedesmus obliquus*	Chl-*a* fluorescence	Inhibition of photosynthesis	76
PVC	1 μm	96 h	0−50 mg/L	*S. costatum*	Growth, Chl-*a*, Photosynthetic efficiency	Inhibition of growth and photosynthesis	64
	1 mm	96 h	0−2000 mg/L	*S. costatum*	Growth, Chl-*a* content, Photosynthetic efficiency	No effect	
	1 μm				Growth, Malondialdehyde (MDA) Assay, SOD activity	Impacted growth rate, 1 μm PVC showed the highest lipid peroxidation, increased SOD levels	72
	74 μm				Growth, Chl-*a*, Photosynthetic efficiency	Decreased growth rate, no effect on Chl-*a* and photosynthetic efficiency	
	1 μm	96 h	0−100 mg/L	*Karenia mikimotoi*	Growth, Chl-*a*, Photosynthetic efficiency	Dose dependent adverse effect on growth, on chlorophyll content and photosynthetic efficiency	77
	10−106 μm (size class)	72 h	1.25×10^3 particles/L	*Phaeodactylum tricornutum*	Growth	No effect on growth	78
PVC (virgin) and UV-aged PVC (60 days)	130−200 μm (size class)	10 days	10−100 mg/L	*C. vulgaris*	Growth, Algal biomass	Growth inhibition was prominent until 96 h	79
UPVC (unplasticized)	250 μm	4 days; 9 days	50, 1000, and 50,000 mg/L	*P. tricornutum*	Growth	Negative impact on the growth rate	80

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Table 1. continued

Polymer	Size	Exposure time	Dosage	Phytoplankton species	Parameters studied	Toxicological effects	Ref
PP	400−1000 μm	78 days	1000 mg/L	*C. reinhardtii*	Growth	Decreased growth rate	59
PE	2−6 μm	72 h	25 mg/L	*Isochrysis galbana*	Growth	No effect on growth under tested conditions	81
	74 μm	96 h	10−100 mg/L	*S. costatum*	Growth	25.3% growth reduction at 96 h (100 mg/L)	72
	150 μm	4 days; 9 days	50, 1000, and 50,000 mg/L	*P. tricornutum*	Growth	4 day exposure did not impact growth	80
	1−500 μm	72 h	25 mg/L	*P. tricornutum*	Growth	No effect on growth under tested conditions	82
PS and PP	6.8−438 μm	72 h	Environmentally relevant concentration (2000−200,000 MP/L) and high concentration (12.5−100 mg/L)	*Raphidocelis subcapitata*	Growth	Interestingly, environmentally relevant concentrations inhibited microalgal growth whereas high concentrations enhanced growth	83
PE and PP	0.5−1 mm^2	30 days	250 mg/L	*Spirulina* sp.	Growth	Reduction in the growth rate	84
PE, PP, PS, PVC, PET	200−600 μm		50−1000 mg/L	*Scenedesmus* sp.	Growth	Growth inhibition	85

Table 2. Summary of Observed Effects of PL on Various Phytoplankton Species in Laboratory Studies

Plastic leachate	Exposure time	Dosage	Phytoplankton species	Parameters studied	Toxicological effects	Ref
HDPE and PVC	48 h	3.125%−50% HDPE 0.25%−10% PVC	*Prochlorococcus*	Growth, Photosynthesis	Inhibition of growth, impaired photosynthetic capacity and genome-wide transcriptional changes are observed	26
PP, PE, and PS	72 h	3.1%−100% leachates	*D. tertiolecta*	Growth, Oxidative stress, DNA damage	Growth inhibition, induced significant DNA damage and elevated ROS production; hormesis phenomenon was detected for PE leachates	98
Car tire rubber (CTR), PP, PET, PS, and PVC	72 h	Different dilutions from 0 to 100%	*R. subcapitata* and *S. costatum*	Growth	PET leachates did not cause growth inhibition; growth inhibition observed in other leachates	27
PUF (polyurethane foam)	5 days	Leachates obtained from 0.1, 0.4, and 1.6 g/L of MP	*C. vulgaris*	Growth, Photosynthesis	Negative impacts on photosynthesis were observed in the higher concentrations of the leachate	88
PE pigmented with lead(II) chromate	4 weeks	Unaged MP (0.75, 1.5, 3.1, 6.1, and 12.2 μg Cr(VI)/L), 2 week-aged MP (1.1, 2.1, 4.2, 8.4, and 16.8 μg Cr(VI)/L), and 4 week-aged MP (1.6, 3.2, 6.4, 12.8, and 25.6 μg Cr(VI)/L)	*M. aeruginosa*	Growth, Photosynthesis	Higher concentrations of plastic leachate had inhibitory effects on growth and photosynthesis	87

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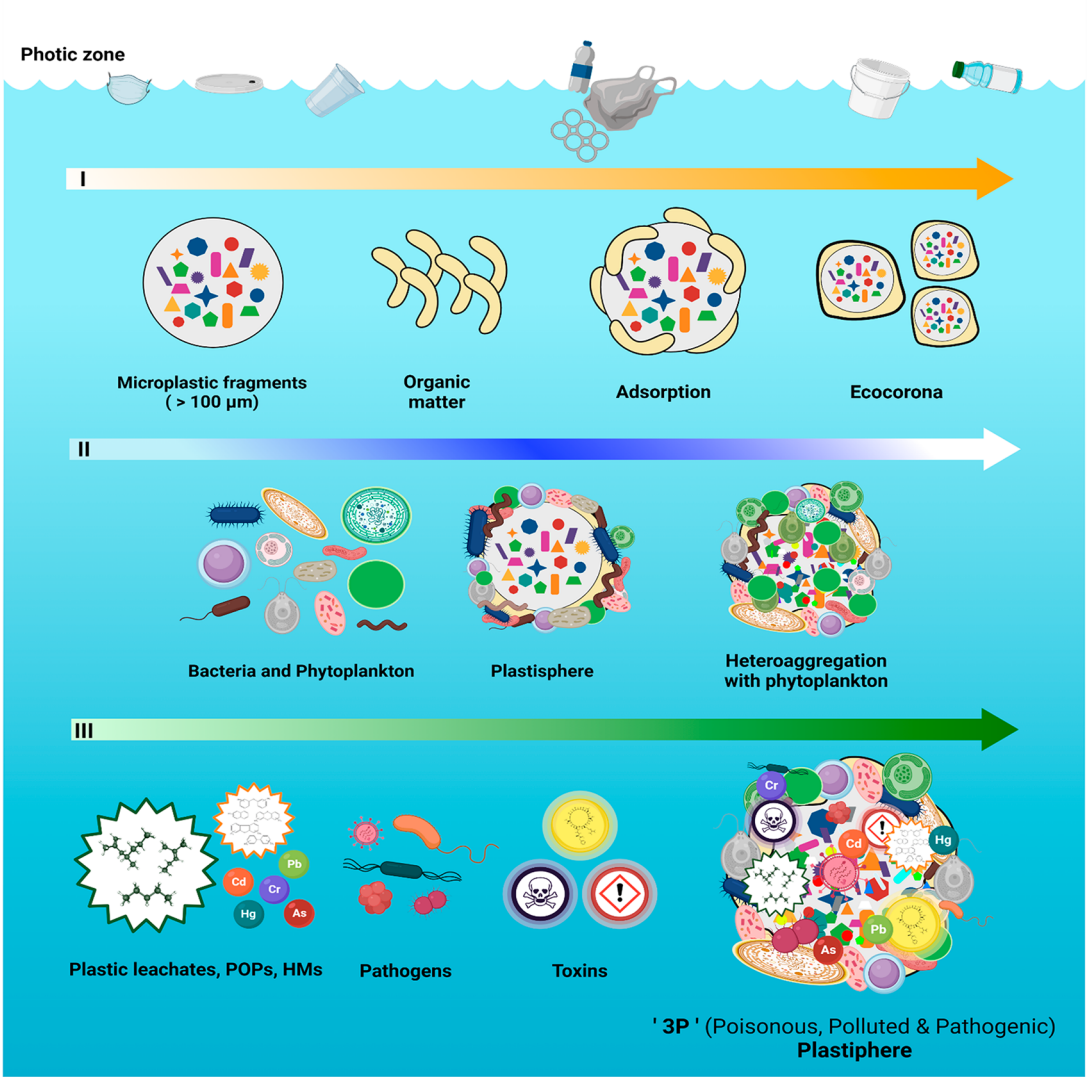

