Microplastics in terrestrial ecosystem

Exploring the menace to the soil-plant-microbe interactions

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Microplastics in terrestrial ecosystem: Exploring the menace to the soil-plant-microbe interactions

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ABSTRACT

Microplastics (MPs), miniscule plastic particles measuring less than 5 mm in size, have become a concern in terrestrial ecosystems, with primarily agricultural and wetland soils being the soils with highest plastic loadings. The adverse effect of MPs might lead to changes in physicochemical and biological characteristics of soil including soil properties, microbial communities, plants, as well as the potential or affirmed correlations among them. Therefore, understanding the risks and effects of MPs, particularly within the soil-plant-microbe context is challenging and have become a subject of substantial scientific inquiry. This comprehensive review is focused on the effects of MPs on the rhizosphere and plant-microbe symbiotic relationships, with implications for plant growth and ecosystem-level nutrient fluxes. MPs alter soil physicochemical properties, microbial community composition, and enzymatic activities in the rhizosphere, influencing nutrient availability and uptake by plants. These changes in the rhizosphere can disrupt plant-microbe symbiotic interactions, such as mycorrhizal associations and nitrogen-fixing symbioses, ultimately impacting plant growth and the cycling of nutrients within ecosystems. Furthermore, we elaborate on the effects of MPs on the rhizosphere and plant-microbe symbiotic relationships carrying implications for plant growth and ecosystem-level nutrient fluxes. Future research directions and solutions to the microplastics menace acknowledging combined effects of MPs and other contaminants, advanced technologies for MPs identification and quantification, and microbial engineering for MPs remediation. This knowledge of MPs-induced impacts on soil-plant-microbe interactions is essential to generate mitigating actions in soil environmental management and conservation.

1. Introduction

It is broadly recognized that the terrestrial environment, particularly agricultural and wetland soils, contains the highest loadings of plastic pollution and act both as a source and sink for microplastics (MPs; particle size <5 mm) [1]. Although the majority of current MPs research predominantly concentrates on marine ecosystems, compelling evidence suggests that the prevalence of MPs in soil surpasses that in oceans by a factor of 4–23 times [2]. MPs have infiltrated soil ecosystems through a myriad of sources and pathways, ranging from direct emissions, the fragmentation of larger plastic debris, the disintegration of synthetic textiles, direct deposition from the atmosphere to the transport via water bodies, resulting that wetlands with low velocity of water settle lots of the plastic pollution originating from urban sources. The utilization of plastic-based mulching and biosolids in agricultural settings also causes the introduction of MPs into agricultural practices [3]. Terrestrial environments have thus become an important "sink" for MPs [3]. The concentrations of MPs surpass 18,760 particles/kg in riparian forests

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[4], 4354 items/kg in mangrove wetlands [5], and 78 particles/kg in farmland soils [6] in China. Internationally, MPs were reported in excess of 78 items/kg in UK agricultural soils [7] and 10,782 ± 7671 items/kg in the mangrove wetlands of northern Brazil [8].

Once, entered the soil, MPs exhibit complex interactions with soil particles, pore- and groundwater and organic matter. Adsorption and absorption of MPs by plants, microbes and all living terrestrial organisms may traffic into food chains [3]. Hence, their presence and potential impact on soil health and ecological systems have become a subject of substantial scientific inquiry. Recently, increasing attention has been given to MPs in soils, with particular focus on various aspects such as analytical methodologies [9,10], occurrences and sources [3,10], transport and distribution [11], ecological and environmental risks [12,13] and mitigation techniques [14]. However, there is a notable scarcity of research addressing the interactions between MPs and the soil-plant-microbe system as well as the MPs menace to the terrestrial ecosystems. The soil-plant-microbe system is of paramount importance in terrestrial ecosystems, facilitating vital functions such as organic matter decomposition, soil structure stability, disease suppression and soil nutrient cycling [15]. Following weathering processes, MPs in soil can fragment into smaller particles, ranging from submicrons to nanometers. MPs in the submicron range can penetrate into finer soil pores and adhere to soil particles more readily than larger particles. This can affect their availability to plant roots and soil microorganisms, potentially leading to increased uptake and accumulation within plant tissues. Nanoplastics differ from MPs in various aspects, including transport properties, interactions with light and natural colloids, surface molecular composition, bioavailability, and release kinetics of plastic additives [16]. However, this review mainly focuses on the impact of MPs, particularly at microscale or submicron-sized, on the soil-plant-microbe system.

Reported data suggest that the presence of MPs has an impact on soil characteristics, plant performance and microbial activities [11,13,17,18], but the integrated impacts of MPs on the soil-plant-microbe feedback loops need to be clarified. The most substantial gaps in the existing literature are: i) mechanisms of phytotoxicity, ii) MPs-microbe associations, and iii) soil-plant-microbe interactions. Addressing these issues can enhance our comprehension of the long-term environmental consequences posed by MPs and facilitate the formulation of strategies for mitigative actions. Therefore, this review presents a systematic summary of the interactions of MPs and the soil-plant-microbe system, focusing on the mechanisms underlying the effects of MPs on soil physicochemical properties, terrestrial plants, and the soil microbial community as well as the interactions of MPs and soil-plant-microbe feedback loops. Drawing from these investigations, we make the fragmented results in literature comprehensive and emphasize the existing research gaps and suggest potential directions for future research. Recommendations for future studies include longitudinal studies assessing MP effects on soil health and plant growth, investigating MP fate in diverse soil types and climates, and promoting interdisciplinary research integrating soil science, ecology, and material science for a holistic understanding of MPs in terrestrial ecosystems. Moreover, incorporating MPs considerations into environmental regulations, restricting certain plastic materials, and promoting sustainable alternatives can help mitigate MPs pollution.

2. Impacts of MPs on soil physicochemical properties

The interactions between MPs and soil physicochemical properties encompass a range of complex effects (Fig. 1 and Table 1). In this section, the MPs-induced effects on soil physicochemical properties including soil texture, aggregation, porosity, water retention and permeability, nutrient and elemental availability will be discussed.

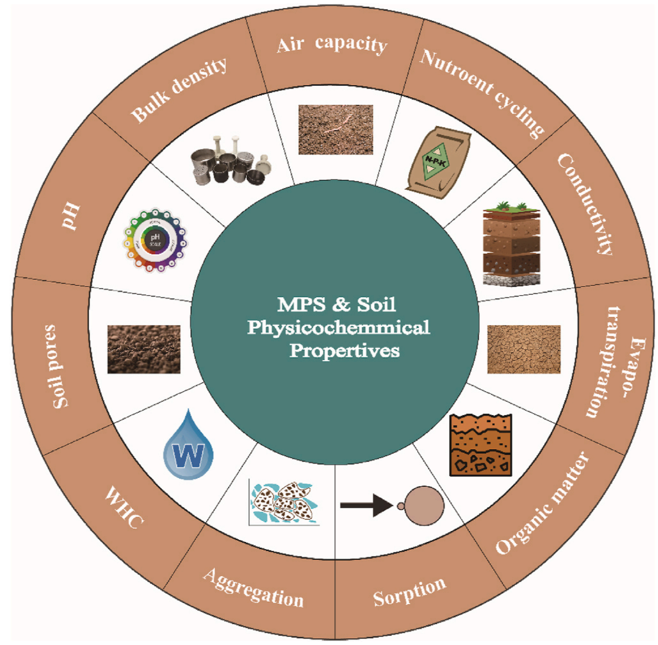

Fig. 1. Interactions between MPs and soil physicochemical properties.

2.1. MPs-induced effects on soil texture

MPs can alter the soil texture by filling up the interstitial spaces between soil particles, reducing the movement of air within the soil. This can result in decreased gas exchange, leading to soil compaction and poor aeration [40]. These effects are dependent on soil types, for instance, sever effects on water stable aggregates and evapotranspiration are more often observed in loamy-sand soil [39]. Moreover, the impact of MPs on soil texture varies based on factors such as concentration, size, shape, and polymer type. For example, soil bulk density decreased and saturated hydraulic conductivity increased with LDPE at concentrations of 1 and 2% w/w, while no significant changes were observed at a concentration of 0.5% w/w [41]. The incorporation of PES fibers and PP granules affected soil physical properties differently, with PES fibers having a more pronounced effect due to their distinct shape compared to soil particles. However, changes in soil properties were gradual, and significant alterations were observed only at higher MPs concentrations, such as 0.5% w/w for polyester fibers and 2% w/w for PP granules [42]. In addition, MPs can alter the soil pH and further affect nutrient availability and affect the performance of plants that are sensitive to soil acidity or alkalinity [43]. For example, the addition of 5% (w/w) LDPE to soil increased the soil pH from 7.4 to 7.7 after 1 h of shaking [44]. Such shifts in soil pH as induced by MPs can interfere with the formation and stability of soil aggregates. Soil aggregates are natural building blocks that give soil its crumbly texture and structural integrity. When MPs are present in soil, they can disrupt the aggregation process. This results in a weaker soil structure that is more susceptible to erosion [45]. The adhesive properties of some MPs also cause soil particles to stick together inappropriately, leading to the formation of unnatural or unstable aggregates. This can disrupt the natural processes of soil formation and reduce soil stability [46].

2.2. MPs-induced effects on soil organic matter

MPs can also interact with soil organic matter, which is a crucial component for soil fertility and structure. The presence of MPs could lead to the formation of novel soil aggregates that might influence organic matter stability and turnover rates. Yan et al. found that PP reacted with soil minerals and humic acid (HA). This process leads to increased soil density and an increased zeta potential of the PP particles

Table 1
The major effects of microplastics on soil physicochemical properties.

