

Review

Polymer bio-weathering and biodegradation induced by soil plastisphere: A comprehensive review

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Abstract: The plastisphere is a newly recognized geospheric layer at a planetary scale, characterized by the presence of microorganisms, primarily as biofilms, that colonize inert and poorly decomposable organic matter, particularly plastics. The stability and diversity of substrate plastic fosters a consistent evolutionary trend among microorganisms, leading to specialized ecological niches that enhance particular physiological traits for plastic degradation. Biofilms have been observed on various types of plastics, including both conventional petroleum-based polymers (like polyethylene and polystyrene) and bioplastics (such as polyhydroxyalkanoates). The characterization of plastisphere objects is crucial and should be conducted with geodetic referencing and spatio-temporal metrics to understand the impacts of climatic and meteorological factors. The dynamic nature of species succession in response to environmental changes necessitates advanced analyzes of microbial communities' potential for plastic degradation. The spatial turnover of core and occasional taxa complicates the precise identification of microbial functions within these communities. The question of "What is in the plastisphere?" emphasizes the need for detailed biogeographical and chemical mapping due to the small size and localized nature of microplastic particles. It is important to differentiate when plastics serve as growth resources (biodegrading) versus mere substrates for microbial growth, raising the question of "Food or just a free ride?" The geochemical and aerochemical activities within the plastisphere are crucial for understanding its broader environmental impacts. These activities include nitrogen metabolism and the biogeochemical cycling of nitrogen, phosphorus, and carbon, which encompasses greenhouse gas emissions associated with plastic degradation. Additionally, trace metals can accumulate in the plastisphere, potentially facilitating photo-Fenton processes that may occur on microplastic surfaces when exposed to sunlight.

Keywords: plastisphere; microplastics; microbial colonization; biodegradation of polymers; platiomics

1. What is the plastisphere from the point of view of a biologist/ecologist?

It is well known that the plastisphere is a new geospheric "shell" of a planetary scale, in which microorganisms (mostly as biofilms [1,2]) and entire ecological communities exist on the inert, poorly decomposable organic matter. The key concepts related to this term are "microbial colonization" and "bacterial colonization" of plastic [3–7]. The ecology of the plastisphere [8,9] has also been seriously discussed in recent years. Stability of the composition of the main plastic substrates leads to the constancy of the evolutionary trend of microorganisms in a given environment due to

which a stable ecological niche is formed for each type of the environment where the corresponding plastic is found [10], in which the evolution of microorganisms occurs in a single direction, resulting in the selection of the particular features of the microorganism physiology optimal for the decomposition of a given type of plastic [11,12]. At the same time, there is a divergence between the lines of microorganisms specialized for different chemical compositions of plastic. One of the most conventional examples of evolution in the plastisphere is the change and, as a rule, enhancement of the antibiotic-resistant elements [13,14]. Thus, it is known that the marine plastisphere selectively enriches microbial assemblages and antibiotic resistance genes during long-term cultivation periods [15]. Selective enrichment of the virulence factor genes in the plastisphere under antibiotic and heavy metal pressures is also well known and widely spread [16]. One of the explanations for this phenomenon is that microplastics accumulate antibiotic-resistant pathogens [17], but some groups believe that the problem is slower antibiotic degradation and higher resistance gene enrichment in the plastisphere [18]. Both versions are of an evolutionary nature, but some of them emphasize the source from which the selection is carried out, while others emphasize the result of this selection in specific conditions. Deciphering the mechanisms shaping the plastisphere antibiotic resistome is a local, but fundamental and actively solved problem of soil microbiology and hydrobiology [19,20]. The resistomes of microorganisms from different hydrophysical sources and industrial effluents (sludges) differ fundamentally, since the conditions/criteria of natural selection differ [21]. The fates of extracellular and intracellular antibiotic resistance genes in activated sludge and plastisphere under the same toxic or pharmacological loads on the environment also differ significantly (and vary in different ways) [22]. Previously conducted studies on the increased inheritance of structure and function of bacterial communities and pathogen propagation in the plastisphere along a river with increasing antibiotic pollution gradient confirm these findings [23].