Figure 1. Metamorphosis of plastic particles into ecocorona (panel I), plastisphere (panel II), and "3P" plastisphere (panel III) during the interaction with organic matter, bacteria, phytoplankton, other eukaryotes, and other components in the aquatic ecosystems. POPs: persistent organic pollutants; HMs: heavy metals.

environmental conditions for the leaching process in PL studies, constitute a few of the many limitations. To highlight the vastly different environmental conditions with respect to MP number, studies on MP presence in open oceans and inland and coastal waterbodies have been tabulated (Tables S1, S3). For example, MP in open oceans are far less than in inland and coastal waterbodies, and huge disparities exist in particle numbers of the various studies. These disparities are attributed to spatial variations in sampling sites, sampling techniques used, e.g., as net pore size, and detection methods used.[93−96] Likewise, chlorophyll *a* content in the open oceans and some prominent inland waterbodies have been presented (Tables S2, S4). The concentrations of MP used in laboratory studies have been extrapolated,[97] and chlorophyll content in these studies have been calculated (Tables S5, S6). These data sets reflect the massive difference in the concentrations of MPs detected in environmental samples and those used in laboratory studies. From these references, the calculated number of MP per mg chlorophyll a (Chl *a*) corresponding to phytoplankton densities for oceans amounts to 38.30 particles/mg Chl *a*, while that for inland and coastal waters is 540.30 particles/mg Chl *a*. Surprisingly, the corresponding number for the laboratory studies is 2.06 particles/mg Chl-*a*. Thus, while laboratory studies employ higher concentrations of MP in the ecotoxicological assessment, the phytoplankton density is also proportionately much higher, which renders these studies environmentally disconnected in terms of both MP and phytoplankton densities employed. In addition, on the basis of particles per volume, the concentrations of MP used were highly disproportionate with those of environmental concentrations. These discrepancies and variances in experimental designs among laboratory studies may obscure the very evidence of MP and PL impacts at subcellular and cellular levels. However, the above data suggest that impacts presented in the laboratory studies cannot be completely discounted and may manifest in the environment on the basis of phytoplankton biomass to MP ratios (SI, Tables S1−S6).

3. IS THE PHYTOPLANKTON COMMUNITY RESILIENT TO OMNIPRESENT MP AND PL?

MP and thereby PL are ubiquitous and already outnumber zooplankton and fish larvae in some ecosystems, and their

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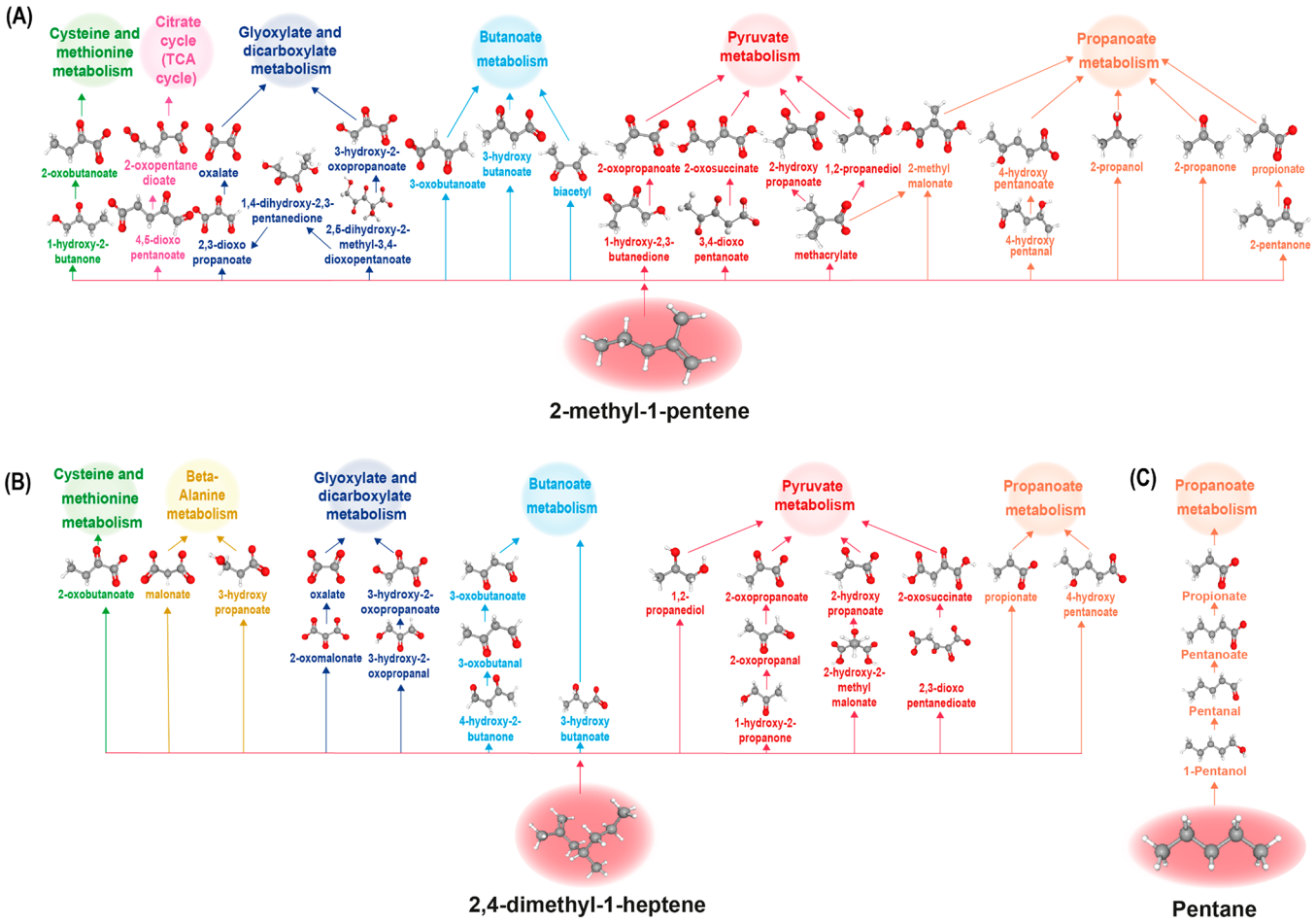