MPs	Concentration	Soil type	Impact	Ref.
PET	0.5%w/w	Vertisol, Entisol, Alfisol	Vertisol: Bulk Density (−), Soil Aggregate Stability (+); Entisol: Bulk Density(N), Soil Aggregate Stability (+); Alfisol: Bulk density(N), Soil Aggregate Stability (+)	[19]
PET	0, 0.1, 0.3%w/w	Nitisol	Bulk Density(N), Soil Aggregate Stability (+)	[20]
PET	0.05, 0.1, 0.2, 0.4%w/w	Loamy Sand	Bulk Density (−), Soil Aggregate Stability (−)	[21]
PET	0,0.1,0.3%,1.0%w/w	Clay	Bulk Density (−)	[22]
PA	0,0.4%w/w	Loamy Sand	Soil Aggregate Stability (−)	[23]
PVC	7,28%w/w	Loessial	DOC(+)	[24]
PVC	7,28%w/w	Huangmian soil	DOC(−)	[25]
PES	0.4%w/w	Loamy Sand	Bulk Density (−)	[26]
PES	0,0.1%w/w	Sandy Silt	Soil Aggregate Stability (−)	[27]
PE	0.5,1,2%w/w	Sandy	Bulk Density (−), Porosity (+), Field Capacity (+), Saturated Hydraulic Conductivity (+), Soil Water Repellency (+), Soil pH(N), Aggregate Stability Index(N), Electrical Conductivity(N)	[28]
PE	0,0.1%w/w	Sandy Clay Loam Soil	Soil pH (−), Soil Aggregate Stability (−)	[29]
PE	0.5,1%w/w	/	Water Evaporation Rate(+)	[30]
PE	0.1, 1, 10%w/w	/	Soil pH (−), Soil DOC(+), Soil CEC (−)	[31]
PE	0.5, 1%w/w	/	Evapotranspiration (+)	[32]
PE	0.25, 0.50, 1, 2%w/w	Albic Luvisol	Water Stability (−), Bulk Density (−), Water-holding Capacity (−)	[33]
LDPE	1%w/w	Sandy Soil	Soil pH (+), conductivity (+), C:N ratio (+)	[34]
PLA, PHB, PE, PS	0.2, 2%w/w	Loamy Sand	Siol pH (+,PLA, PHB, 2%), Siol pH (-, PE, PS, 2%), Soil pH(N, PE, PS, PLA, PHB, 0.2%); Soil DOC (+, PLA, PHB); NH_4^+-N, NO_3^--N, available P, Zn and Pb availability (-, PLA, PHB)	[35]
HDPE, PS	0.1, 1, 10%w/w	/	Soil pH (-, HDPE), soil pH(N, PS) DTPA-Extractable Cd (+)	[36]
PE, PLA	0.1, 1, 10%w/w	/	Soil pH (+), DTPA-Extractable Cd (+)	[37]
PE, PP, PET, PVC	0.02, 0.1, 0.2%w/w	Silty-Clay Soil	Soil pH(N), Conductivity(N), Porosity(N), Organic Matter Content(N)	[38]
PA, HDPE	0.25, 0.5, 1, 2%w/w	Loamy Sand	Bulk Density (−), Soil Aggregate Stability (−)	[21]
PP, PS, PA, PET, PET*, HDPE	0.05%, 0.10%, 0.20%, and 0.40% w/w	Loamy Sand	Bulk Density (-, PP、PS、PET、PET*、HDPE) Water Stable Aggregates (-, PS、PA、PET*) Evapotranspiration (+,PS、PA、PET、PET*、HDPE)	[39]

NOTE:/, no information; Polyester (PET); polyethylene terephthalate (PET*); Polyamide (PA); Polyethersulfone (PES); Polypropylene (PP); Polyvinyl chloride (PVC); Polystyrene (PS); Polyethylene (PE); Low Density Polyethylene (LDPE); Low Density Polyethylene (HDPE); Positive effect (+), negative effect (−), no significant effect (N).

[47]. Additionally, the interaction between PP and HA resulted in increased PP surface roughness, accelerating the degree of surface oxidation and enhancing the characteristic signal [48]. Soil organic matter consists of plant and animal residues in various stages of decomposition. MPs can act as physical barriers, impeding the access of soil microorganisms and decomposers to organic matter. This can lead to a slowdown in the decomposition process, resulting in the accumulation of organic matter in the soil. Liu et al. [24] demonstrated that PP significantly enhance the accumulation of organic matter in soil and promote the release of soil nutrients, including dissolved organic nitrogen, carbon, and phosphorus. MPs can interfere with the decomposition of organic matter by altering the microbial community functioning responsible for the breakdown process. For instance, exposure to LDPE MPs significantly reduced the microbial functional genes associated with hemicellulose (*abfA* and *manB*) degradation [49]. Some MPs may serve as substrates for microbial growth, attracting certain microbial species while repelling others and ultimately affect the efficiency of organic matter decomposition [50].

2.3. MPs-induced effects on soil water retention and permeability

The presence of MPs in the soil can affect its permeability and hydraulic conductivity. MPs, particularly the smaller particles, can fill up the soil pores and interstitial spaces, reducing the rate at which water can move through the soil, which is more sever in sandy or in clay-sandy soils [51]. MPs can also effectively bind soil particles, promoting the formation of large soil aggregates and increasing the presence of large soil pores [46]. Experiments testing various PE content (0%, 0.1%, 0.2%, 0.4%, and 0.6%) explored their impact on agricultural soil infiltration. A 0.2% PE content significantly decreased infiltration rate by 11.7% ($p < 0.05$), attributed to MPs accumulation impeding water flow. Exceeding 0.2%, MPs-soil interaction formed macropores, enhancing preferential flow and infiltration [52]. Due to their hydrophobic nature, some MPs can repel water and promote surface runoff as water tends to flow over the surface under these conditions leading to soil erosion and nutrient loss [46]. As a result, the water-holding capacity of a soil may decrease, leading to poor water retention and uneven water distribution in the soil. When water cannot penetrate the soil easily, it can lead to surface runoff, soil erosion, and reduced water availability for plant roots. It has been reported that six microplastics (polyester fibers, polyamide beads, and four fragments: PE, PET, PP and PS) significantly altered soil water cycling and spring onion (*Allium fistulosum*) performance, affecting biomass, elemental composition, and root traits [39]. In addition, extensive plastic film coverage can influence soil water evapotranspiration, exacerbating soil drying and cracking. Experimental findings revealed that soil treated with 2 mm PE exhibited a faster evaporation rate compared to 5 mm or 10 mm PE-treated soil, and the evaporation rate increased with higher PE content [30]. MPs can also interact with plant roots, leading to increased (e.g., polyester (PES)) or decreased (e.g., PA) plant evapotranspiration, thereby affecting the soil moisture content [17].

2.4. MPs-induced effects on nutrient and elemental availability

MPs in the soil ecosystem can significantly influence nutrient and elemental availability. The adsorption of essential nutrients, such as nitrogen, phosphorus, potassium, and other elements, by MPs can lead to diminished nutrient availability for plants and soil microorganisms, potentially impacting their growth and productivity [53]. The binding of nutrients to MPs results in the formation of small nutrient reservoirs, effectively sequestering nutrients on the plastic surfaces and hindering their release back into the soil matrix. This reduces the pool of available nutrients for plant uptake and microbial activity [12]. Research conducted by Brown et al. (2023) and Shi et al. (2022a) demonstrated that

MPs composed of PHBV, PE, and PLA can decrease the bioavailability of soil N [54,55]. However, under specific environmental conditions, including changes in factors like temperature, pH, and moisture, or due to microbial activity, the bound nutrients can gradually be released from the MPs into the soil. This localized nutrient enrichment in the vicinity of the MPs can lead to enhanced nutrient availability for nearby plants and soil microorganisms, potentially fostering plant growth and microbial activity [43]. Such localized nutrient enrichment can be particularly advantageous in nutrient-deficient soils or during specific stages of plant growth. Nevertheless, excessive or uncontrolled nutrient release from MPs may disrupt nutrient distribution in the soil, potentially adversely impacting plant communities and disturbing nutrient cycling processes [18]. Spiking 1% and 5% (w/w) of PE) and PVC in an acid soil revealed that PE promoted the abundance of bacterial families associated with nitrogen fixation, while both PE and PVC inhibited FDAse activity and stimulated urease and acid phosphatase activities [56]. In a study by Liu et al. (2022), the nutrient-acquisition potential of crops and microbes was examined under treatments with PE and PVC at concentrations of 0%, 1%, and 5% (w/w). Higher doses of PE facilitated increased N uptake by roots. In contrast, PVC did not promote microbial decomposition of soil organic matter for N and P acquisition. Instead, PVC induced wheat plants to efficiently acquire available nutrients within a confined root zone [57]. The disruption on nutrient distribution induced by MPs alters nutrient availability, consequently affecting soil microbial activity, plant growth and productivity.

3. Impacts of MPs on terrestrial plants

The effects of MPs on terrestrial plants are mainly described through the aspects of MPs absorption/accumulation/translocation in plants, plants oxidative stress, plant metabolism and growth traits, and plants species interactions (Fig. 2).

3.1. Absorption, accumulation, and translocation of MPs in plants

Once introduced into the soil, MPs exhibit the capacity to be assimilated by plants through their root systems. MPs can adhere to the surfaces of roots, and as the roots grow and explore the soil, and encased or embedded in the root tissues. Plant roots might be capable of actively taking up MPs through endocytosis, a process where the cell membrane engulfs particles and forms vesicles that are transported into the cell [58]. Despite the fact that MPs might encounter challenges in penetrating plants cellulose-rich cell walls due to their high molecular weight or large size [59], it is noteworthy that MPs exhibit an intriguing ability to induce contortions and deformations within these cellular barriers, resulting in the creation of enlarged apertures, thereby facilitating the entry of larger particles [60]. Remarkably, MPs of dimensions less than 2 μm, endowed with mechanical flexibility, can access plant tissues through minor crevices within roots or the apoplast, as well as capitalizing on root senescence, mechanical disruptions, or incursions attributable to subterranean herbivores [61]. Moreover, the aggregation of MPs proximate to root hairs, adhesion to root exteriors, and subsequent occlusion of seed capsule pores potentially curtails the absorption of water and nutrients, inhibits respiratory processes in plants, and

