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# Construction of an efficient polystyrene-degrading microbial consortium based on degrading and non-degrading bacteria predominant in biofilms of marine plastic debris

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Expanded polystyrene (EPS) has caused significant pollution in marine environments, with potential EPS-degrading bacteria identified on long-term floating EPS biofilms. However, studies on bacterial interactions and consortium reconstruction based on *in-situ* bacterial diversity remain limited. Marine EPS wastes of different sizes were collected from subtropical coast of Xiamen island, and subjected to bacterial diversity analyses. Co-occurrence network and bacterial characterization revealed that *Rhodobacterales* and *Rhizobiales* play important roles in polystyrene (PS) degradation. Bacterial isolation characterization confirmed that *Fulvimarina pelagi*, *Pseudosulfitobacter pseudonitzschiae*, *Devosia nitrariae*, *Cytobacillus kochii*, and *Cytobacillus oceanisediminis* as novel PS-degraders. Based on their abundance *in situ* and PS degradation activity, a consortium was constructed, constituted of *F. pelagi*, *P. halotolerans*. and *O. granulosus*, showed a high degradation capability with PS weight loss by 18.9% in 45 days. These results contribute to marine plastic pollution remediation and resources recycling.

KEYWORDS

**expanded polystyrene (EPS), biodegradation, consortium, marine bacteria, construction**

# 1 Introduction

It is estimated that 4-23 million metric tonnes of plastic pollution per year enter the ocean as part of the Global Plastic Cycle (Borrelle et al., 2020). As reported, the density of plastics in the ocean is increasing, with microplastic pollution levels in seawater and sediment environments ranging from 0.001 to 140 particles/$m^3$ and 0.2 to 8,266 particles/$m^3$, respectively (Thushari and Senevirathna, 2020). Polystyrene (PS) is a thermoplastic resin produced through the radical polymerization of styrene monomers with the form of general purpose polystyrene (GPPS), high impact polystyrene (HIPS), and EPS (Muthukumar et al, 2024). Its molecular formula, $(C_8H_8)n$, primarily consists of benzene rings, vinyl groups, and single bonds. Benzene rings constitute the repeating units of the polymer, connected by vinyl groups and single bonds (Salisu et al., 2022). An annual growth rate of 4% is expected between 2021 and 2026 (Muthukumar et al., 2024).

Expanded polystyrene (EPS) is a material known for its low cost, ease of processing, and high buoyancy, making it suitable for various applications such as shockproof packaging and fast-food containers (Matjašič et al., 2021). It is widely used as a buoy in marine aquaculture. However, its recycling rate is extremely low (Ali et al., 2021), and it acts as a potential carrier of biotic or abiotic pollutants. EPS is also prone to fragmentation due to physical, mechanical, and biological forces, resulting in significant marine debris that disperses globally through ocean currents (Chelomin et al., 2023).

So far, diverse marine bacteria residing on the surfaces of EPS or PS have been observed, but few have been isolated and confirmed in their role in the plastic biosphere. Bacteria from *Flavobacteriaceae*, *Hyphomonadaceae*, *Rhodobacteraceae*, *Comamonadaceae*, *Alcanivoracaceae*, *Oceanospirillaceae*, *Vibrionaceae* families, *Pseudoalteromonas* (Guezennec, 2002), *Bacillus* (Mohan et al., 2016), and *Vibrio* (Zanchetta et al., 2003) have been retrieved from PS surface in the North Sea, the Baltic Sea and other coastal waters. We found that marine bacteria of *Sphingomonadaceae, Rhodanobacteraceae, Rhizobiaceae, Dermacoccaceae, Rhodocyclaceae, Hyphomicrobiaceae*, and *Methyloligellaceae* constituted the major compositions of the PS-degradation consortium, derived from EPS samples from a subtropical mangrove area (Liu et al., 2023). In our latest report, bacteria of *Flavobacteriaceae*, *Rhodobacteraceae*, *Halomonadaceae*, *Exiguobacteriaceae*, *Vibrionaceae*, and *Pseudoalteromonadaceae* were found predominant on EPS surface biofilms in the coast of Xiamen (Zhang et al., 2024). Recently, we also discovered that the main EPS-degrading bacteria in the gut of EPS-ingesting clamworms, which were mainly composed of *Acinetobacter* and *Ruegeria* (Zhao et al., 2024). These studies convey the high diversity of PS associated marine bacteria.