Figure 2. Prediction of biotransformation pathways of the major PP leachates: (A) 2-methyl-1-pentene, (B) 2,4-dimethyl-1-heptene, (C) pentane. The carbon atoms are depicted in gray, and oxygen atoms are depicted in red. An extended pathway prediction is available as Figures S1 and S2 for 2(A) and 2(B), respectively, only key products and intermediates are summarized here.

diversity of size and shape mimics that of most phytoplankton species.[99] With the numbers increasing every year, MP may perhaps exceed phytoplankton cell density at least in certain "hotspots" in highly polluted habitats.[100] Increasing MP density renders the interplay between phytoplankton, bacterioplankton, and MP more dynamic and interesting. Microbial attachment on MP[39,101,102] as well as MP hydrophobicity and the corresponding attachment of organic matter on MP have been well documented.[14] As detailed in Figure 1, when plastic particles enter the water, observable changes occur on the plastic surfaces. The immediate attachment of organic and in some cases inorganic substances on the plastic surface[14] aids in reducing particle hydrophobicity and rapidly attracts microorganisms, often within hours, as depicted in panels I and II[35,103−105] (Figure 1). In fact, a recent study on coastal waters reveals that microbial succession occurs rapidly during initial colonization. Bacteroidetes predominate in the first hours, but are quickly masked by Gammaproteobacteria followed by Alphaproteobacteria in the next days. Likewise, in sunlit coastal waters, diatoms initially power the plastisphere followed by brown algae a few days later. In relatively dark regions such as caves, the marine-dissolved organic matter supports the plastisphere.[105]

Other studies also show that the plastisphere is sustained by phototrophic microorganisms, which provide fixed organic carbon.[35,102] Interestingly, analyses of the composition of the heterotrophic prokaryotic community indicate that the plastisphere selects some key members of the phycosphere, which points to the important role of photoautotrophs on MP, at least temporarily.[37,38,101,106,107] As mentioned earlier, stress-induced EPS excretion by microalgae may stimulate phycosphere microbial communities in the plastisphere.[39,42] In addition, the plastisphere also includes the entire microbial food web with primary producers such as cyanobacteria and heterotrophs including decomposers and secondary producers such as heterotrophic protozoa and small animals.[38,39,108] Although research in this domain is still in its infancy, it is obvious that plastisphere microbial communities gradually become distinct from their planktonic counterparts. Importantly, this microbial community can also influence the fates of MP and PL.[92,109] Therefore, the corresponding alterations in metabolic pathways, lifestyles, and biogeochemical cycling have been envisaged by these studies. At the same time, the plastisphere is by itself divergent, and the composition of the plastisphere is influenced by numerous and partly rapidly changing factors. These include seasons, surrounding habitats, nutritional availability, polymer type, and stage of microbial succession in the plastisphere.[42,102,110,111] Yet, feedbacks and interactions between chemical compounds of MP origin, in particular PL, and microbial community dynamics remain largely unknown.

Alterations of the natural temporal succession in microbial communities of various waterbodies have been observed in the presence of plastic fragments. It has been shown in different

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aquatic ecosystems that the plastisphere leads to different temporal patterns in microbial successions.[35,112] The distinctiveness of the plastisphere communities suggests that the plastic fragments interfere with the natural selection of aquatic microorganisms. This can be attributed to alterations in growth and metabolism of individual organisms in the natural plankton community. Increased stress and even apoptosis of more sensitive species can supply additional energy sources for other heterotrophic microorganisms which may lead to distinct changes in the microbial community structure in the plastisphere.[113] For instance, among photoautotrophic organisms, in freshwater and brackish waters, *Chlorella* and *Scenedesmus* genera are two of the most ubiquitous and resilient organisms which have been found to be resistant to various organic compounds in wastewater.[114−116] They also seem to be highly resilient against MP even at high concentrations.[58,88,117] Therefore, phytoplankton diversity in the presence of MP is likely much lower than that of the surrounding planktonic community as the presence of MP may select for the dominance of a few tolerant organisms.[38,117] These massive alterations in microbial community structure may also occur in a dose-dependent manner as it has been found for individual organisms.[63,75,77] Another recent study[118] argues that the microbial community structure in the plastisphere is diverse and influenced by the local species and nutrient pools, but relatively less on MP polymer type. Nevertheless, the study did not test for any dose dependency.[118] Nearly all studies report on the presence of cyanobacteria, diatoms, and green algae in the plastisphere, with gradual succession in microbial communities and increasing dominance of cyanobacteria.[117] These studies verify that changes in the community structure of the phototrophs occur in highly polluted areas with high concentrations of MP and PL.[119] Therefore, we assume that pronounced differences in microbial communities and the entire aquatic food chain occur in highly MP-contaminated near-shore waters (Tables S3, S4).[119] Consequently, progressive succession of the phytoplankton communities and their associated phycosphere bacterial communities toward more niche-specific hydrocarbon-degrading communities[109−112,120−122] may have profound effects on aquatic food web dynamics and energy transfer and thus ecosystem functioning.

3.1. Initial PL Biotransformation Pathways and the Plastisphere. Synthetic polymers degrade naturally due to biotic and abiotic processes. To test, explore, and expand our understanding of the influences of possible leachate products and leaching scenarios on phytoplankton, PP was considered for biotransformation pathway prediction as it currently is the most-produced polymer class.[3] Major degradation products of this polymer are ROOH, RCOR, pentane, 2-methyl-1-pentene, and 2,4-dimethyl-1-heptene.[123,124] The transformation products which were predicted using the EAWAG-BBD tool can serve as organic substrates for bacteria and microalgae or can lead to toxic stress by themselves or in combination with other substances in aquatic ecosystems. Figure 2 is a simplified version of pathways considering the final leached products. The selected leachates are key products of the PP leaching process which are potentially taken up by the plastisphere microbial community. Yet, there are several intermediates apart from the products indicated in the simplified figure which may also have a detrimental effect on the plastisphere microbiota due to their reactive natures (Figures S1, S2).