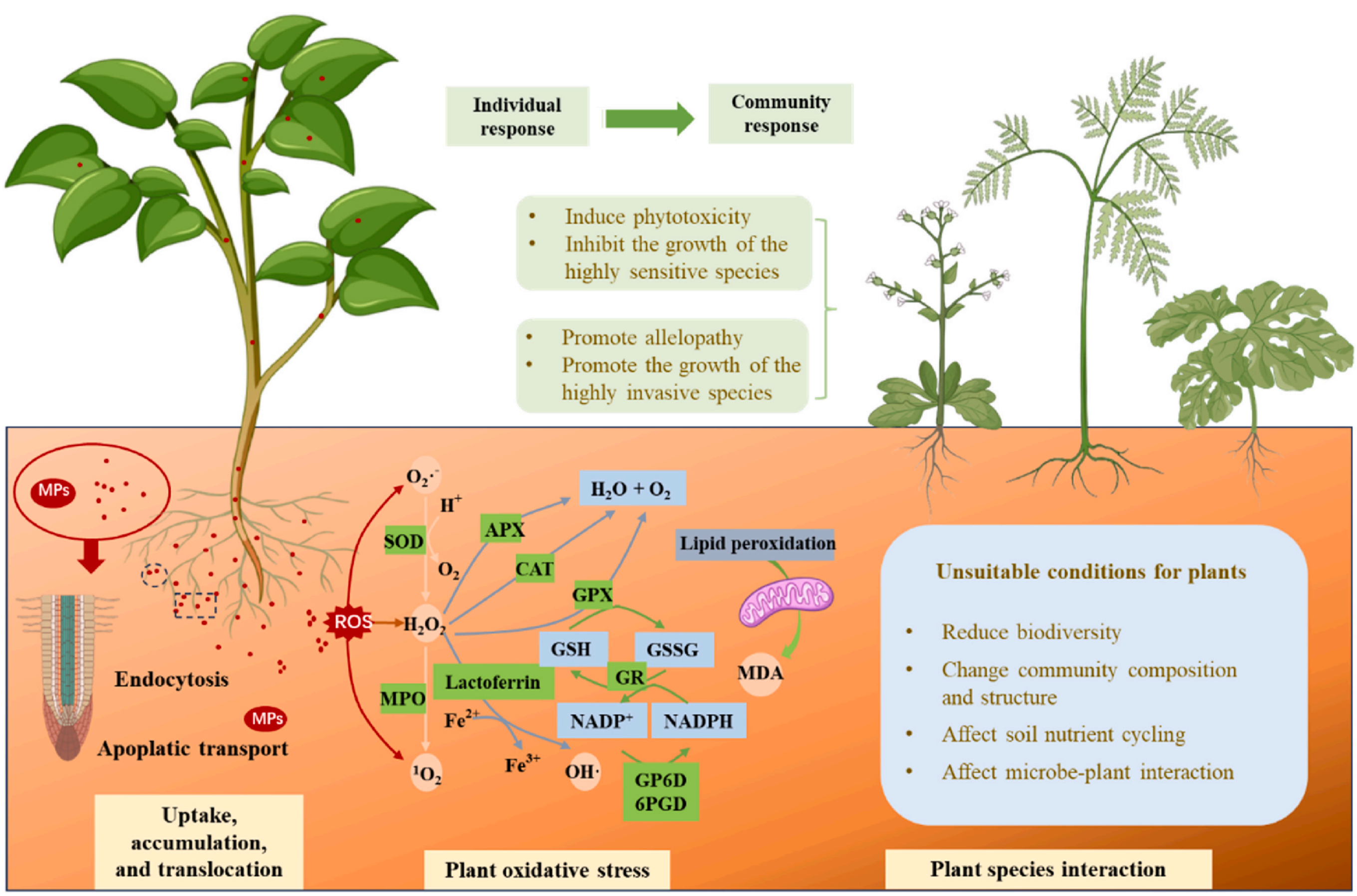

Fig. 2. Impact of MPs on terrestrial plants including individual and community response. ROS for reactive oxygen species; $O_2^{\cdot-}$ for superoxide anions; H_2O_2 for hydrogen peroxide; OH· for hydroxyl radicals; $^1O_2$ for singlet oxygen; CAT for catalase; SOD for superoxide dismutase; APX for ascorbate peroxidases; MDA for malondialdehyde; GPX for glutathione peroxidase; GR for glutathione reductase. GSH for glutathione; GSSG for glutathione disulfide; $NADP^+$/NADPH: nicotinamide adenine dinucleotide phosphate; GP6D: glucose-6-phosphate dehydrogenase; 6PGD: 6-phosphogluconate dehydrogenase.

consequently engenders delays in seed germination and the accrual of both above-ground and subterranean biomass [62].

MPs are amenable to absorption by roots, enabling their transit to higher sections of plants such as the stem, leaf, flower, fruit, and seed. A prominent conduit for the translocation of MPs within plants is the apoplastic pathway. MPs that permeate incomplete Casparian strips during root development can move upwards into aerial parts through the apoplast pathway along vascular bundle cell walls [58]. Noteworthy observations encompass the presence of micro-sized (2 μm) PS microbeads within leaf vasculature, as evidenced by scanning electron microscopy in lettuce and wheat [61]. Recently, using a confocal laser scanning microscope, the presence of 1 μm fluorescently-labeled PS microspheres within the leaf veins of rice plants further confirm that micro-sized plastic particles possess the capacity for upward translocation, traversing from root regions to the higher aerial segments of the plant [63].

The adsorption, accumulation and translocation of MPs within plants can elicit either positive or negative effects, dependent on plant species and the characteristics of the MPs, including their size, shape, surface charge, and chemical composition [64]. The size and shape of MPs significantly influence their absorption and translocation by plants. The smaller MPs, resembling soil particles, may penetrate plant tissues more readily, while irregularly shaped MPs can enhance attachment and interaction with plant surfaces due to their increased surface area [65]. Moreover, the chemical properties of MPs, such as hydrophobicity, surface charge, and functional groups, dictate their interactions with plant tissues. Hydrophobic MPs tend to adhere more strongly to root surfaces, while charged or functionalized MPs may exhibit distinct interactions with plant cell membranes [66].

3.2. Plants oxidative stress in response to MPs

3.2.1. Reactive oxygen species production

Oxidative stress occurs when there's an imbalance between the production of harmful reactive oxygen species (ROS) and the ability of plants to detoxify or repair the damage. Overproduction of ROS due to MPs was detected in several plants: garden cress (*Lepidium sativum*) [67], rice (*Oryza sativa* L.) [68], broad bean (*Vicia faba*) [69], spring barley (*Hordeum vulgare* L.) [70], etc. The intensity of ROS induction is contingent upon variables including MPs composition, dimensions, concentration, and exposure duration. For instance, in lettuce, PE (23 μm at 1 mg/mL) triggered a notable augmentation (25.3%) in H_2O_2 levels in leaves and a parallel increase in roots after two-week exposure [71]. Exposure to MPs can trigger the overproduction of ROS like superoxide anions ($O_2\cdot^-$), hydrogen peroxide (H_2O_2), hydroxyl radicals (OH·), and singlet oxygen ($^1O_2$), resulting in irreversible harm to plant cells [72]. These ROS species predominantly localize within various plant organelles, including chloroplasts, mitochondria, peroxisomes, and the endoplasmic reticulum [11]. Once generated, ROS propagate through cellular compartments, inducing oxidative damage to lipids, proteins, and nucleic acids. MPs induce lipid peroxidation by attacking unsaturated fatty acids in cellular membranes, disrupting membrane integrity [73]. This damage results in the formation of malondialdehyde (MDA) as a byproduct. Elevated levels of MDA are indicative of increased oxidative stress and cellular damage. It has been evidenced that MPs-induced heightened ROS production is often paralleled by an escalation in lipid peroxidation [69]. Moreover, oxidative stress induction or impairment of antioxidant systems is regarded as the primary cause of cellular/genotoxicity. Mechanical contact of MPs with root surfaces and the internalization of smaller fragments in various cellular compartments are believed to contribute to oxidative damage [11]. These small particles oxidize protein molecules, modify amino acids, and disrupt protein structure and function. DNA damage, including strand breaks, base modifications, and DNA adduct formation, occurs due to oxidative stress, leading to genomic instability [74].

3.2.2. Key antioxidant enzymes

The occurrence of plants oxidative stress is related with the activities of key antioxidant enzymes such as superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX) [11]. SOD functions to catalyzes the dismutation of $O_2\cdot^-$ into O_2 and H_2O_2. CAT serves to break down H_2O_2 into water and O_2. POX including ascorbate oxidases (APX) and glutathione peroxidases (GPX), catalyzes the reduction of H_2O_2 and other peroxides, effectively neutralizing these ROS that can cause oxidative damage to plant cells. Additionally, POX plays a crucial role in various physiological processes, including lignin biosynthesis, wound healing, and defense responses against pathogens. The effect of exposure concentration, size and type of MPs on antioxidant enzymes varies across different plants (promotion or inhibition). For instance, 2-week exposure of PE (23 μm at 250 mg/L and 500 mg/L) increased the SOD, CAT and POX content in the root of *Lactuca sativa*, while the increases in CAT and POX content are not significant when the exposure concentration increases to 1000 mg/L [71]. The influence of PS (at a concentration of 140 mg/L) on *Utricularia vulgaris* depended on the MPs size, where 1 μm PS significantly inhibited POX, whilst 2 and 5 μm PS significantly increased SOD, and 5 μm PS significantly decreased CAT [75]. The influence of PS (5-μm at 10, 50 and 100 mg/L) on *Vicia faba* demonstrated significant increases in SOD and POX activities [69]. Conversely, in leaves of *Oryza sativa* L., PS exposure leads to a dose-dependent reduction in SOD activity, which is statistically significant ($p < 0.05$) and varies with PS concentrations (50, 250, and 500 mg/L) [68].

The oxidative stress induced by different types of MPs varies depending on their size, shape, and chemical composition. Studies have shown that smaller MPs tend to penetrate plant tissues more easily, potentially leading to greater oxidative stress compared to larger MPs. When MPs degrade into nano-sized particles, their surface-to-mass ratio increases and gives the particles ability to penetrate directly through lipid membranes [76]. The chemical composition of MPs also plays a crucial role in their impact on oxidative stress in plants. For example, PE have been shown to induce significant oxidative stress in plants due to their hydrophobic nature and slow degradation rate, leading to prolonged exposure [67]. Moreover, the impact on oxidative stress is contingent upon variables including MPs concentration and exposure duration. For instance, in lettuce, PE at 1 mg/mL triggered a notable augmentation (25.3%) in H_2O_2 levels in leaves and a parallel increase in roots after two-week exposure [71].

3.3. MPs-induced effects on plants

3.3.1. Phytotoxicity induced by MPs

MPs have the potential to induce phytotoxicity by perturbing the plant hormone balance, nutrient metabolism, and nutrient uptake. Upon exposure to MPs, plants may upregulate the expression of genes involved in stress perception, signal transduction, and defense responses. These genes encode various proteins, including transcription factors, chaperones, and enzymes, which play crucial roles in mitigating the adverse effects of MPs. Additionally, MPs have the potential to induce phytotoxicity by perturbing the plant hormone balance and nutrient metabolism. MPs-induced alterations in metabolic pathways can lead to a deceleration in the synthesis of plant compounds [77]. Exposure to 2 g/mL PS (5.64 ± 0.07 μm) disrupted redox homeostasis, carbohydrate metabolism, and phytohormone regulatory networks in barley [70], and PS (<50 μm) exposure significantly interfered with metabolic pathways in rice (*Oryza sativa* L.) leaves [68]. At the cellular level, MPs may induce alterations in cell wall composition and thickness, affecting cell integrity and permeability. As discussed in section 3.2, MPs can disrupt cellular membranes, leading to changes in membrane fluidity and ion permeability. Additionally, MPs can generate ROS within plant cells, leading to oxidative damage and cellular dysfunction [11].