Although more and more bacteria that can degrade PS plastic have been isolated from both terrestrial and marine environments. Few show the degradation potential with untreated plastic weight loss over 8% (James-Pearson et al., 2023; Sanluis-Verdes et al., 2022). For an example, we found that marine bacteria of *Novosphingobium, Gordonia, Stappia, Mesobacillus, Alcanivorax, Flexivirga, Cytobacillus, Thioclava*, and *Thalassospira* showed PS degradation capability in a pure culture. Among them the key degrading bacteria of *Gordonia* showed relatively high weight losses of 4.69% to 7.73% for 30 days (Liu et al., 2023). Previously, PS-degrading bacteria *Rhodococcus ruber* showed 0.8% weight loss of PS films after eight weeks of incubation (Mor and Sivan, 2008), and strain *Exiguobacterium* sp. YT2 isolated from the gut of mealworms showed 7.4% weight loss of PS pieces (2500 mg/L) over a 60-day-incubation (Yang et al., 2015). The studies conducted thus far on plastic biodegradation have typically focused on individual isolates.

It is recognized that in natural environments, biofilms form on plastic surfaces and highlighting the role of the bacterial cooperation in biofilm in plastic biodegradation. However, the interactions and synergistic mechanisms of plastic degradation between different strains within the microbial consortium are not well understood. In the case of aromatic-aliphatic copolyester plastics, marine microbial consortia exhibit stronger degradation capabilities (Meyer-Cifuentes et al., 2020). And, microorganisms in the consortium could effectively cooperate through various enzymatic activities, metabolic processes, and other pathways, thereby increasing the rate of plastic degradation (Zhang et al., 2023). To date, there has been a paucity of efficient microbial consortia capable of degrading plastics. Furthermore, the degradation efficacy of engineered bacterial consortia remains suboptimal. The consortium composed of *Rhodococcus* sp., *Shewanella* sp., *Pseudomonas* sp. which used seawater containing PS as the sole carbon source, had the weight loss 2.3% after 6 months (Syranidou et al., 2017). Two consortia consisted of *Bacillus flexus* + *Pseudomonas azotoformans* and *B. flexus* + *B. subtilis*, respectively, with a weight loss of 1.95% and 1.45% after one year of culture (Aravinthan et al., 2016).

This study aims to optimize a marine PS-degrading microbial consortium. EPS wastes were sampled from the coast of Xiamen Island at the Jiulong River Estuary, followed by 16S rRNA gene amplicon sequencing to observe the bacterial abundance in environments samples and recombinant consortium. Scanning Electron Microscope (SEM), Water Contact Angle (WCA), Attenuated Total Reflectance Fourier Transform Infrared Spectroscopy (ATR-FTIR), were used for the evaluation of the PS-degrading ability of the constructed consortium and weight loss of each consortium was quantified. The results have expanded the PS-degrading bacterial diversity on marine EPS plastic and microplastics, and provided insight into the interactions of in biofilms on plastic surfaces, which leads to the construction of an efficient degrading consortium.

# 2 Materials and methods

## 2.1 Sample collection and experiment design

EPS wastes, seawater, and surface sandy sediments were collected from the coast of Xiamen Island, and macro-pieces of EPS with microplastic formations on the surface were specially

selected (Figures 1a, b). The EPS samples were named LP (larger than 5 mm, Figures 1c, d), MP (smaller than 5 mm, collected from the surface of LP, Figure 1c), seawater (nearshore seawater), and sand (surface sediment). In the lab, to incubate PS-degrading bacteria, the LP and MP sample were respectively resuspended in 50 mL centrifuge tubes containing 40 mL liquid MMC medium (pH = 7.4, NaCl 20 g/L, $NH_4Cl$ 0.67 g/L, KCl 0.7 g/L, $NaNO_3$ 1.06 g/L, $KH_2PO_4$, 2.0 g/L, $Na_2HPO_4{\cdot}12H_2O$ 7.65 g/L, $MgSO_4{\cdot}7H_2O$ 3.5 g/L in 1 L of deionized water), then samples were vortexed for 10 minutes using a Vortex Genie (Scientific Industries, Inc., USA). Subsequently, they were centrifuged at 7000 rpm and 4°C for 10 minutes using an Eppendorf centrifuge (Germany), and the supernatant was removed. The remaining was used for DNA extraction and isolation of the PS-degrading bacteria.