In the limit, experiments in this area include plastisphere microbiome exposures to sub-lethal antibiotic concentrations [24]. However, microorganisms survive: it has been previously found that the plastisphere enriches antibiotic resistance genes and potential pathogenic bacteria [25], and the formation of specific bacterial communities contributes to the enrichment of antibiotic resistance genes in the plastisphere [26]. It has also been proven and illustrated with time resolution that the temporal dynamics of antibiotic resistome in the plastisphere during microbial colonization has a decisive influence on the possibility of colonization and biodegradation of plastics by microorganisms [27]. Therefore, it is clear that this evolutionary criterion is the main source of survival for a multi-species community of microorganisms as a whole. Hence, the methods of analysis and control/monitoring of these microorganism communities do not relate to the genomics of individual species, but to the metagenomics of the entire community and metatranscriptomics of the plastisphere [28] (the applicability of nanopore sequencing technologies to metagenomics has been considered in [29,30]). In addition, such methods must take into account the environmental factors in accordance with which selection takes place, including abiotic and xenobiotic factors, in particular, the presence of permanent toxicological and pharmacological contaminants (for example, long-term application of organic ferti-

lizer prompting the dispersal of antibiotic resistance genes and their health risks in the soil plastisphere [31]).

2. Biodiversity of the plastisphere

It should be noted that the biodiversity of the plastisphere includes not only bacteria on plastic in the soil or hydrosphere [32]. It is necessary to analyze plastisphere development in relation to the surrounding biotic communities [33], including all inter- and intra-domain interactions in the plastisphere [34]. Phytoplankton and zooplankton are found in the plastisphere in the hydrosphere [35,36], and recently it has also been proposed to take into account diatoms and macroinvertebrates [37]. The soil plastisphere also includes inhabitants of the rhizosphere [38], not excluding (but not limited to) nodule nitrogen-fixing bacteria and protozoa living at the interface between plastic and the environment in functional communities in plastic-mulching croplands [39]. Some taxa of organisms can be considered specific only for the soil or only for the aquatic plastisphere, while others can be both aquatic and terrestrial. For example, various fungi and slime molds in the plastisphere are found not only in soil / in farmland, but also across different river functional zones [40–42]. Obviously, viruses and plasmids, occurring in different bacteria (not only bacteriophages), can be found in the plastisphere of freshwater, saltwater, soil, edaphological, and other habitats [43–45] (from a biogeographical standpoint, the soil plastisphere is a special case of the terrestrial plastisphere [46,47]). However, in this report, due to the limited experimental possibilities, we consider only microorganisms and only in soil and swampy edaphological environments.

3. Biotopes of the plastisphere

Currently, the following types or biotopes of aquatic plastispheres are distinguished in accordance with the differences between microbial compositions, functions, assembly, and networks in the freshwater and seawater ecosystems [48–50] (as a roadmap for research projects of various biogeographic localizations of research, see [51]):

- Freshwater plastisphere [52–55], including river plastisphere [56–58] and urban riverine plastisphere [59],
 - Persistent rainwater plastisphere [60],
 - Marine plastisphere [61–65] (including shallow water or surface water ones [66]),
 - Lacustrine plastisphere [67,68],
 - Coastal plastisphere [69],
 - Estuarine plastisphere [70–73],
 - Beach plastisphere [74], etc.
- Hybrid dispersed or soft matter carrier-based “biotopes” of plastisphere include:
- Sediment-driven plastisphere community assembly on plastic debris [75] (including exotic anoxic salt marsh sediments [76])
 - Technogenic and anthropogenic municipal wastewater and municipal solid wastes [77,78];

- Soils and wetlands, which we discuss in detail in this paper, etc.