The impacts of MPs on plants at the whole-plant level can manifest as reduced growth and productivity and altered physiological functions [77]. The exposure to MPs has been confirmed to significantly alter plants growth traits, encompassing parameters such as biomass, leaf surface area, seed germination and fruit development [58]. Plant responses to MPs are inherently variable, contingent upon the specific attributes of the MPs and the botanical species under consideration. For instance, PVC has been observed to exert pronounced growth inhibition on *Lepidium sativum* in contrast to PE and PP, as manifested in compromised germination rates and diminished plant height [67]. The repercussions of residual starch-based biodegradable plastic film residues on *Triticum aestivum* growth surpassed those of LDPE plastic film residues in terms of biomass and foliar quality [78]. In contrast, experiments with *Allium fistulosum* revealed that PES, PS, high-density polyethylene (HDPE), PET, and PP lead to notable increases in root biomass [17]. Additionally, the impact of MPs on plants varies with concentration, with lower concentrations causing more significant physiological effects. This could result from aggregational responses at higher concentrations, potentially alleviating phytotoxicity [79].

3.3.2. Effects of MPs on plant species interactions

While studies on the effects of MPs on plants have primarily focused on population-level impacts, few experimental findings show effects on complex plant communities [80]. Beyond individual plant effects, MPs also exert substantial influence on plant-plant interactions, intraspecific clustering, and community structure. For instance, MPs-induced modifications in soil structure promoted the proliferation of drought-tolerant plant species [81]. Moreover, MPs can reshape the plant community composition by bolstering the growth of invasive species like *Calamagrostis* that has encroached upon several significant semi-natural steppes in central Europe, culminating in a decline in the biodiversity of steppe plant communities [26]. MPs also exert an impact on plant communities through allelopathic interactions. Allelopathy entails the alteration of plant growth, development, and metabolism via compounds secreted by plants, ultimately influencing biomass. Within a plant community comprising seven distinct species, the introduction of MPs led to diminished growth in *Festuca*, while concurrently fostering heightened growth in *Hieracium*, a genus known for its allelopathic potential to inhibit neighboring species germination and growth [26]. However, MPs tolerance in certain plants could lead to increased biomass due to resource competition within the community, offsetting negative community-level impacts [80]. Given potential effects of MPs on plant species dominance and community structure, it is imperative that future research prioritize the investigation of cascade effects on ecosystem functions.

4. Impacts of MPs on soil microorganisms

MPs engage in complex interactions with soil microorganisms (Fig. 3). In this section, we will elaborate on the biofilm formation on MPs surface, MPs toxicity on soil microorganisms and microbial community, and microbial degradation of MPs.

4.1. MPs as microbial habitats and biofilm formation

4.1.1. Microbial colonization on MPs surface

Various microorganisms, including bacteria, fungi, algae, and protozoa, can colonize and form biofilms on MPs surfaces. MPs can serve as microbial habitats in the environment, offering a unique environment for microbial colonization due to their high surface area and large numbers of attachment sites for strains to be attached. Initially, cells and extracellular DNA (eDNA) undergo a reversible attachment to the surface of MPs through weak interactions like van der Waals forces, electrostatic forces, hydrophobic interactions, and hydrogen bonding [82]. The molecular-specific interactions involving the outer membrane, flagella, pili, and proteins then lead to a stronger and irreversible adhesion [82]. Within a short period, microbial cells form multilayered clusters on MPs surfaces, aided by threadlike extracellular polymeric substances (EPSs) composed of exopolysaccharides, amyloid-like proteins, lipids, and humic substances [83]. EPSs, rich in functional groups, serve as effective adhesives by offering abundant adsorption sites for cells and eDNA. This adhesion is facilitated through electron-supply receptor action, hydrogen bonding, and ligand exchange mechanisms [84]. EPSs also support microbial survival through quorum sensing and serve critical roles in nutrient adsorption and cellular protection, facilitating close attachment to the MPs surface [85]. Continuous attachment and metabolic processes result in the development of mature biofilm networks on MPs. At the mature stage, new cell and eDNA adhesion persist due to cell division and stable biofilm is formed.

The biofilm formation on MPs can alter the composition and the alpha diversity (richness, evenness, and diversity) of microbial community. Studies have shown that biofilms on MPs can harbor distinct microbial communities, where significantly higher abundances of *Pirellulaceae*, *Phycisphaerales*, *Cyclobacteriaceae*, and *Roseococcus* were observed in the biofilms formed on PE and PP [86]. Moreover, biofilm formation on MPs can influence microbial activity and function. The biofilm matrix provides a protective environment for microorganisms, facilitating metabolic interactions, resource sharing, and niche differentiation within the microbial community. This unique habitat offered by MPs alters microbial functions, potentially influencing the ecological roles of microbial communities. Specifically, pathways related to amino acid metabolism and metabolism of cofactors and vitamins have been found to be increased in biofilms formed on MPs, reflecting adaptations of microbial metabolism to MP-associated substrates and nutrients [86].

4.1.2. Implications of the microplastisphere

MPs acting as a microbial habitat influence soil microbial communities by providing a substrate for colonization and growth, altering community composition, diversity and abundance [87]. The presence of biofilms on MPs can have positive as well as negative implications. On the one hand, biofilm formation on MPs can yield beneficial effects, as the robust structure of the biofilm offers physical support and protection against external mechanical damage during the transportation of MPs [88]. Additionally, it enhances the biodegradation of the plastic due to the enzymatic activities of specific microorganisms within the biofilm that facilitate the breakdown of polymer chains (microbial-assisted plastic degradation) [89]. Moreover, the biofilm serves as a nutrient reservoir, favoring certain taxa that utilizing MPs as a carbon source, which can further contribute to the degradation process [90]. On the other hand, MPs can function as carriers for pollutants, facilitating their transport and accumulation in soil environments, and impeding microbial communities' capacity to degrade pollutants [91]. These changes can disrupt microbial functioning, affecting nutrient cycling, organic matter decomposition, and pollutant degradation processes.

MPs may play a role in the spread and deposition of microbial diseases as the plastisphere constitute a potential distinct habitat for pathogens, such as *Vibrio parahaemolyticus*, *Escherichia Shigella*, *Stenotrophomonas maltophilia* and *Bacillus cereus* [92,93]. The microplastisphere also facilitate early enrichment of antibiotic resistance genes (ARGs) through the primary attachment of antibiotic-resistant bacteria (ARB) carrying intracellular ARGs (iARGs) and initial adsorption of extracellular ARGs (eARGs). ARB (e.g. *Vibrio* spp., *Pseudomonas mendocina* and *Pseudomonas monteilii*) with higher density and closer adhesion have been observed in the plastisphere [94]. The transmission of ARGs is closely associated with bacterial growth through horizontal gene transfer (HGT) mechanisms, including conjugation, transformation, and transduction [88]. Higher ARG abundance were found on plastisphere of MPs compared to natural substrates like quartz sand [95]. Biofilms containing sulfonamide resistance genes (*sul 1* and *sul 2*) and the associated mobile genetic element (*intI 1*) were also found to be formed on both PE and PS [96]. Furthermore, larger and highly weathered MPs, as well as those in soil after prolonged vegetable cultivation, have a propensity to adsorb more hydrophobic antibiotics, potentially contributing to increased ARG abundance associated with

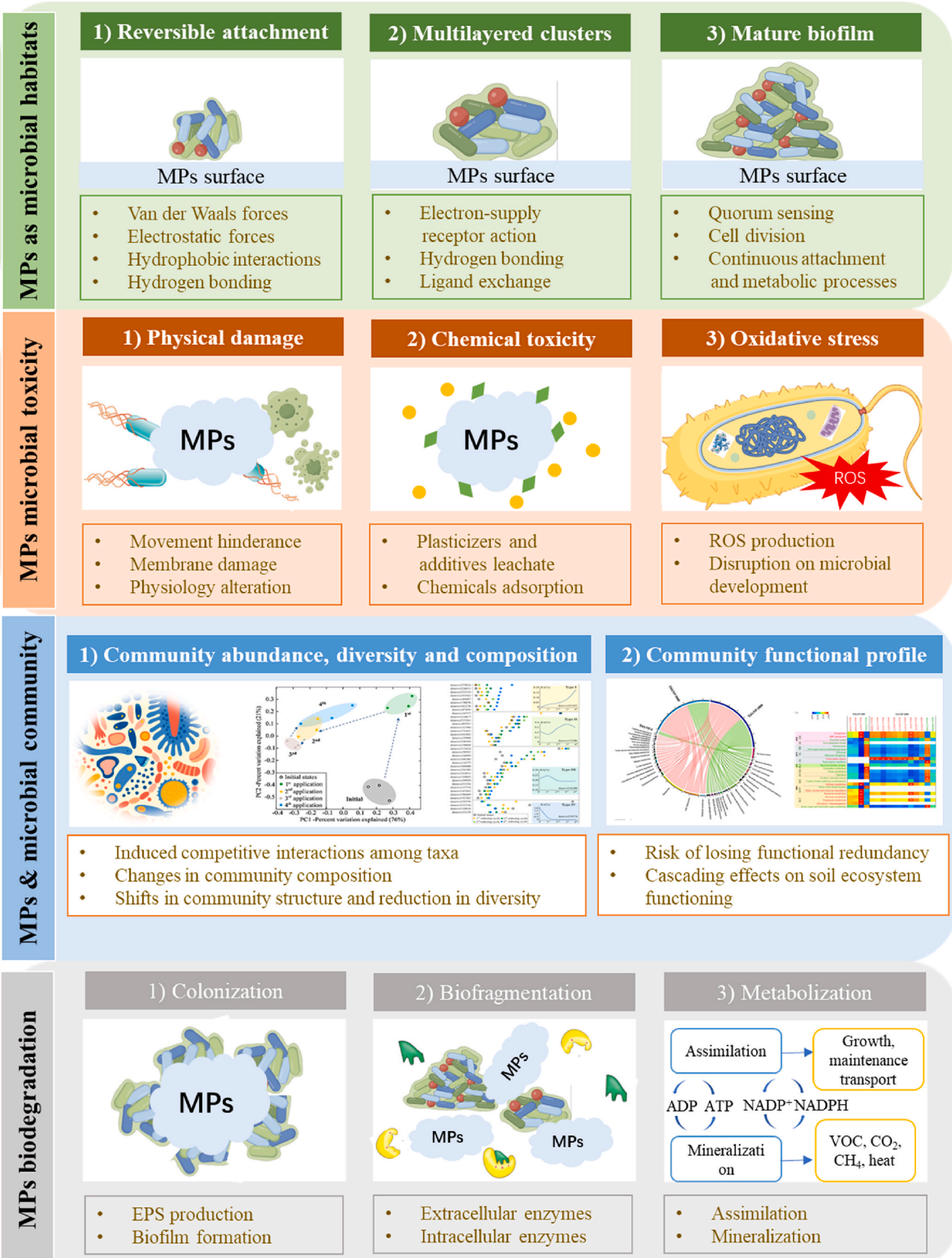

Fig. 3. Interactions between MPs and soil microorganisms. (A) Microbial colonization and biofilm formation on MPs surface; (B) toxicity of MPs on microorganisms; (C) impact of MPs on soil microbial community, (D) microbial degradation process of MPs.

antibiotic resistance in MPs [97].