Biotransformation rules presented in the predicted pathways comprise of a set of biocatalytic reactions catalyzed by several basic enzymes such as esterases, lipases, and cutinases.[109,111,120,122,125] These enzymes or equivalents might drive biotransformation/biodegradation in the plastisphere microbiota. One of the three organic leachates selected here (pentane) and structurally similar compounds to other two leachates also represent volatile organic compounds (VOCs) which are emitted during predatory pressure or apoptosis and lead to cell death in some key phytoplankton species.[126,127] Also, their leachate intermediates constitute VOCs of algae, cyanobacteria, and heterotrophic bacteria and may also serve as signaling molecules.[126−128] This "biomimicry" by these PL may elicit the "cry wolf" effect in cellular defense mechanisms and in phytoplankton cell-to-cell communication, altering the predatory pressure for phytoplankton. Moreover, many of the final products might be utilized by phototrophs capable of mixotrophy and heterotrophy. This further skews the plastisphere microbial diversity toward specific hydrocarbon degraders.[109,120] Therefore, the interplay of VOCs, signal molecules, their relevant concentrations to elicit signaling, the possible change in microbial community structure of the plastisphere, and the impact on grazers provide interesting, but yet largely open, research questions. If explored, the proposed studies might help document indirect and intangible impacts of PL on photosynthetic microorganisms and may delineate the more specific PL impacts from those of MP.

3.2. Vectors of Anthropogenic Pollutants Driving Plastisphere Composition. It has been mentioned earlier that the plastisphere attracts antibiotic-resistant bacteria, and the plastisphere is a hotspot for hydrocarbon-degrading bacteria.[45,129,130] Adsorption of pollutants including heavy metals is viewed as a major reason for microbial multiresistances associated to MP. Furthermore, several mechanisms such as hydrogen-bonding-mediated, and hydrophobic and electrostatic interactions-mediated adsorption of organic molecules and heavy metals are proposed to occur on MP.[129,131,132] Matter adsorption is highly influenced by several environmental factors, such as MP characteristics and age, the surrounding medium, organic matter, and nutrient concentrations in the ecocorona.[132] Additionally, adsorption to MP in the ecocorona will facilitate interactions between anthropogenic pollutants such as heavy metals, PAHs, PCBs, pesticides, and other natural organic matter with the microbial community in the plastisphere.[130] The presence of different functional groups with varying polarities facilitates interactions of other pollutants with MP, their additives, and PL. For instance, the presence of benzene rings on PS causes strong affinity to nonpolar compounds through $\pi-\pi$ interactions. Therefore, PS has a high sorption capacity for aromatic compounds, which shows that the chemical structures of MP monomers influence pollutant composition and pathogenic microorganisms in the plastisphere.[133] Several studies are emerging on the combined toxicities of MP with PAHs,[80,134] PCBs and pesticides,[81,135] plastic additives,[58] antibiotics,[73] and heavy metals.[79,87,136] The sources of some of these pollutants, however, remain unclear as some heavy metals and organic pollutants can also leach from MP.[26,57,87,130,137] As a result, these MP serve as emerging hotspots of pathogenic and hydrocarbon-degrading bacteria vastly different from their planktonic counterparts.[130] Thus, they form niches facilitating accelerated microbial evolution in the plastisphere through horizontal gene transfer of potentially hazardous genes such as antibiotic resistance genes.[45] They may also constitute "future sinks" of pathogenic and/or invasive microorganisms and pollutants which potentially affect human and ecosystem

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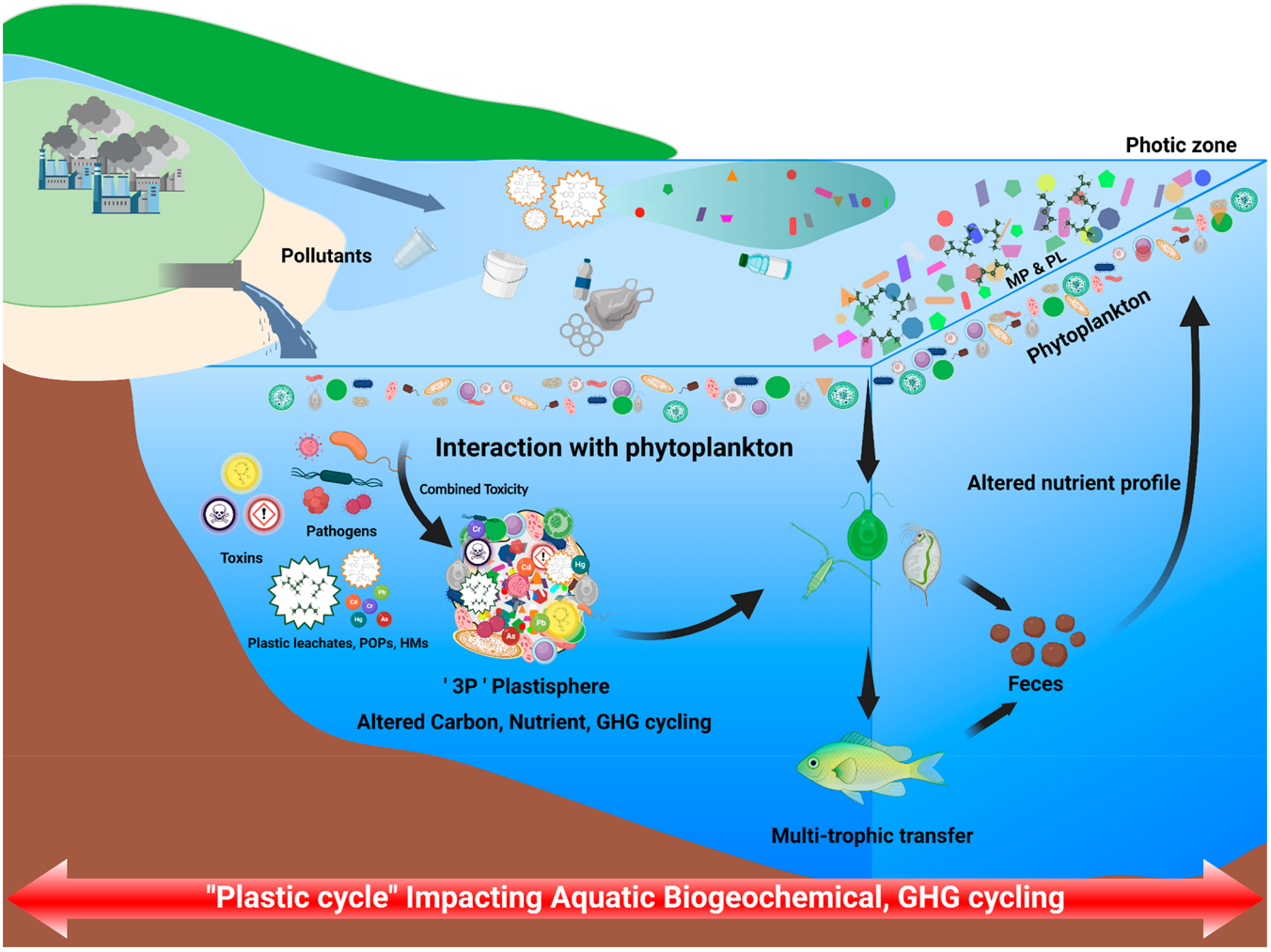