In fact, the determination of plastisphere biotopes requires taking into account biogeographic conditions, since the biotopes of the Arctic seas are not equivalent to the southern marine or Mediterranean biotopes, just as the terrestrial biotopes of the plastisphere in the permafrost and talik areas differ from the cryozone biotopes in the Antarctic area. Plastic-degrading microbial strains isolated from the alpine and Arctic terrestrial plastisphere differ significantly [79]. Marine biotopes of the plastisphere depend on the water salinity and can be more similar to freshwater biotopes in low salinity limits. At the same time, in some salt lakes, halophilic microbial species make the emerging communities similar to marine ones. The phenomenon of dependence of microplastic biodegradability responses of plastisphere antibiotic resistance to freshwater-seawater shift is known, which has been observed in onshore marine aquaculture zones [80].

At the same time, the influence of climate on the formation of plastisphere biotopes is known. Global warming as a trend certainly affects the change in the species composition of biofilms and plastisphere biotopes, as well as the composition of volatile and non-volatile products released during the plastic biodegradation under appropriate conditions [81]. However, single extreme weather events are also considered an important factor for the evolution of plastisphere [82] (although they are believed to have almost no effect on the additive biodegradation process). An example of such events is typhoon-induced turbulence, which redistributed microplastics, leading to the reformation of the plastisphere community [83]. Perhaps, within the framework of the catastrophe theory, this result can be generalized to many factors of diverse origin, as a result of which or after which the microbial community passes a bifurcation point and qualitatively changes its metabolic and microecological profile.

4. Geochemical and aerochemical activity of the plastisphere

Geochemical and aerochemical activity of the plastisphere includes the nitrogen metabolism of microbes and the biogeochemical cycles of nitrogen [84,85], phosphorus [86], carbon [87,88] (including greenhouse gas cycling by the plastisphere [89]), as well as bioaccumulation of trace metals in the plastisphere [90,91]. Due to the presence of metals, including iron, one can speculate about the possibility of photo-Fenton processes on the surface of microplastics and other elements of the plastisphere during their open exposure, including in the ocean [92]. More precisely, the geochemical activity of the plastisphere can be considered through the prism of the ion channel activity [93] or the analysis of the extended phenotype of microorganisms of the corresponding habitats [94,95]. However, this area of scientific research is beyond the experimental background of our paper.

5. Is the boundary between biodegradable and non-biodegradable plastics constant within the plastisphere?

Biofilms and other manifestations of the plastisphere are known on such widely used plastics (both petroleum-based polymers [96] and microbially generated bioplastics, such as PHB) as: polyethylene [97–101]; polypropylene [102]; polyethylene

terephthalate [103,104]; polystyrene [105]; polyurethane [106]; polybutylene succinate or poly(butylene succinate-co-adipate) [107,108]; polyhydroxyalkanoates [109]; poly (lactic acid)/Poly (butylene adipate-co-terephthalate) [110]; nylon [111].

The above list includes both biodegradable polymers and non-degradable ones [112–115]. However, in the plastisphere a strict classification of plastics to one of the above categories is not always evident, and each new plastic-degrading enzyme discovered in the plastisphere [116] shifts the boundary of this uncertainty or extended interpretation (especially if we subsequently proceed from the shotgun metagenomics of the plastisphere microbiome, which allows to understand the potential of enzymatic production and plastic degradation of specific microbial communities developed under specific conditions [117]). The boundaries between non-degradable and biodegradable materials in the plastisphere are also shifted by “plastiomics” (a branch of science studying “plastiome”: plastisphere-enriched mobile resistome [118]; one of the new multi-omics disciplines leading to a complete analysis of microbial diversity in the plastisphere and multi-OMIC characterisation of biodegradation and microbial community succession [119–121]). As it is known, specific components that are resistant to biodegradation or antimicrobial in nature are often included in plastics. As a result of the evolution in the plastisphere, there is a selection for antimicrobial resistance [122] and development of a set of genes responsible for the resistance to these additives, the so-called “resistome” (partly included into the scope of “plastiomics” (see above)). Therefore, at present, the adaptation of microorganisms to spread in the plastisphere is usually considered as a pathway for antimicrobial-resistant bacteria spread to the environment [123]. In particular, it follows from this that the next generations and new strains of microorganisms will decompose materials resistant to the earlier forms (as correlates of their niches and changing environmental conditions [124,125]) of the same microorganisms! The taxonomic boundaries of biodegradation will change rapidly.