4.2. Toxicity of MPs to soil microorganisms

4.2.1. Physical effects of MPs on microorganisms

The physical effects of MPs on microorganisms can have significant implications for their survival and functioning. The small size and irregular shape of MPs can result in physical interactions with microorganisms at the cellular level. MPs hinder the movement of motile microorganisms by impeding their motility. Microorganisms lack a rigid cell wall are particularly vulnerable to the hindrance caused by MPs due to their rapid movement and cell membrane fluidity. This can disrupt the normal behavior and ecological interactions of motile microorganisms in the environment [98]. In addition, MPs can come into direct contact with the cell membranes of microorganisms. The sharp edges and abrasive surfaces of MPs cause physical damage to the cell membrane, leading to breaches and leakage of cellular contents. This damage can compromise the integrity and stability of the cell, affecting its overall health and viability [99]. The sharpness and roughness of microfragments could induce cellular damage by physical means [100]. Even without causing immediate cell lysis, MPs can exert physical stress on microorganisms, leading to sublethal effects, including cell morphology, cellular physiology alteration and growth reduction [98].

4.2.2. Chemical toxicity of MPs on microorganisms

The chemical toxicity of MPs can pose significant risks to microorganisms in the surrounding environment. MPs are not chemically inert; they can contain a range of additives, plasticizers, and other chemicals that were either intentionally added during manufacturing or absorbed from the environment [101]. When MPs are present in soil habitats, these chemicals can leach into the surrounding environment, leading to potential toxic effects on microorganisms [102]. The chemicals leached from MPs can inhibit the growth and reproduction of microorganisms. Certain additives and plasticizers may disrupt cellular processes critical for microbial proliferation, leading to reduced population sizes [103]. HDPE and PVC leachate containing MPs exhibited inhibitory effects on the growth of the *Prochlorococcus* and reduced photosynthesis in *Isochrysis galbana* and *Skeletonema costatum*, and the extent of these effects was negatively correlated with the concentration of MPs in the leachate [104,105]. Chemicals released from MPs can interfere with microbial metabolic pathways. This interference may affect energy production, nutrient utilization, and biosynthesis, causing metabolic disturbances and alter microbial functioning [106]. MPs was found to inhibit the metabolic activity of intestinal flora based on the reduced production of short chain fatty acids. These effects were mainly contributed by the release of phthalates. *Acidaminococcus* and *Morganella* were simultaneously correlated to the release of phthalates (PAEs) and the inhibition of metabolic activity of intestinal microbiota and can be used as indicators for the intestinal exposure of MPs and additives [103].

The presence of MPs can trigger the production of ROS in microorganisms, leading to oxidative stress and potential cellular damage [107]. Oxidative stress occurs when ROS levels overwhelm the natural cellular defense mechanisms, leading to damage of lipids, proteins, and DNA [108]. Oxidative stress-induced damage to cellular components can impair microorganism's essential functions, disrupting normal cellular metabolism and compromising overall cellular health. Prolonged exposure to ROS induced by MPs can result in reduced microbial growth and viability. High levels of oxidative stress can lead to cell death and decreased microbial population sizes [72]. Exposure to MPs, especially small-sized particles, has been observed to exert significant cell pressure and cause cell membrane damage in microorganisms. This phenomenon can be attributed to the high specific surface area of smaller MPs, which increases their potential contact area with microbial cells. As a result, a larger proportion of active groups on the MPs surface can interact with microbial cells, leading to the catalysis of ROS production and activation of signaling pathways associated with inflammation and apoptosis [76].

4.3. MPs-induced effects on soil microbial community

4.3.1. Soil microbial community structure and diversity alterations induced by MPs

MPs have the potential to accumulate in specific soil regions, leading to localized effects on the microbial community. They can significantly influence the abundance and composition of soil microorganisms, causing shifts in the overall community structure. The responses of different microbial taxa to MPs exposure can vary based on factors such as their morphology, physiology, and ecological niche. Certain microorganisms may thrive in MPs-rich environments due to their adaptability for attachment and growth, while others may experience stress and reduced fitness, leading to declines in their abundance or activity. For instance, compostable plastic micro-films composed of polycaprolactone (PCL), polybutylene adipate terephthalate (PBAT), polyhydroxyalkanoate (PHA), polylactic acid (PLA), and various starch-based biopolymers have been shown to increase the abundance of specific fungal genera such as *Aspergillus*, *Fusarium*, and *Penicillium* [109,110]. Conversely, PLA have been observed to have adverse effects on arbuscular mycorrhizal fungi (AMF) diversity and community composition, possibly due to chemical toxicity after biodegradation [37]. Studies focusing on different types of MPs powders have demonstrated that PVC had the most substantial effects on bacterial communities, with the relative abundance of Desulfobacteraceae and Desulfobulbaceae increased, while Chromatiaceae and Sedimenticolaceae were decreased [111]. The presence of MPs can lead to competitive interactions among microbial taxa, as certain microorganisms may outcompete others for MPs attachment sites or available nutrients, thereby altering community dominance. MPs-induced stressors may result in reductions in the abundance of sensitive microorganisms, potentially disrupting the balance of microbial interactions and reducing overall community diversity in the soil ecosystem.

4.3.2. MPs-induced soil microbial community functioning

The reduction in microbial diversity induced by MPs can have profound implications for the soil microbial community functioning. The relationship between microbial diversity and functional diversity in the soil ecosystem is intricately connected and plays a vital role in maintaining ecosystem stability. A diverse microbial community harbors a broad spectrum of metabolic capabilities, enabling efficient resource utilization, nutrient cycling, and organic matter decomposition [112]. However, the reduction in microbial diversity caused by MPs can lead to the risk of losing functional redundancy. MPs may adsorb and concentrate certain organic and inorganic compounds, affecting their availability to microorganisms. This can lead to changes in microbial nutrient uptake and metabolism, potentially disrupting nutrient cycling processes in the soil ecosystem. In a study conducted in farmland ecosystems, the presence of PE and PVC was found to have significant effects on soil nitrogen cycling. These MPs influenced essential nitrogen functional microorganisms and related enzymatic activities, suggesting potential disruptions in the nitrogen cycling process [113]. Furthermore, the addition of PVC was observed to decrease the abundance of essential metabolic function genes, such as those involved in carbohydrate metabolism, a crucial process in the soil carbon cycle [114]. Consequently, these changes in soil microbial community functioning can lead to shifts in soil ecosystem dynamics, reduced nutrient cycling efficiency, and alterations in plant-microbe interactions.

4.4. Microbial degradation of MPs

4.4.1. MPs-induced microbial degradation processes

Microbial degradation of MPs refers to the process by which microorganisms, such as bacteria and fungi, break down and biodegrade MPs particles in the environment. Studies have identified several microbial species capable of degrading specific types of MPs. For instance, *Pseudomonas citronellolis*, *Pseudomonas putida*, *Bacillus fexus*, *Aspergillus* sp., and *Phanerochaete chrysosporium* were identified as effective degraders of PVC [115]. *Ideonella sakaiensis* and *Streptomyces* scabies are capable to biodegrade the amorphous PET by utilizing two hydrolytic enzymes (PET hydrolase and mono (2-hydroxyethyl) terephthalate hydrolase) [116,117]. *Bacillus cereus*, *Phanerochaete chrysosporium*, and *Trametes versicolor* were found to degrade PE, and *Rhodococcus* sp., *Sphingobacterium* sp., *Vibrio* sp., *Xanthomonas* sp., and *Pseudomonas* sp., demonstrated proficiency in degrading PS and PP [118,119]. Moreover, fungi have also shown promise as efficient degraders of various types of MPs. Fungal species, including *Phormidium lucidum* and *Oscillatoria subbrevis*, exhibited high efficiency in the degradation of LDPE [120]. *Scenedesmus dimorphus*, *Navicula pupula*, and *Anabaena spiroides* have been involved in the biodegradation of HDPE and LDPE [121]. Algae are also under close attention for their biodegradation ability of plastics, where some microalgae can use MPs as carbon sources for their growth. Additionally, certain algal species, such as *Anabaena spiroides*, *Scenedesmus dimorphus*, *Navicula pupula*, and *Spirulina* sp., have demonstrated the ability to biodegrade PE, PET, and PP [122]. The discovery of these microorganisms to degrade various types of MPs presents promising opportunities for developing eco-friendly strategies to combat the pervasive issue of MPs pollution in the environment.

The degradation of MPs by microbes occurs through a combination of physical, chemical, and biological mechanisms. MPs in the environment provide a surface for microbial attachment and colonization. The biofilm formation on MPs due to the microbial EPS production facilitates the enzymatic degradation process [15]. Several microbial enzymes are known to be capable of degrading polymers into monomers. Phenylacetaldehyde dehydrogenase, styrene monooxygenase, styrene-oxide isomerase, and serine hydrolase have been linked to MPs breakdown, with acetyl-CoA serving as the last monomer in the tricarboxylic acid (TCA) cycle [89]. Both extracellular and intracellular enzymes play an important role in the cleavage of MPs particles. Microorganisms capable of degrading MPs first produce specific extracellular enzymes, targeting the polymer chains of MPs by using an exogenous carbon reservoir to break down MPs polymers into smaller fragments such as oligomers, dimers and monomers [123]. Once the MPs are cleaved into small molecules by extracellular enzymes, intracellular degradation engages the breakdown of stored endogenous carbon by accumulating several microorganisms itself [124]. After the enzymatic hydrolysis, the microbial cells can take up the degraded products and utilize them as carbon and energy sources for growth and metabolism [90]. Some microorganisms are more efficient in assimilating the breakdown products, while others may leave behind smaller plastic fragments in the environment, leading to the fragmentation of MPs into even smaller particles. Over time, repeated degradation and fragmentation processes can further reduce the MPs size.