## 2.2 DNA extraction, 16s rRNA gene amplification and sequencing

Total DNA was extracted strictly according to the instructions provided by the commercial environmental sample DNA extraction kit (QIAGEN, Germany). The purity and concentration of the extracted DNA were measured using NanoDrop2000 (Thermo, U.S.A) and stored at -80°C for high-throughput sequencing. The V3 - V4 region of the 16S rRNA gene was amplified using the universal bacterial primers 341F (5'- ATGCGTAGCCGACCT GAGA-3') and 805R (5'-CGTCAGACTTTCGTCCATTGC-3'), and then sequencing was performed using the Illumina HiSeq 4000 platform (Illumina, U.S.A).

Purified amplicons were pooled in equimolar amounts and paired-end sequenced (2 ×300) on an Illumina MiSeq platform (Illumina, San Diego, USA) according to the standard protocols by Sangon Biotech Co., Ltd. (Shanghai, China). Raw reads were deposited into the National Genomics Data Center database (Accession Number: CRA018003).

## 2.3 Data processing and statistical analyses

All 16S rRNA sequences were analyzed using QIIME v1.9.1 (Caporaso et al., 2010). Then, operational taxonomic units (OTUs) with a 97% similarity cut-off were clustered using UPARSE (version 7.1) (Edgar, 2013), and chimeric sequences were checked and removed using UCHIME (Edgar et al., 2011). The taxonomy of each OTU representative sequence was analyzed by the RDP Classifier (http://rdp.cme.msu.edu/) against the 16S rRNA database Silva (Release132: http://www.arb-silva.de) using a confidence threshold of 0.7.

We calculated all possible Spearman's rank correlations between OTUs with more than fifty sequences (306 OTUs). This previous filtering step removed genus with relative abundance less than 0.005, reduced network complexity, facilitating the

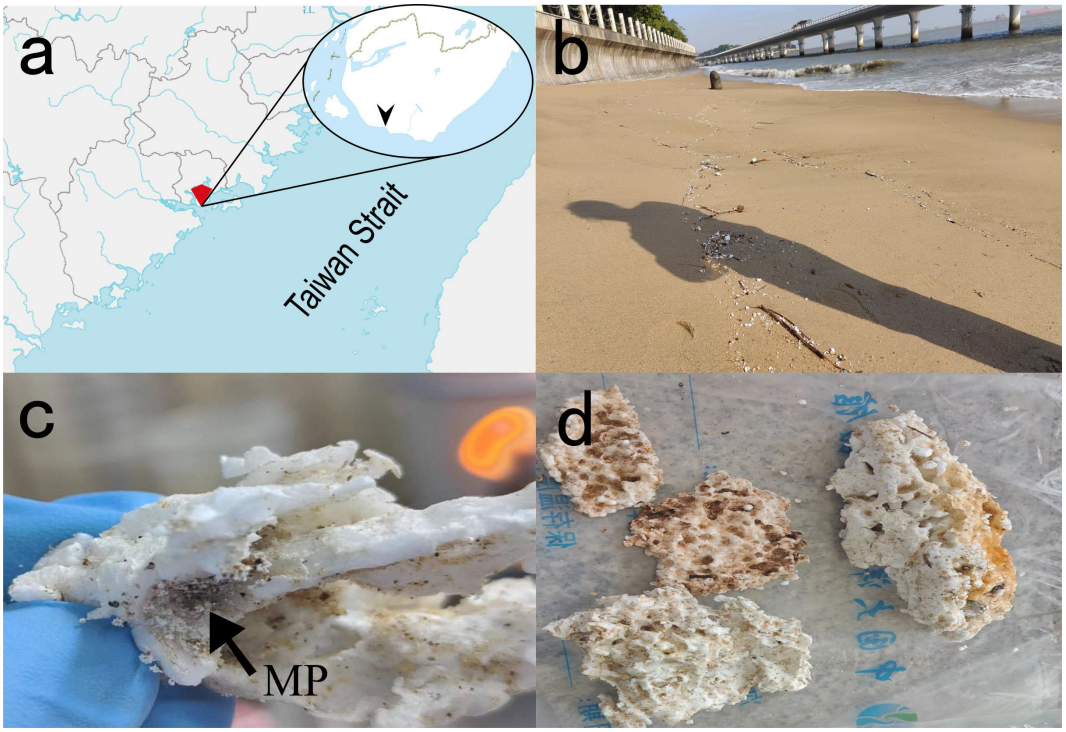


FIGURE 1
ESP debris in Bai-cheng beach of Xiamen Island and sampled items. **(a)**, Map of sampling sites; **(b)**, Xiamen Island coast; **(c)**, MP, particles smaller than 5 mm indicated by arrows; **(d)**, LP, plastics larger than 5 mm.

determination of the core community. We considered a valid co-occurrence event to be a robust correlation if Spearman's correlation coefficient (ρ) was both >0.7 and statistically significant (P-value <0.05) (Lu et al., 2022). To describe the topology of the resulting network, a set of measures (average node connectivity, average path length, diameter, cumulative degree distribution, clustering coefficient, and modularity) was calculated. All statistical analyses were carried out in the R environment (http://www.r-project.org) using Hmisc (Wu et al., 2023) and igraph packages (Layeghifard et al., 2018). Networks were explored and visualized with the interactive platform Gephi v 0.10.1 (Bastian et al., 2009).