Figure 3. The plastic cycle fundamentally alters aquatic ecosystems through direct and indirect impacts on phytoplankton, bottom-up and top-down impacts on the entire food chain, and knock-on effects on biogeochemical and GHG cycling.

health.[46,137−139] It is also important to note that ingestion of these pathogenic and pollutant-laden MP, and the potential desorption of MP pollutants under low pH conditions, e.g., in the gut of zooplankton and fish, will have devastating consequences on higher trophic levels and even humans.[140−142]

In addition to pathogens and pollutants, natural and anthropogenic toxins are another burden of the plastisphere, making it highly harmful for humans and the environment.[55,56] For example, analogues of the cyanobacterial toxin microcystin are present on MP, even up to eight different microcystin analogues on PP MP.[56] Furthermore, microcystins are present on nearly all polymer types, i.e., PVC, PP, PE, PET, but predilection is MP size-dependent. MP also seem to increase toxin levels within *M. aeruginosa* (see Section 4), which taken together renders these microbial vectors very poisonous.[52,55,56] Another point of concern is that the photosynthetic community within the plastisphere may well erode over time because of the emergence of pathogenic, multidrug resistant-, and pollutant-degrading bacteria and eukaryotes, which can differ from microbial communities in the phycosphere as has been demonstrated in mesocosm studies.[118] Yet, these studies do not consider the multitude of other anthropogenic pollutants present in the natural environment.[117,118] Even hydrocarbon-degrading cyanobacteria such as *Phormidium* sp. have been found on marine plastic debris which is in stark contrast to planktonic communities in natural seawater and mesocosms.[120,143] Thus, it is very likely that these substances exert a considerable selection pressure for organisms with special capabilities such as antibiotic resistance, hydrocarbon degradation, and heavy metal adsorption, resulting in drastically different microbial communities in the plastisphere which have the potential to gradually alter the natural planktonic communities over time.[120,122] Moreover, increased gene transfer will alter microbial functions and accelerate genetic evolution of the microbial community with so far unknown consequences for aquatic ecosystems and their functions.[45,138,144] In summary, as shown in panel III of Figure 1, these substances render the plastisphere pathogenic, pollutant laden and poisonous, which in turn drive changes in microbial community structure and alter aquatic ecosystems more severely than ever before[55,120,130,138] (Figure 1).

4. CAN AQUATIC ECOSYSTEMS BEAR THIS LETHAL BURDEN ON PRIMARY PRODUCERS?

Whereas we have discussed studies demonstrating MP and PL impacts on organismal and community scales in the previous sections, in this section, we focus on effects on ecosystem structure, functions, and services.[145] Some of the major documented impacts on individual organisms include growth and metabolism and thus on community composition including

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acceleration of microbial succession and horizontal gene transfer. This possibly alters biogeochemical cycling[144,146] and thus ecosystem functions and related services. MP and PL may thus drastically and manifold alter aquatic ecosystems in the long run.[48] Consequently, harmful and even lethal impacts of MP and PL on individual organisms as well as communities and their manifestations at the ecosystem level are discussed in combination.

4.1. Primary Productivity Impacts via MP and PL. MP impacts on primary productivities in terrestrial ecosystems have been proven beyond doubt, especially in certain ecosystems such as grasslands and agroecosystems.[147,148] Almost all soil studies agree that MP and PL controlled microbial community successions and, therefore, shifts in plant species dominance.[145,148,149] Recently, a global study on farmland ecosystems has summarized that MP have a higher impact on soil fungal communities than their bacterial counterparts, and overall microbial diversity and function of the farmland ecosystems are greatly affected via MP-induced effects on pathogen diversity.[150] Growing evidence has pointed to changes in ecosystems structure, functions, and services due to MP and their additives in the terrestrial ecosystems.[149] Such scenarios also rapidly develop in aquatic ecosystems, especially since freshwater and terrestrial ecosystems are closely interlinked and the sheer extension of the marine ecosystems.[145]

In most of the studies reviewed, it has been found that photosynthesis and primary productivity of phytoplankton are affected in the presence of MP and PL, in some cases even irreversibly (Tables 1 and 2). When PL and other pollutants, which are adsorbed to and often concentrated on these vectors, occur in combination with other stressors, the impacts on primary productivity is particularly strong.[24,122,151] In cases showing positive impacts on primary productivity, changes in community composition and the dominance of particular species need to be considered, as throughout time, species dominance leads to blooms and associated ecological impacts.[152] In some cases, the gradual dominance of bloom-forming phytoplankton and increased toxin formation can be observed, which may in turn control primary productivities of entire ecosystems, as toxic algae can constitute keystone species with the ability to control grazers and other phytoplankton species.[52,55,153] Similarly, the gradual succession of the plastisphere from a predominantly phycosphere community to a poisonous, pathogenic, and pollutant-degrading community (see Section 5) will further impact primary productivity. In contrast, the phycosphere microbiome has the potential to enhance microalgal growth[154,155] and also counteract possible harmful effects as has been observed on MP. However, at this stage, the impacts of MP and PL on primary productivity is difficult to quantify due to differences in methods used and the diversity of algal responses. Several studies suggest an increase in net community oxygen production and thus primary production in the plastisphere.[86,108,118] Yet, this might occur at the cost of diversity in species and biogeochemical cycling, which eventually alter ecosystem productivity[120,144,146] (Figure 3).

4.2. Bottom-up and Top-down Impacts. The direct impacts of MP and additives on several grazers have been well documented.[29,156,157] Indirect impacts on primary consumers, and higher trophic levels, are through MP impacts on the primary producers. A primary direct MP effect on grazers is via ingestion of MP- and PL-associated phytoplankton. As MP can also act as vectors, in addition to their reduced nutritional value and the resultant direct MP impacts on the grazers' health, indirect impacts of the vectors should be also accounted for. First, toxins which are adsorbed to MP have acute toxicological impacts on grazers and fishes, which are often lethal, and might lead to a slow degradation of the ecosystem, preceded by massive toxic algal blooms and fish deaths. Second, pathogenic and drug-resistant bacteria associated with the plastisphere will have acute and chronic impacts on grazers as well as secondary and tertiary consumers, thus impacting the entire food web. Third, MP-associated pollutants (either leached or adsorbed) create a secondary impact apart from primary MP impacts. These impacts are not easy to quantify as they are dependent on MP type, pollutant adsorbed, environmental conditions, and grazer type. Further, active desorption of chemicals can occur in the grazer's gut after MP ingestion due to the low pH conditions severely altering their microbiome, prey preference, and nutritional quality for the higher trophic states. These MP effects on the grazer's gut may have reverse effects on ocean productivity.[141,158] Overall, phytoplankton interactions with MP and PL have direct and indirect impacts on zooplankton and the higher trophic states with profound consequences for predator fitness and survival.