4.4.2. Microbial degradation of MPs under anoxic conditions

In addition to aerobic degradation, MPs degradation under anoxic conditions, characterized by limited oxygen levels or even the absence of oxygen, is also a subject of growing interest in diverse environments [125]. An investigation into bacterial colonization dynamics in anoxic sediment revealed distinct microbial communities associated with different MPs types, with PVC recruiting a unique community enriched in sulfate-reducing bacteria [87]. While anoxic degradation rates generally lag behind aerobic degradation rates, anoxic microorganisms exhibit potential in degrading specific MPs types. For instance, the facultative anaerobic bacterium *Shewanella oneidensis*, prevalent in alternating anoxic-oxic regions, has been observed to generate hydroxyl radicals (·OH) during such conditions, contributing to the MPs degradation [126]. Chen et al. provided evidence for degradation of PS under different anoxic/oxic conditions in sediments by setting up pure-culture experiment inoculating the S. oneidensis strain MR-1 [127]. Degradative enzymes, including thiol peroxidase (*tpx*), alkyl hydroperoxide reductase C (*ahpC*) and bacterioferritin comigratory protein (*bcp*) and changes in lipid A and biofilm-associated proteins have been implicated in MPs biodegradation under anoxic conditions [128]. The comprehension of anaerobic MPs degradation remains dynamic, necessitating further investigations into specific metabolic pathways and enzymes involved to develop effective and sustainable solutions for MPs pollution mitigation in diverse environments.

4.4.3. MPs degradation driven by environmental factors

Environmental factors such as temperature, pH, and humidity exert significant control over the microbial degradation of MPs in terrestrial environments, impacting degradation efficiency and kinetics [129]. Elevated temperatures generally enhance microbial degradation by accelerating enzymatic reactions and microbial growth rates. Studies have indicated that higher temperatures promote MP degradation by stimulating microbial enzymatic activity and facilitating the assimilation of carbon derived from MPs by microorganisms [130]. Soil pH is also a critical determinant, as variations can alter the electrostatic interactions between plastics and contaminants, influencing sorption behavior. Alkaline environments often exhibit reduced adsorption behavior of plastics, while acidic or neutral conditions tend to favor adsorption [131]. Humidity levels can also affect the microbial degradation of MPs, particularly in terrestrial environments. Moisture availability influences microbial growth, activity, and biofilm formation on MP surfaces. Furthermore, humidity levels influence microbial activity and biofilm formation on MP surfaces, with adequate moisture enhancing degradation processes. However, excessively dry or waterlogged conditions can inhibit microbial activity, limiting nutrient availability and impeding MP degradation [132]. Additionally, environmental conditions such as nutrient availability, oxygen levels, and organic matter content can also influence MPs degradation processes by modulating microbial metabolism and community dynamics [129].

4.4.4. Microbial-mediated MPs bioremediation

Microbial degradation stands as a practical, environmentally sound, and economically feasible strategy for MPs remediation, leveraging natural microbial processes to decompose and detoxify plastic waste [133]. In contrast to conventional approaches like mechanical extraction or incineration, microbial degradation avoids the creation of secondary pollutants and ecological disruption. Moreover, its ability to target MPs directly in situ offers a non-invasive remediation option without requiring extensive infrastructure [134]. However, the effectiveness and efficiency of employing microorganisms for MPs remediation in real-world scenarios are influenced by various factors. Although certain microorganisms have demonstrated MPs degradation capabilities under laboratory conditions, their performance in complex environmental matrices remains incompletely understood. The rate of MP degradation by microorganisms may be slow, requiring extended treatment times to achieve significant reductions in MP pollution levels [135]. While microbial degradation holds promise as a potential strategy for addressing MPs pollution, its practical application in real-world scenarios requires further consideration of various technical, economic, and ecological factors.

5. Impacts of MPs on soil-plant-microbe interactions

As MPs function as both microenvironments for microbes and vectors for the transport of contaminants, their presence may mediate the transfer of harmful substances within soil-plant-microbe system, thus affecting the health and functional dynamics of terrestrial ecosystems. Effects of MPs on plant-microbe symbiotic relationships encompass shifts in mycorrhizal associations and nitrogen-fixing bacterial communities, carrying implications for plant growth and ecosystem-level nutrient fluxes (Fig. 4 and Table 2).

5.1. Rhizosphere-MPs interactions

The rhizosphere is the region of soil surrounding plant roots, where

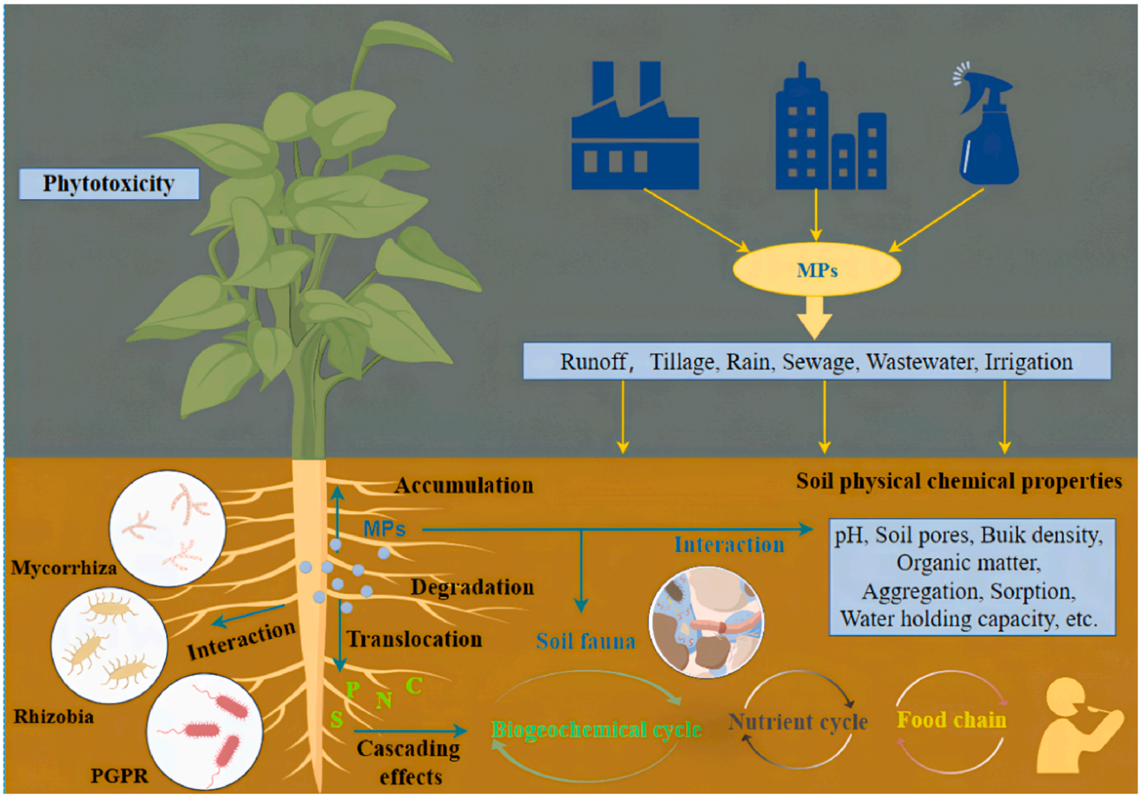

Fig. 4. Impacts of MPs on the soil-plant-microbe interaction.

complex interactions occur between plants and microorganisms. MPs can interfere with the rhizosphere ecology, affecting nutrient availability, water movement, and microbial colonization. Root exudates (i.e. plant-derived primary and secondary metabolites) and soil organisms (e.g., bacteria, archaea, fungi, arthropods, nematodes, and earthworms) stand as primary drivers of rhizosphere processes [13]. MPs have been observed adhering to plant roots at the soil-root interface, impeding nutrient uptake and altering rhizosphere composition and characteristics [139]. Bioturbation by soil organisms, notably anecic earthworms and collembola, also contributes to MPs vertical and horizontal transport within soil profiles up to several centimeters [140]. Moreover, the uptake and transformation of nutrients by plant roots are slowed by MPs, resulting in declines in biomass and microbial activity and changes in the composition and rhizosphere characteristics [141]. For instance, PES microfiber notably amplifies the presence of AMF structures like hyphae, arbuscules, and coils within the rhizosphere. These effects are potentially tied to modifications in soil structure and water dynamics caused by PES [17].

The microbial communities within the rhizosphere exhibit dynamic responses to MPs, leading to alterations in microbial diversity, activity, and functionality. Investigations assessing the impact of LDPE and PLA on the rhizosphere bacterial communities of *Phaseolus vulgaris* at concentrations of 0.5%, 1.0%, and 2.5% (w/w) revealed shifts in microbial community composition. Specifically, the abundance of *Comamonadaceae* was elevated across all MP treatments, while *Rhizobiaceae* demonstrated the highest abundance in the 2.5% LDPE treatment and the lowest in the 2.5% PLA treatment [142]. Additionally, microbial activity in the rhizosphere can be influenced by MPs, resulting in changes observed in enzymatic activities associated with nutrient cycling and organic matter decomposition. For instance, three types of microplastics (PE, PVC, and PS) at a concentration of 2% and a particle size of 200 μm were investigated for their impact on wheat rhizosphere bacterial communities. Exposure to PS decreased most functional category levels, while PE and PVC enhanced certain functional categories, with PVC showing improvements in xenobiotics biodegradation and metabolism [143]. The changes in functionality of microbial communities potentially lead to disruptions in essential ecosystem processes such as nutrient cycling and plant-microbe interactions. For instance, starch-based biodegradable plastics elicit alterations in rhizosphere microbial constituents, promoting heightened abundance of *Bacillus* and *Variovorax* while simultaneously stimulating the production of volatile compounds such as dodecanal. These volatile compounds, in turn, might influence plant growth patterns [78]. In essence, the interplay between MPs and the rhizosphere constitutes a complex phenomenon that intricately weaves together plant physiology, microbial ecology, and soil processes.