## 2.4 Morphological observations of PS film surface by SEM

Microbial attachment and the subsequent formation of a stable biofilm on the surface of plastics are crucial initial steps in the degradation process, as the biofilm is known to enhance bacterial proliferation and biodegradation (Meera et al., 2022). In the temperature range of 25 ~ 30°C, the oxidation range of PS is more extensive (Matyakubov and Lee, 2024). Biofilms on the surface of LP and MP were examined using SEM (LEO-1530, Germany), and biofilms formed on PS films by the six constructed consortia after 45 days at 28 °C were also observed. PS films treated by the consortium were randomly collected and treated with 2% SDS for 4 h at 50 °C to remove extracellular secretions or biofilms from the PS film surface and observed by SEM (Kim et al., 2020).

## 2.5 Isolation, identification, and degradation activity assays of the PS-degrading bacteria from EPS debris

To isolate pure culture strains from EPS plastic surfaces, the samples described in Part 2.1 were used for gradient dilution and cultivated on Marine Broth 2216 (BD Difco) and R2A medium (BD Difco) plates for 5-7 days. The individual colonies were selected and transferred to fresh media of the same type of plates for cultivation. This process was repeated until pure cultures were obtained. Next, single colonies were selected and subjected to PCR using the 27F (5′-AGA GTT TGA TCC TGG CTC AG-3′) and 1492R (5′-TAC GGC TAC CTT GTT ACG ACT T-3′) primers. The PCR products were purified and sequenced. Lastly, the amplified DNA sequences were aligned with organisms present in the EzbioCloud database (https://www.ezbiocloud.net/) and the GenBank database using the Basic Local Alignment Search Tool (BLAST). Confirmed pure cultures were preserved in 25% glycerol and stored at -80°C. Additionally, these cultures were deposited in the Marine Culture Collection of China (MCCC).

The degradation ability of the obtained pure culture strains was verified with PS (Sigma, GF94795701, 150 mm × 150 mm × 0.19 mm) as the sole carbon source. Based on the biomass increase of the strains at 28°C and 150 rpm over a period of 10 days, bacteria exhibiting the ability to degrade PS were screened.

## 2.6 Evaluation of plastic weight loss after bacterial treatments

PS films (1.5 cm×1.5 cm) were weighed and immersed in 75% ethanol for 24 hours, then dried after the ethanol removed. Four bacterial strains, namely *Paracoccus halotolerans, Fulvimarina pelagi, Pseudosulfitobacter pseudonitzschiae* and *Oceanicola granulosus*, were inoculated into liquid culture media Marine Broth 2216 or R2A. Cell growth was determined by measuring the $OD_{600}$ with a spectrophotometer. When the $OD_{600}$ of each bacterial strain reached a value between 0.6 and 0.8 (indicating nearly equivalent bacterial numbers), equal volumes of each strain in different combinations of the consortium were combined in a 1:1 ratio. The mixture was centrifuged at 5000 rpm for 5 minutes, and the supernatant was discarded, then cells were resuspended in MMC, and this process was repeated three times to thoroughly discard the original medium. Subsequently, inoculation was performed at a volume ratio of 2% into MMC medium containing PS films (4 pieces, 1.5 cm×1.5 cm). Three biological replicates were set up, and each replicate with a 2% inoculum was inoculated into 100 mL/250 mL MMC liquid medium. The cultures were incubated at 150 rpm and 28°C for 45 days. Finally, the surface biofilm was removed with 2% SDS for 4 h at 50°C (Kyaw et al, 2012), followed by washing with sterile water and drying. The weight of the films was measured, and the weight loss rate was calculated.