6. The importance of imaging and mapping studies and microscopy techniques for the characterization of the plastisphere objects

It follows from the above that characterization of the plastisphere objects should be carried out discretely and with geodetic referencing in the biogeographical aspect, and with a spatio-temporal metric during the study of climatic and meteorological influences on the plastisphere. Moreover, from the above theoretical and bibliographic prerequisites follows the need to introduce microscopic or high-resolution microanalytical methods (including MALDI imaging or confocal Raman microscopy) into the studies of the plastisphere and products of its biological and/or ecological activity.

Indeed, almost five years ago, a conventional paper asked the following question: Who is where in the Plastisphere, and why does it matter [126]? It would not have been possible to answer this question without high-resolution (or position-sensitive) biogeographical and chemical/ecological maps (unprecedented for other biotopes in terms of resolution due to the small size of the objects of study and their localization, for example, on microplastic particles). If we talk about microplastics and other objects of the plastisphere, we also need to distinguish when it acts as a resource for growth (i.e., biodegrades), and when it acts just as a substrate on which

microorganisms grow using completely different resources of the environment (the question: “Food or just a free ride?” is relevant both for single particles or fragmented plastic films, and for the global diversity of the plastisphere as a whole [127]). The well-known phenomenon of spatial turnover of core and occasional taxa in the plastisphere also complicates the possibility of precise position-sensitive identification of functions / biochemical roles of microorganisms in the microbial community and in multilayer films of the plastisphere [128]. The spatiotemporal succession of species in a multi-species microbial community, in accordance with the changing environmental conditions (climatic or substrate-dependent, including their transformations during biodegradation of multilayer or multicomponent composites, including laminate fragments and bioplastics reinforced with non-biodegradable components), requires spatiotemporal and cepstral analysis of microbial communities in the plastisphere and their potentials for plastic degradation [129]. In the latter case, both divergent processes and convergent processes can occur in populations or microbial communities during spatiotemporal succession effects and turnover of microbial species [130,131].

For this reason, many authors have recently advocated imaging of microscopic communities on plastic marine debris to establish the spatial structure in the plastisphere [132], and also address this problem from the standpoint of materials scientists analyzing biodegradable plastics, and also postulate the necessity of the numerical description of nano- and microplastics’ surfaces in the plastisphere [133]. Other authors (usually with better technical equipment in the laboratories) suggest not only imaging of the plastisphere samples, but also microanalysis, including local stable-isotope analysis and nanoSIMS single-cell imaging, which reveals soil plastisphere colonizers [134].

Collaborative teams perform the studies of the single samples at the microscopic level and create databases correlating such studies of the microscopic samples with the geographic maps of their localization and metagenomic representations of the evolution of microbial communities. The highest level of skill is considered to be the analysis of the impact of microbial communities from the plastisphere on the results of microplastic absorption by other species of living organisms that differ in dynamic localization and migration maps, biogeographical, and trophic characteristics. As an example of the latter approach, one can consider the latest work on the impacts of microplastics and the associated plastisphere on physiological, biochemical, and genetic expression and gut microbiota of the filter-feeder amphioxus [135]. This trend is expected to be popular in the near future.