5.2. MPs-induced effects on plant-microbe symbiosis

5.2.1. MPs-induced effects on mycorrhizal fungi

MPs can have significant impacts on symbiotic relationships between microbes and plants, disrupting the delicate balance that supports plant growth and ecosystem functioning. Plants form beneficial symbiotic relationships with various microorganisms, such as mycorrhizal fungi, plant growth-promoting rhizobacteria (PGPR). MPs can interfere with the establishment and functioning of these symbiotic associations, leading to reduced nutrient uptake and nitrogen fixation for plants. Mycorrhizal fungi, forming symbiotic partnerships with plants, play a pivotal role in nutrient uptake facilitation and plant health promotion [144]. Nevertheless, the introduction of MPs into soil matrices can elicit both direct and indirect repercussions on mycorrhizal fungi. MPs may serve as physical barriers, impeding the hyphal extension of mycorrhizal fungi and constricting their nutrient accessibility in the soil [145]. Additionally, MPs can adsorb essential nutrients, leading to diminished nutrient availability for mycorrhizal fungi, thereby compromising their nutrient acquisition efficacy and support for plant nutrient uptake [145]. Moreover, MPs can engender alterations in the composition and abundance of the soil microbial community, including mycorrhizal

Table 2
The effects of MPs on soil-plant-microbe interaction.

MPs	Concentration	Plant species	Soil type	Impact	Ref.
PA, PEHD, PES, PET, PP, PS	PES: 0.2% w/w; PA, PEHD, PET, PP, PS: 2.0% w/w	Spring onion (*Allium fistulosum*)	Loamy sandy soil	**Soil environment:** Soil density (-, Bulk soil, PEHD, PES, PET, PP, and PS; +, Rhizosphere, PEHD, PES, PET, PP, and PS); Water stable aggregates (+, Rhizosphere, PA, PES, PET, and PP); Evapotranspiration (+, PES; -, PA); Water availability (-, plant-MPs interaction); Microbial metabolic activity (-, plant-MPs (PA, PEHD, and PET)); **Root traits:** Total root length (+); Root average diameter (−); Total root area (+); **Leaf traits and total biomass:** Dry biomass (-, PA; +, PES); Total biomass (+, PA; +, PES); Water content of plant (+, PA; -, PES, PET, PP); Leaf nitrogen content (+, PA, -, PES).	[17]
LDPE; starch-based biodegradable plastic (Bio)	1% w/w	Wheat (*Triticum aestivum*)	Sandy soil from the agricultural land	**Plant development:** Plant height (N, Bio; N, LDPE); Tillers (-, Bio; N, LDPE); fruits (N, Bio; N, LDPE); **Plant biomass** (-, Bio; -, LDPE); **Vegetative growth:** Leaf area (-, Bio; N, LDPE); Number of leaves (-, Bio; N, LDPE); Relative chlorophyll content (N, Bio; N, LDPE); Stem diameter (-, Bio; N, LDPE).	[78]
HDPE, PS, PLA	0, 1% and 10% w/w	Peanut (variety Luhua no. 8)	Farmland soil	**Soil nutrients:** Soil NO_3^--N (-,10% PS, 1%, 10% PLA; +,1% PS, 1%, 10% HDPE) (-, 10% HDPE); Soil NH_4^+-N content (+, 1%, 10% HDPE, 1% PS; -, 10% PS, 1%, 10% PLA); **Soil enzyme activity:** Urease (-, 10%HDPE; +10% PLA); FDAse (+, 10% HDPE; −1% PS); **Soil N-fixing bacterial communities:** Shannon index (+, 1% HDPE; -, 1% PS); Simpson index (-, 1% HDPE; +, 1% PS); ACE and Chao indices (+, 1% HDPE; -, 10% PLA); **Plant traits:** Shoot biomass (N); Root biomass (+, 1%, 10% HDPE); Plant height (+, 1%, 10% PS and PLA); Shoot N content (-, 10% PS and 1%, 10% PLA); Root N content (-, 10% PS and PLA); Chlorophyll *a* (+, 1%, 10% PLA).	[136]
HDPE, PLA	0, 0.1%, 1% and 10% w/w	Maize (*Zea mays* L. var. Wannuoyihao)	Vegetable farmland soil	**Biomass** (+, 10%HDPE, 0.1%, 1% PLA; -, 10% PLA); **Shoot/root ratio of Zn concentration in plant** (-, 1% HDPE, 0.1%, 1%, 10% PLA); **Soil** pH (+, 0.1%, 10% HDPE, 10% PLA; -, 1% PLA)	[137]
PS, PVC, PP and PE	1% w/w	*Bacopa* sp.	Soil	**Soil properties:** soil organic matter (+, PE, PP, PS; N); TP (-, PVC, PS); TN (-, PP, PVC, PS); K (-, PE, PP); pH (N); **Soil enzymatic activities:** Sucrase activity (-, PS, PVC, PE, PP); Urease activity (-, PP; +, PS, PVC); Catalase activity (-, PP, PE); **Bacterial communities:** Shannon index (-, PS, PP, PE); Chao index (-, PS, PP, PE); **Plant traits:** Germination (-, PS, PVC, PP and PE); Fresh weight (-, PS, PVC, PP, PE); Plant height (-, PVC, PP, PE); Starch content (+, PVC, PE); MDA (+, PVC); POD (+, PS, PVC, PP, PE); CAT (-, PS); APX (+, PP).	[138]

fungi, potentially perturbing their competitive dynamics and functional proficiency [146]. The establishment and maintenance of symbiotic associations between mycorrhizal fungi and plant roots may also be affected by MPs-induced shifts in microbial communities and nutrient availability.

5.2.2. *MPs-induced effects on PGPR*

The presence of MPs in the soil-plant-microbe system can exert substantial implications for PGPR, such as nitrogen-fixing bacteria and the associated nitrogen cycling processes. Nitrogen-fixing bacteria, particularly rhizobia engaging in symbiotic interactions with specific plant species, play a pivotal role in the conversion of atmospheric nitrogen into utilizable forms for plants [147]. However, the impact of MPs on these bacteria involves multifaceted mechanisms. Firstly, MPs restrict the mobility and establishment of PGPR in the proximity of plant roots, where the symbiotic association occurs. This impedes the formation and sustenance of the advantageous mutualism, resulting in reduced nitrogen fixation, phosphorus solubilization and plant growth hormones production [136]. Secondly, the interaction between MPs and the essential nutrients from the soil diminished the nutrients bioavailability to PGPR. Consequently, the capacity of these microorganisms for plant benefit is compromised, leading to potential nutrient deficiencies [148]. In addition, perturbations of MPs on PGPR microbial community dynamics may disrupt competitive interactions among microbial taxa, consequently influencing the overall activity and functionality [116].

5.2.3. *MPs interactions with pathogenic microorganisms*

MPs serve as carriers for harmful pathogenic bacteria, facilitating their dissemination and colonization in plant tissues. Pathogenic fungal taxa such as *Candida*, *Fusarium*, and *Rhodotorula* are frequently found colonizing plastic surfaces of medical, industrial, and household appliances, indicating that MPs could potentially contribute to the accumulation and dissemination of fungal pathogens in soil environments subjected to substantial influxes of plastic solid waste [149]. Moreover, MPs act as vectors for transporting invasive microbes in the environment, contributing to the accumulation and spread of fungal pathogens in soil environments, causing negative effects on rhizosphere microbial communities and plant productivity [150]. In addition, the invasion of plant pathogens can potentially disrupt the accumulation of MPs by plants. Pathogen-induced root damage and physiological changes may interfere with MPs uptake and translocation within plants, while alterations in root exudates could affect the availability and retention of MPs in the soil-plant system [80]. Furthermore, pathogen-induced stress responses and modifications to rhizosphere microbial communities may indirectly influence MPs fate and behavior.

5.2.4. *Long-term and cumulative effects of MPs*

MPs exhibit accumulation and slow degradation rates in soil owing to their intrinsic resistance to biotic and abiotic degradation processes. Once deposited in soil environments, MPs persist over extended periods, gradually accumulating. Physical weathering mechanisms, such as fragmentation and abrasion, may generate smaller particles termed microplastics, albeit at a sluggish pace in terrestrial settings [151]. While certain plastics may undergo chemical degradation over time due to exposure to environmental factors like sunlight and moisture, the overall degradation rate remains generally sluggish [152]. Biological degradation, facilitated by soil microorganisms, also contributes to MP breakdown; however, the efficiency of this process varies depending on factors such as plastic type, microbial community composition, and prevailing environmental conditions [90]. Over time, the accumulation of MPs in soil ecosystems can lead to a gradual increase in MPs concentrations. Persistent exposure to MPs may result in the gradual deterioration of soil health, characterized by declines in soil fertility and disruptions to nutrient cycling processes. These changes can influence crucial soil functions, such as organic matter decomposition, nutrient cycling, and soil carbon sequestration [153]. As MPs accumulate in the rhizosphere, they may interfere with rhizosphere microbial community, affecting root development, nutrient uptake and water absorption capacities, ultimately compromising plant health and productivity [13].

The long-term presence of MPs in the soil environment creates microniches that can impact plant-microbe symbiosis and have significant ecological and evolutionary implications. MPs, along with their surroundings, offer selective conditions that can serve as hotspots for horizontal gene transfer (HGT) and microbial evolution [154]. Soil microbes, crucial for soil health and nutrient cycling, interact extensively with hosts like terrestrial plants, potentially leading to cascading effects on plant-microbe interactions. Continuous exposure to MPs disrupts the microbial ecology, affecting nutrient cycling and soil fertility [155]. This disruption can lead to reduced crop productivity, altered plant community composition, and shifts in ecosystem dynamics over time [156].