Other direct MP impacts on grazers, e.g., inhibition of mobility, further decreases foraging of phytoplankton biomass. In addition, mobility inhibition makes the grazers more susceptible to other predators, e.g., larval damselflies.[157] Consequently, the trophic cascade is altered, and these behavior-mediated interactions change plankton dynamics and primary productivity.[157] Other indirect MP impacts are overlapping size range between MP and phytoplankton, odor distinct or similar to prey species confusing primary consumers to ingest these MP and associated pollutants, and harmful microorganisms[26,159] which may lead to profound consequences for ocean productivity.[159] These direct and indirect impacts were studied extensively in *D. magna*, which is a freshwater keystone species. The studies show that in the absence of this freshwater keystone species (due to inhibitory MP effects) invasive species may benefit.[30,99,157] This predilection for invasive species is often facilitated by the much longer exposure times of plastic fragments to microorganisms than of natural substrates which are more rapidly removed from the water column. The higher durability and buoyancy of MP enable their long-distance transport and long-term persistence which increase MP exposure to different microbial communities in time and space and thus promote MP colonization by invasive species.[138,157,160] MP and their associated chemicals and microorganisms are proven to disperse via aerosols and thus can also reach the most remote aquatic ecosystems.[161−163] These remote ecosystems can be severely impacted by MP affecting ecosystem resistance and resilience to changing environmental factors such as climate.[164,165] In fact, MP are known to impact habitat-forming corals by directly affecting primary productivity and consequently the supply of fixed organic carbon from the photoautotrophs to their coral hosts.[143,157,165] MP- and PL-induced risks to these habitats have massive impacts on biodiversity, trophic levels, and biogeochemical cycling and may gradually change these ecosystems into a different system state[166] with pronounced effects on climate and oceanic productivity even at the global level.[167]

4.3. Biogeochemical Cycling: Emerging Losses in Ecosystem Functions. Following world scientists' warnings to humanity on the current threats faced by global ecosystems, threats faced by ocean ecosystems and of the microbial world

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were included.[2,168,169] Thereby, the increasing predominance of MP constitutes one of the major threats to human existence.[2,20,94,169,174,175] The dissolved organic carbon (DOC) secreted by primary producers serves as a carbon source for heterotrophic bacteria.[60,107,170,171] Presently, it has been estimated that DOC released from marine plastics globally is nearly 23,600 t/year,[166] and DOC leached from MP is identical to some VOCs released by phytoplankton (see Section 5). The huge amounts of DOC from anthropogenic MP completely alter the signature of ocean DOC and interfere with signaling mechanisms and cell-to-cell communications—eventually endangering prey defense and predatory preferences. In lakes, PL at environmentally relevant concentrations elicited efficient bacterial growth than natural DOC because the PL were more accessible for bacterial utilization.[171] Thus, further changes in oceanic carbon cycling due to the massive release of MP-DOC and subsequent changes in planktonic community profiles toward pathogenic and pollutant-degrading heterotrophic bacteria are suggested to greatly alter the entire biogeochemical cycling.[120,128,167,171] Further, MP have been shown to impact minor nutrient cycling, e.g., rupture of the siliceous cell walls of marine diatoms, and diatoms are one of the major groups in oceans as well as in the plastisphere.[63,65,134] Another nutrient cycle impacted by MP is cycling of Fe which is an integral part of primary productivity.[158] Desorption processes of pollutants from MP at low pH conditions in the gut of zooplankton reduces the efficiency of lithogenic Fe, which is essential for primary productivity.[158,172]

The plastisphere also serves as hotspots of greenhouse gases (GHG) cycling and CO_2 and N_2O consumption and production.[146,173] Although the role of plastisphere photoautotrophs is not consistent across samples, some of the phycosphere bacteria hold prominent roles in GHG cycling. Methane and ethylene are also known to be produced from plastics, especially aged plastics, although the observed impacts are highly local, and the global impacts are insignificant for methane at present emission rates, but emission rates for other hydrocarbons have global relevance.[121] A recent study has demonstrated that biofilm formation in the estuarine plastisphere provides anoxic microzones thereby increasing denitrifying activity and nearly 2-fold higher N_2O production in plastisphere compared to bulk waters.[146] MP are also known to affect the sedimentary microbial community and adversely impact nitrogen cycling, especially PVC MP, which affect both nitrification and denitrification.[32] Although this directly affects biogeochemical cycling, the effect of inhibition of these processes on the release of nitrogen and further assimilation by the primary producers is obvious, but rarely investigated.[32] Additional studies have found that the plastisphere alters nitrogen cycling, albeit positively.[57,99,140] Global temperature increase can also directly or in combination influence the rate of leaching of hazardous chemicals from plastic wastes and help to accelerate hydrocarbon cycling.[24] The reduced sinking rate of microorganisms due to heteroaggregation with low-density plastics alter cycling of various nutrients in the waterbody.[69] In areas with a massive MP contamination, a substantial decrease in diatom sinking rates presumably causes a reduced availability and low quality of carbon for export flux and filter feeders in deeper water layers.[14,23] To a large extent, the impacts of MP and PL on biogeochemical cycling in the affected aquatic ecosystems is collateral, with a severe potential to harm many aquatic nutrient cycles.[138,172] The influence of the plastic cycle on biogeochemical cycles is so widely distributed that MP and PL influences on Earth system processes are unquestioned, and the extent of MP in the environment is seen as a marker for the Anthropocene epoch[23,173,174] (Figure 3).

Cumulative MP and PL impacts on key primary producers and hence phytoplankton community dynamics in both marine and freshwater ecosystems in combination with several physical, chemical, and biological processes in aquatic ecosystems point to massive, but still largely unknown, effects on ecosystem services. MP and PL effects on the above-mentioned biogeochemical cycles and "knock on" effects on GHG cycling have the potential to further disturb the global climate. In particular, MP impacts on biodiversity, trophic structure, and functioning of aquatic food webs are undermining related provisioning services in the long term. Conclusively, the majority of services of aquatic ecosystems are severely threatened by the increasingly dominance of the the plastic cycle in human-altered aquatic ecosystems in the Anthropocene[174] (Figure 3). Thus, it remains questionable whether we have already crossed the threshold at which MP and associated PL irreversibly change aquatic ecosystem structure and functionings.