7. Novel techniques in the soil plastisphere investigations

Now, let us turn to the soil and the effect of microflora from the soil plastisphere on the biodegradation of plastics in it, since it is the central object of our experimental study. We will also not limit ourselves to bacteria, since the soil fungi also play a significant role in biodegradation. In our early works using lab-on-a-chip or optofluidic sensors with a polymer coating buried in the soil, we have found that during biodegradation, the image quality on the buried sensor changes due to the polymer decomposition or the effect of microorganisms and the environment on it [136–

139]. Later, we tried to study this effect from the standpoint of mass spectrometry (to ensure the “omics approach”) or other localized chemical analysis [140–144], but we made a mistake in the chip design - it turned out that the polymer in hybrid chips is ionized by the laser beam and affects the experimental results. Therefore, it is necessary to create chips that do not contain any other polymers (neither in the form of adhesives, nor in the form of sealants, coloring or protective coatings) if we want to accurately study biodegradation or soil-geochemical degradation of specific polymers in the soil plastisphere.

The soil plastisphere is probably the most well-studied part of the global plastisphere. Optimal research methods have been developed for it, influencing factors and ecological conditions have been identified, complete or almost complete biogeochemical deciphering of the mechanisms shaping the plastisphere microbiota in soil has been performed, the roles of individual species and distributions of different decomposer organisms at the interfaces of abiogenic and bioinert matter (rare and abundant microorganisms between the plastisphere and soils) have been studied [145–147]. Redox processes and the effects of pH on shaping plastisphere bacterial communities in soil have been studied, including their dependence on the content of microelements and chemical contaminants in the soil [148]. In the case of soil, multiple effects of heavy metals and disinfectants on antibiotic resistance genes and virulence factor genes in the plastisphere from diverse soils/ecosystems have also been studied [149,150], not only for microorganisms, but also for the soil mesofauna. In this regard, these effects can be considered the most predictable, in relation to the biogeochemical effects for exotic biotopes, and the soil can be considered a natural laboratory or bio-testing ground for practicing skills in working with ecological, biogeochemical and materials science (biodegradation) aspects of the plastisphere (if we do not take into account such conceptual generalizations like “continental-scale microcosm” [151] which blur the term meaning).

8. Soil plastisphere species and infectious diseases

In specific cases of practical importance specific polymers or polymer composites of the known origin decompose in the soil, either of technogenic (not containing pathogenic microflora) or of anthropogenic genesis (for example, masks and respirators accumulated in the soil during the COVID pandemic, potentially containing bacteria from the human exhalation [152,153], as well as special filters of infectious medical institutions). Porous and fibrous materials, including non-woven ones, are assemblers for the terrestrial plastisphere microbiome [154], but their efficiency strongly depends on the properties of the material, including its porosity [155,156], since the pore sizes must correspond to the sizes of microorganisms and be at least no smaller than them. Non-degradable microplastics from the mulching residues are often found in the soil [157]. In some cases, even potentially biodegradable components will not be able to be decomposed, due to the discrepancy between the size of the possible colony-forming unit and the size of the remaining stable fragment of the polymer or composite [158]. In some cases, fragments of controlled-release fertilizer coatings may also be found in the soil. Despite the progressiveness of the entire approach to controlled-release fertilizer application, may preclude its wide use for agri-

cultural practice, since the environmental consequences may be quite disastrous [159].

9. Future prospects and challenges

In conclusion, we would like to dwell in detail on the methods of studying platisphere and biodegradable microplastics beyond the conventional scanning electron microscopy, which are capable of providing images and data for correlation-spectral analysis, 2D FFT spectral measurements, calculations of integral spatial characteristics (ISCs) and integral frequency characteristics (IFCs). Since the second decade of the twenty-first century is the era of “big data” diagnostics of the state of micro-objects using single microscopy methods no longer satisfy the requirements of multiparametric control and spectral multiplexing in the protocols for identifying the chemical components of (micro)objects [160–162]. To date, the results in the field of analysis of biodegradable microplastics will be obtained within the framework of correlative microscopy and spectroscopy workflow [163].