5.3. Potential consequences for terrestrial ecosystem

5.3.1. MPs-induced effects on biogeochemical processes

The impact of MPs on the soil-plant-microbe system can trigger cascading effects that reverberate through soil biogeochemical processes. The intricate interplay between these components can disrupt nutrient cycling, carbon sequestration, and overall ecosystem functioning [1]. The presence of MPs in soil triggers a chain of effects on soil structure, porosity, and water retention, which intricately interlink with nutrient availability, leaching, and transport processes. For instance, MPs can affect soil CO_2 and N_2O emissions by altering soil properties, affecting oxygen levels, water content, and temperature. The presence of MPs may enhance soil oxygenation through improved permeability, disrupting the natural carbon-oxygen balance and inhibiting CO_2 fixation [129]. Simultaneously, increased oxygen can hinder denitrification, which contributes to decreased N_2O emissions [157]. Changes in soil properties can subsequently alter microbial community diversity and functioning, and then influence decomposition rates, nutrient mineralization, and the cycling of elements like carbon and nitrogen. Studies have revealed that MPs in soil can change the abundance of *Actinomyces*, *Bacteroides* and *Chloroflexi* to influence carbon solubilization, degradation and fixation, respectively [158]. MPs can also affect the nitrogen cycle by changing the abundance of genes associated with the nitrogen cycle. Research indicates that MPs can reshape soil microbial composition, affecting ammonification and nitrification-related bacteria, including nitrosative bacteria, ammonia-oxidizing bacteria, *Chloroflexi*, and *Rhodoplanes*, consequently influencing nitrification and denitrification processes [1]. Moreover, MPs-induced alterations in plant growth, nutrient metabolism, and species interactions can modify the quantity and quality of organic matter inputs to the soil. This can subsequently impact microbial communities engaged in decomposition and nutrient cycling processes. For instance, MPs can impact the decomposition of litter, a crucial process for carbon and nutrient cycling, by modifying soil properties like aggregate stability, aeration, and water content, alongside their interactions with decomposing enzymes and soil carbon storage [80]. Furthermore, the capacity of MPs to adsorb chemical compounds further magnifies their impact on biogeochemical processes [159]. These particles can bind to nutrients and contaminants, altering their availability and distribution in the environment. Such changes can have profound implications for nutrient uptake by plants, microbial activities, and the fate of soil organic matter, underscoring the far-reaching consequences of MPs on soil biogeochemical dynamics.

5.3.2. Cascading effects on food web dynamics and human health

The impact of MPs on the soil-plant-microbe system has the potential to cascade through soil food web dynamics, disrupting interactions among soil microorganisms, plants, and organisms across trophic levels. MPs infiltrate various trophic levels within soil ecosystems, affecting the behavior, interactions, and populations of soil organisms. At the base of the soil food web, microorganisms can inadvertently ingest MPs, altering their activity and community composition. This, in turn, affects nutrient cycling processes and the availability of resources for higher trophic levels [43]. MPs can also accumulate in detritivores and filter feeders, potentially impacting their fitness, reproduction, and, consequently, the flow of energy and nutrients through the food web [160]. There is evidence demonstrating the transfer of MPs from soil to chickens, as observed in traditional Mayan home gardens. This phenomenon is highlighted by the escalating MPs concentrations observed along the pathway, starting from the soil (0.87 ± 1.9 particles/g), progressing to earthworm casts (14.8 ± 28.8 particles/g), and ultimately culminating in chicken feces (129.8 ± 82.3 particles/g) [161]. The altered interactions and dynamics within the soil food web can have cascading effects on ecosystem functioning, including nutrient cycling, decomposition, and plant growth. Moreover, MPs in soil-plant-microbe system also raises concerns regarding their potential transfer to the human food chain. Crops cultivated in MPs-contaminated soils can accumulate these particles, possibly leading to human consumption through food consumption [58]. In essence, the impacts of MPs on soil food web dynamics and human health are complex and interconnected. Studying these impacts comprehensively is crucial for understanding the multifaceted repercussions of MPs contamination in soil ecosystems and its potential implications for both the environment and human health.

6. Conclusions and future directions

MPs are a menace to soil-plant-microbe systems and the concentrations found in the environment increase over time making the problems larger and larger. This review has elucidated how MPs impact the physical and chemical properties of soils, leading to biochemical changes and altered growth in plants. Moreover, the interactions between MPs and soil microorganisms are elucidated. MPs serving as microbial habitats can interact with soil microorganisms, altering the microbial community structure, diversity and functioning. Alternatively, the potential microbial degradation of MPs presents promising opportunities for MPs mitigation strategies. Further, the importance of the interaction between MPs and the plant's rhizosphere and how this affects the relationship between plants and microbes are discussed. This interaction can have far-reaching consequences for terrestrial ecosystems, influencing biogeochemical processes and food web dynamics. While advancements have been achieved in the study of MPs in soil-plant-microbe systems, certain limitations and shortcomings persist. We plea for concerted efforts to address the challenges posed by MPs within the complex realm of soil-plant-microbe interactions, ultimately enabling informed actions to preserve terrestrial ecosystems. Below are suggestions for further relevant studies.

1) MPs associated with chemical contaminants

The combined effects of MPs and contaminants in the soil-plant-microbe system need to be further studied, as understanding these interactions is crucial for assessing their potential ecological and human health impacts. MPs in the environment can act as carriers or sinks for various chemical contaminants, including heavy metals, persistent organic pollutants (POPs), and other toxic substances [159]. These contaminants can adsorb onto the surface of MPs, creating a potential risk for the transfer of pollutants through the food chain and their introduction into ecosystems. The presence of contaminants on MPs can alter their fate, behavior, and interactions with organisms in the soil-plant-microbe system [162]. The uptake of MPs combined with contaminants by plants can lead to bioaccumulation and biomagnification, concentrating toxic substances in the food web and potentially posing risks to higher trophic levels, including humans. Furthermore, the presence of contaminants on MPs can also influence their biodegradation rates and interactions with microorganisms. Some contaminants may act as inhibitors or accelerators of MPs degradation, affecting the persistence of MPs in the environment.

2) Identifying and quantifying MPs in soil-plant-microbe system

The diverse set of extraction methods, identification techniques, and size fractionations in research published hinder cross-study comparisons. Addressing challenges requires collaboration, development of standardized protocols, and advanced techniques for comprehensive understanding the fate and ecological impact of MPs on the soil-plant-microbe system. Because MPs undergo physical, chemical, and biological transformations within the soil-plant-microbe system, these dynamics make it challenging to measure the actual abundance. Moreover, the low concentrations of MPs in soil-plant-microbe system necessitate the utilization of highly sensitive detection and quantification methods. An interdisciplinary approach that combines field observations, experimental manipulations, molecular analyses, and modeling efforts will be essential for advancing our understanding of MPs' impact on soil-plant-microbe system and developing effective management strategies to mitigate their adverse effects. Experimental studies are needed to elucidate the mechanisms underlying the interactions between MPs and soil-plant-microbe system. These studies can employ controlled laboratory experiments to investigate the effects of MPs on soil physicochemical properties, plant growth and physiology, microbial community composition and function, and ecosystem processes such as nutrient cycling and carbon sequestration. Advanced molecular techniques, such as metagenomics and metatranscriptomics, can be used to characterize MPs ecotoxicity and identify key genes and metabolic pathways involved in MPs degradation and detoxification [163]. Furthermore, modeling approaches can be employed to predict the long-term impacts of MPs. This can involve the development of mechanistic models that integrate data on MPs transport, transformation, and biological interactions of MPs pollution in soil and its effects on soil-plant-microbe system over time [164].

3) Microbial engineering strategies for MPs remediation

Microbial engineering strategies hold promise in contributing to the reduction of MPs in the terrestrial environment. These strategies leverage the unique abilities of microorganisms to degrade, transform, or sequester MPs, and thus contribute to environmental cleanup efforts. One approach involves the genetic modification of microorganisms to enhance their plastic-degrading capabilities. Researchers have identified enzymes, such as PETases lipases, esterases, and cutinases, capable of breaking down specific plastic polymers like PET [165]. Genetically engineered microbes (GEMs) can be used to optimize the expression of these enzymes within microorganisms, boosting their efficiency in plastic degradation [166]. Additionally, synthetic biology techniques enable the creation of synthetic microbial consortia with complementary plastic-degrading enzymes, enhancing degradation rates and expanding the range of plastic types that can be targeted. Another strategy involves harnessing naturally occurring plastic-degrading microorganisms and enhancing their activity through environmental manipulation or selective enrichment. By isolating and cultivating microorganisms from plastic-contaminated environments, researchers can potentially identify strains with high plastic-degrading potential. Subsequently, optimizing growth conditions and microbial interactions can enhance their plastic degradation abilities. Furthermore, metagenomics approaches offer insights into microbial communities that naturally degrade plastics [166]. This information can guide the development of strategies to promote the growth and activity of these plastic-degrading microbes through targeted amendments or environmental management.

4) Advanced technologies in MPs mitigation

Researching novel remediation approaches, such as phytoremediation, bioaugmentation, and soil amendments, can help mitigate MP pollution in terrestrial ecosystems. These strategies leverage technological advancements, interdisciplinary collaborations, and nature-based solutions to tackle the complex challenges associated with MPs pollution. In addition, blockchain-based systems can help identify sources of MP pollution, hold responsible parties accountable, and incentivize sustainable practices throughout the product lifecycle [167]. Electrokinetic remediation can enhance the removal of MPs from contaminated soils by creating electroosmotic flow and ion migration, facilitating the transport of MPs towards collection electrodes [168]. Nanotechnology applications utilize nanomaterials with high adsorption capacities to capture and remove MPs from soil and water environments [169].

Advanced methods for monitoring and evaluating the presence and impact of MPs in terrestrial ecosystems involve a multidisciplinary approach that integrates various analytical techniques and methodologies. These include microscopy techniques such as optical microscopy, spectroscopic and chromatographic techniques [170]. Remote sensing and geospatial analysis detect changes in soil properties and map the distribution of MPs in terrestrial ecosystems [171]. Genomic and metagenomic approaches, including next-generation sequencing, reveal microbial community responses to MPs contamination [163]. Isotopic labeling techniques like stable isotope probing track the fate of MPs and their interactions with soil biota [172]. Through the integration of these advanced methods, researchers can comprehensively assess the occurrence, distribution, fate, and ecological impacts of MPs in terrestrial environments, guiding the development of effective management and mitigation strategies.

CRediT authorship contribution statement

Yujia Zhai: Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Junhong Bai:** Writing – review & editing. **Pengfei Chang:** Visualization, Writing – original draft. **Zhe Liu:** Writing – original draft. **Yaqi Wang:** Writing – original draft. **Gang Liu:** Writing – review & editing, Supervision, Conceptualization, Funding acquisition. **Baoshan Cui:** Funding acquisition, Conceptualization, Writing – review & editing. **Willie Peijnenburg:** Writing – review & editing. **Martina G. Vijver:** Writing – review & editing, Conceptualization.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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