4.4. Phytoplankton's Defense to MP and PL Able to Combat or Escalate Threats? Although complete biodegradation of MPs in water samples has not been reported, microbial degradation of plastics has been demonstrated from several environmental isolates.[175−177] Microbial degradation of the plastic matrix is aided by external abiotic factors leading to changes in physical, mechanical, and chemical matrix properties.[121,178] Among phytoplankton, two filamentous cyanobacterial species, *Phormidium lucidum* and *Oscillatoria subbrevis*, have shown remarkable weakening of polymer crystallinity, weight, and thickness while rapidly colonizing the PE film surface. EPS secretion by the phytoplankton enlarges the pores that eventually crack into smaller fragments.[179] Similarly, *Spirulina* sp. formed new functional groups such as carbonyl, carboxylic acid, and hydroxyl groups on the PP and PE MP surfaces making them more prone to further microbial degradation.[84]

One of the emerging mechanistic insights involved in MP degradation is the increased production of EPS, which in turn modifies the physicochemical properties of the associated polymer.[180] Addition of microplastics is reported to stimulate EPS secretion in *Chlorella* sp. (1.4 times) and *Phaeodactylum tricornutum* (2.2 times).[181] EPS composition and amount varies based on the polymer type and phytoplankton species,[59,182] and studies suggest that a higher protein−carbohydrate ratio of the EPS will result in better aggregation and eventually higher sinking rates of MP-phytoplankton because of the gel-like sticky characteristic.[180,182] Other typical defense mechanisms of phytoplankton include production of cellular pigments such as chlorophyll *a*, chlorophyll *b*, and carotenoids that act as antioxidants.[183] Further, synthesis of antioxidant enzymes has been reported in several studies (Tables 1 and 2).

On the contrary, because of these self-ameliorative processes by phytoplankton, heteroaggregation and sinking of MP and phytoplankton may eventually lower primary productivity and displace MP from surface waters to subsurface waters and sediments.[64,69,184] Likewise, the increased synthesis of EPS signifies the release of photosynthetically fixed DOC which could be otherwise used by organisms for cell division and growth. For example, the increased DOC release may also attract and amend the innate phycosphere bacterial community of the phytoplankton.[61,111,171] These self-ameliorative processes are defined by environmental factors, and thus may not keep pace

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with the burgeoning plastic input. Consequently, further comprehensive studies on various defense and ameliorative mechanisms of phytoplankton toward MP, PL, and associated pollutants are needed to shed light on the eventual fate and transport of MP, and phytoplankton, and their cumulative impact on biogeochemical cycling.

Meanwhile, in the near term, without any effective conservation and mitigation measures, there is a high risk that plastics of all sizes as well as associated chemicals will harm environmental and human health to a nontolerable level with profound consequences for all life on Earth.

5. CITATION NETWORK ANALYSES

Citation network analyses (CNA) performed with VOS viewer software[131] visualize all studies published in PubMed using a combination of keywords such as "Microplastics", "Phytoplankton", "Photosynthetic Microorganisms", "Plastic Leachate", and "Aquatic Photosynthetic Microorganisms" in the last 50 years (1972−2022). CNA help in understanding concerted networks of studies in a particular field, the evolution of a field, and possible future directions. From the networks, it is apparent that *Chlorella* species and diatoms are the predominant phytoplankton groups in most studies (Figure S3a). In the case of polymers, more focus has been given to PS, followed by PE, PP, and PVC, which are the most-produced polymers and are presently indispensable for human life (Figure S3b). Yet, little focus is given to PET as it is known to be degraded biologically.[175,185] Marine ecosystems are comparatively widely studied presumably due to the high number of researchers in the field. In contrast, freshwater ecosystems are less studied and thus are represented by a separate node in both MP and PL networks (Figure S3). Studies on freshwater ecosystems, however, have gained momentum after 2015. CNA reveal that the major impacts of MP and PL on autotrophs are related to photosynthesis, growth as well as gene expression. The role of MP as vectors of antibiotic-resistant microorganisms is widely studied and represented by a node specific to antibiotics. The separate node for nanoplastics reveals their role in causing toxicity to autotrophs and an increasing trend for such studies. The cumulative toxicity of MP, PL, and other anthropogenic pollutants is an emerging field of interest.

Like in the case of MP, widely studied organisms for PL toxicity are eukaryotic microalgae and cyanobacteria (Figure S3b). Biotransformation in the environment and the subcellular and molecular level impacts of these chemicals are growing areas of research. DNA damage and growth inhibition caused by PL from PE, PS, and PP show the direct impact of PL on the entire biota. PL toxicity is accompanied by heavy metal toxicity, especially Cr, which is another derivative from plastic additives. The final synthesis from these networks shows that growth inhibition, photosynthesis, oxidative stress, DNA damage, and gene expression are the major findings of studies at the cellular level, while alterations in food chain, biotransformation, and biological availability represent the most commonly studied community- and ecosystem-scale impacts. In addition, the prominent and distinct nodes for combined toxicity, antibiotics, heavy metals, nanoplastics, and plastic additives indicate the emerging trends in this area.

6. RESEARCH NEEDS AND FUTURE DIRECTIONS

Although research on MP, PL, and nanoplastics has rapidly advanced and evolved in the recent years, it is still very much in its infancy with respect to the vast scope for further research. Here, we discuss major existing knowledge gaps, potential research directions, and policy imperatives to support a global consensus on standardizing research methods and building research networks, as well as policy and public outreach for addressing the issue from conservation and mitigation viewpoints.

1. The need to organize research on MP, and especially emerging research on PL, is reemphasized by this review. For instance, while MP and PL impacts are predominantly harmful to phytoplankton, it is difficult to generalize this trend for effective policy measures due to the lack of any consensus.[49] The lack of consensus can be attributed to the manifold, nonstandardized methods and experimental designs. Therefore, uniform guidelines on MP research are needed and also applied to studies on PL and combined toxicity studies with respect to model organisms at each trophic state and at various temporal and spatial scales. Lack of uniformity will lead to meaningless end points, preventing useful information for policy advocacy and hampering solution seekers. Profiling the plastic additives is often very difficult and a humongous exercise due to the diversity of plastic materials and of additives used by manufacturers. The concentrations of individual chemical species in PL are challenging to quantify as these compounds are often present in trace amounts, at times lower than analytical detection limits, except for a few additives that are added in high amounts and leach in quantifiable concentrations.[24,27,151,186] Responsible manufacturing, regulation of additive usage, additive profiling and labeling by manufacturers, and increasing awareness on the generation of PL represent promising directions for policy advices and mitigation measures.
2. In the case of PL, environmental concentrations are a few orders of magnitude lower than most dosages used in experimental studies. However, the mixtures of chemicals and other stressors in the environment cause cumulative toxicity, as the combined toxicity is usually higher than just the sum of toxicity of the individual components, and every chemical will interact synergistically or antagonistically and thus affect overall toxicity.[24,187] Further, the laboratory-scale experiments employing single species toxicity or communities in laboratory-controlled environments are vastly different from the much more complex environmental conditions. MP and PL concentrations in natural environments, although low, are increasing on a yearly basis and will even increase faster in the post-COVID era than previously predicted.[11] Therefore, *in situ* MP and PL toxicities for phytoplankton need to be explored; e.g., only a few mesocosm studies are yet available.[118]
3. For a meaningful comparison between studies, the factors influencing the spatial and temporal distributions of MP and PL in all aquatic ecosystems need to be understood in detail and normalized across experimental designs. Long-term large-scale experiments, environmentally relevant concentrations, and *in situ* conditions can be achieved after such standardization. More cutting-edge research on combined toxicity, synergistic, and antagonistic interactions of MP, other pollutants, and leached compounds could be then enabled allowing for analysis of global

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patterns. Consequently, these advances will provide conclusive, ecosystem level analyses allowing for effective advice to policymakers, stakeholders, and managers to better mitigate the negative effects of the ever increasing global plastics pollution.