It can be assumed that the methods for calculating ISC will be used not only for the full electron micrographs, but also for studying spatial distributions of individual elements of pollutants or of the “living matter” of the platisphere during multichannel X-ray mapping using energy-dispersive (EDS) and wavelength-dispersive (WDS) X-ray spectroscopy [163–169], or electron probe microanalysis [170,171], scanning electron microscopy with combined backscattered electron and X-ray imaging (SEM-BEX) [172]. To characterize adhesion and electrostatic charging of the surface of microplastics biodegraded in the platisphere under the action of biological agents, it is also possible to propose surface charge mapping using a technique compatible with scanning electron microscopy [173–177] (as well as the charge of biomolecules at the interface of the plastic and the living biological / biodegradation agent [178]). Correlation spectral analysis can be performed using a two-dimensional Fourier transform and calculation of integral spatial characteristics, correlating the distributions of individual pollutant elements (obtained from EDS, WDS, etc.) and individual charged regions of the biodegradable microplastic sample. We could also focus on correlation techniques for X-ray tomography and neutron tomography of microplastics [179–183], but since these are rather exotic techniques, we will not dwell on them and move on directly to optical microscopy.

In the field of optical microscopy of polymer biodegradation and biodestruction processes, as well as in optical microscopy of microplastics and structures associated with biological weathering in the platisphere, a revolutionary breakthrough in correlative and multiparametric microscopy methods is expected [184–186] (although conventional optical microscopy is not disappearing from the research protocols [187–190], and new methods of microscopic visualization and particle counting of microplastics continue to be developed, approaching the diversity of flow cytometry methods and cell/particle sorting techniques [191–193]).

The following microscopy techniques for microplastics or polymer biodegradation products are expected to be developed rapidly in the near future and will provide the basis for obtaining images that can be correlated and compared using descriptors obtained from a two-dimensional Fourier transform:

1. Hyperspectral microscopy, including dark-field hyperspectral microscopy and AI-based / CNN-based microplastics classification techniques [194–197];
2. Polarized light optical microscopy and polarization-sensitive holographic microscopy [198–200];
3. Fluorescence microscopy techniques [201–204], including:
 - 3.1. Fluorescence lifetime imaging microscopy (FLIM) [205–207]
 - 3.2. Comparative and correlative Raman and fluorescence microscopy [208]
 - 3.3. Correlative fluorescence microscopy and infrared spectroscopy (or microscopy), or correlative fluorescence microscopy and FTIR microscopy [209,210];
4. Conventional infrared microscopy [211,212] or/and FTIR microscopy [213–220];
5. Raman microscopy [221–231], including hyperspectral Raman microscopy [232,233] and multicolor coherent Raman scattering microscopy [234];
6. Confocal laser scanning microscopy [235,236];
7. Atomic force microscopy [237–239] and related correlative techniques such as atomic force microscopy coupled with infrared spectroscopy (AFM-IR) [240,241];
8. Lenless (shadow) microscopy or lenless diffraction imaging and lenless digital holography [242–245];
9. Different types of holographic imaging with microplastic identification (including holographic classification and deep learning) [246–253].

Images of microplastics and active biodegradation agents on them can be correlated, colocalized, processed using machine intelligence, and stored in reference databases/databanks for machine learning and automatic sample identification. All of them can be analyzed and compared in real time using software such as QAVIS (POI FEB RAS), which allows obtaining two-dimensional Fourier spectra and calculating their integral spatial and frequency characteristics in real time during the experiment/measurement process [254–257]. This software and this approach to comparative analysis of multi-channel images are especially convenient for microexperiments that use multi-channel imaging methods (not only hyperspectral microscopy, but also full-Stokes polarized light microscopy [258], multi-angle microscopic or microporometric measurements of polymers [155,156], correlative light and electron microscopy [259–262], etc.).

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