4. With respect to the particular focus of this review on the impacts of MP and PL on phytoplankton, several open research questions remain. One of the foremost considering the magnitude of the issue is the release of huge amounts of MP-DOC and its influence on algal-DOC, microbial community structure, grazers, and aquatic ecosystems. Furthermore, the interplay of VOCs, signal molecules, and the mimicking by PL molecules are related scientific questions of prominence.
5. PL degradation pathways presented here would facilitate experimental interventions on interactions and feedbacks between PL and microbial community dynamics. Elucidating fate, degradation, and biotransformation mechanisms of PL including MP-DOC will improve our understanding of the actual impact of the plastics cycle on biogeochemical cycling and GHG concentrations.
6. Therefore, detailed, *in situ* experiments to validate recent, overwhelming evidence on alteration of nutrient cycles, especially nitrogen and phosphorus, and micronutrients need to be urgently commissioned.
7. Alternatively, to alleviate the vast differences between environmental conditions and MP abundances used in laboratory-scale studies, single cell approaches coupled to toxicomics would exemplify the actual impacts of MP and PL on phytoplankton thereby neutralizing most variables.
8. Modeling the spatial distribution and abundance of floating MP in surface and subsurface open oceans has been extensively performed.[93,94,96,97] However, application of toxicodynamic and/or toxicokinetic modeling for interactions of MP and PL with phytoplankton is urgently required. In addition, model development to elucidate the impacts of combined toxicities of MP vectors is particularly pertinent.
9. The "3P" plastisphere is a dangerous, emerging phenomenon, which may drastically change aquatic microbial communities, and severely impact human health, if left unexplored and unchecked.
10. Quantification of losses or gain in primary productivity due to the plastics cycle after the above cumulative research progress including standardization methods and normalization of influencing factors in freshwater and marine ecosystems needs coordinated global efforts.
11. The impacts of MP and PL from specialized hazardous waste streams such as e-waste on primary producers need to be elucidated. Likewise, delineating the specific impacts of PL from MP need to be considered for effective mitigation measures.
12. For effective mitigation, once the standardized guidelines are set for detection and quantification, global standards specific to MP in water and wastewater quality analysis need to be endorsed. Despite the review's focus on MP and PL, problems posed by nanoplastics cannot be ignored and viewed in isolation. Nevertheless, a global consensus on such standards for MP, and possibly for nanoplastics, form an essential first step.
13. Such a global consensus is not possible without definitive studies on socio-economic losses, in particular, specific revenue losses due to harmful MP and PL impacts. Likewise, intense studies on quantifying human health impacts of MP and PL through transdisciplinary approaches are essential for policy changes at a global scale. Thus, this alarming threat also offers new opportunities from mitigation and policy prescription perspectives.
14. Although feasible, long-term solutions are difficult to fathom, efforts on engineering PET-degrading enzymes are emerging and offer much promise for mitigation, although such efforts may rapidly increase the CO_2 pool in the atmosphere. The enzymes involved in biotransformation reactions presented here may well be tested for increasing polymer degradation as a mitigation measure.
15. Advancing research on utilities for treating MP in wastewater allows us to control at least one of the major MP point sources. Furthermore, viable upcycling or recycling and bioplastics are some of the many mitigation pathways in future.

All these efforts need be urgently devised and executed in parallel as global MP and PL threats are raging. To maintain the integrity and former steady state of natural aquatic ecosystems requires a coordinated global effort.

7. CONCLUSIONS

MP remain for up to several hundred years in the environment to an extent rendering them as reliable markers for the Anthropocene. In toxicological parlance, it is a chronic and terminal problem for aquatic ecosystems without any currently feasible solutions. While environmentally relevant and higher MP concentrations have been extensively tested mainly in the laboratory, environmentally relevant exposure times are hardly achieved (usually a few hours to a few months in lab experiments). With the predicted future increase in plastic fragments, their environmental impacts remain largely unknown, in particular as current predictions neglect the post-COVID plastic litter increase. MP and PL in combination with other anthropogenic pollutants suggest a highly underestimated potential to profoundly alter ecosystem structure and functions, which may lead to a new and unfavorable steady state in aquatic ecosystems. Net effects of these impacts and responses through phytoplankton self-defenses on ecosystem structure and functions remain to be studied. Presently, evidence from all studies on the impact of MP, PL, and their related hazards indicate that phytoplankton is "under siege" at subcellular, organismal, community, and ecosystem levels, and the danger is escalating. In view of the above-described urgency and the gross negligence shown so far, a massive, global scale-up in public awareness in coordination with all responsible stakeholders, augmented by scientific progress through integrated research at all levels across the globe, and alternate environmentally friendly pathways need to be urgently adopted. To this end, a global network of scientists working on MP and PL aquatic ecotoxicity and mitigation measures must first come together in an endeavor to collectively research and inform society and governments on possible threats and solutions.

■ ASSOCIATED CONTENT

Supporting Information

The Supporting Information is available free of charge at https://pubs.acs.org/doi/10.1021/acs.est.2c05817.

Sampling, characterization, and identification of MP from surface waters with reference to phytoplankton; prepara-

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tion and characterization of PL; summary of a few studies on MP and chlorophyll *a* concentration in open oceans, inland, and coastal regions, and laboratory studies (Tables S1−S6) (PDF)

Figure S1: Complete biotransformation pathways of major PP degradation products, 2-methyl-1-pentene derived using the EAWAG-BBD-PPS databases. Figure S2: Complete biotransformation pathways of other major PP degradation products, 2,4-dimethyl-1-heptene derived using the EAWAG-BBD-PPS databases. Figure S3: CNA of studies conducted in the last 50 years (1972−2022) on microplastics and phytoplankton (A) and plastic leachates and phytoplankton (B) (ZIP)

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Author Contributions

#C.A. and S.A.B. are co-first authors. R.R. conceptualized the review. All authors contributed to the interpretation of the data and the discussion of the results presented in the review. All authors have given approval to the final version of the manuscript.

Notes

The authors declare no competing financial interest.

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