## 2.7 PS surface hydrophilicity examination

After microbial consortium growth using PS film as the sole carbon source, the characteristics of plastic surface may change, resulting in alterations in the hydrophobicity of the PS film (Zhang et al., 2022). Randomly selected PS films from each microbial consortium were subjected to contact angle measurements (OCA20, German Data Physics company). Briefly, 2 μL of pure water was deposited on the surface of PS film at 1 μL/s at room temperature. The contact angles formed by the left and right edges of the water droplet in contact with the PS film were measured as indicators of PS degradation. Measurements were taken at 4-5 points on the surface of each PS film (Jaleh et al., 2011).

## 2.8 ATR-FTIR analysis

PS films degraded by the different consortia were randomly selected for analysis after the biofilms on the PS surface were removed with 2% SDS and dried. The changes in the structure of the PS films due to the bacterial incubation were analyzed using ATR-FTIR spectroscopy, with a Thermo Scientific iS50 (Nicolet iS50, USA) infrared spectrometer with an integrated attenuated

total reflection ATR attachment. Briefly, the measurement spectra range was from 4000-400 $cm^{-1}$, and the data were treated using OMNIC software. Images were taken with a spectral resolution of 4 $cm^{-1}$ over an average of 32 scans. The data were transformed using N-B strong apodization and Mertz phase correction according to a protocol for plastic identification. All the ATR-FTIR spectra measured were compared with the spectra in a commercial library (Cross Sections Wizard, Polymer Laminate Films).

### 2.9 Cultivation conditions and treatment of microbial consortium

Microbial cultivation with PS as a growth substrate was conducted at 28°C and 150 rpm. The flasks were shaken once a day during the incubation period to prevent bacterial attachment to the flask walls. On the 10th, 20th, and 35th days, three replicates were randomly sampled, followed by the remaining three replicates the on 45th day. Subsequently, all supernatants obtained from the centrifugation of the replicates were subjected to high-throughput sequencing to observe changes in species ratios.

## 3 Results and discussion

### 3.1 Observation of biofilms on the surface of *in-situ* EPS

Biofilm formation by microorganisms on the surface of plastics is a prerequisite for biodegradation (Bhagwat et al., 2021). Subsequently, plastics are degraded by internal and external enzymes secreted by these microorganisms (Sivan et al., 2006). The released monomers or mesostates serve as a carbon source that can be readily absorbed by microorganisms, leading to an increase in microbial biomass (Degli-Innocenti, 2014). SEM observations showed obvious biodegradation on the surfaces of macro- and microplastic debris, the latter rotten more severely (Figure 2). The irregular structure of the EPS and the obvious biofilm on the surface indicate that it was degraded in the marine environment, suggesting the presence of bacterial strains capable of degrading EPS on the surface.

### 3.2 Diversity and co-occurrence network analysis of indigenous bacterial communities on EPS debris

To explore the diversity and composition of bacterial communities on the surfaces of EPS in coastal, we performed high-throughput 16S rRNA sequencing analysis on environmental samples, including nearshore seawater, surface sandy sediment, and various sizes of EPS debris collected from the coast of Xiamen Island. In total, we identified 30 phyla, 82 classes, 150 orders, 325 families, and 813 genera of bacteria. Figure 3a showed the relative abundance of taxa at the order level, the top 10 orders on *in-situ* macroplastics as *Rhizobiales* (18.58%), *Pseudonocardiales* (16.5%), *Sphingomonadales* (9.42%), *Bacillales* (8.33%), *Rhodobacterales* (7.15%), *Rubrobacterales* (4.91%), *Rhodothermales* (4%), *Frankiales* (3.88%), *Thermomicrobiales* (1.89%), and *Sphingomonadales* (1.7%). The top 10 orders in surface of *in-situ* microplastics were *Rhizobiales* (23.25%), *Sphingomonadales* (9.86%), *Rhodothermales* (7.97%), *Rhodobacterales* (5.61%), *Frankiales* (4.56%), *Bacillales* (4.12%), *Propionibacteriales* (3.81%), *Microtrichales* (3.4%), *Rubrobacterales* (3.12%), and *Pseudonocardiales* (2.34%). The relative abundance of *Pseudonocardiales* on *in-situ* microplastics significantly decreased compared to macroplastics, indicating variations in bacterial consortium composition across various plastic sizes.

*In-situ* seawater samples exhibited a high diversity of bacterial communities dominated by *Rhodobacterales* (39.81%), *Pseudomonadales* (25.31%), *Flavobacteriales* (15.98%), *Enterobacterales* (3.04%), *Sphingomonadales* (2.1%), and *Bdellovibrionales* (1.08%). Bacterial communities in surface sandy sediments displayed distinct composition, the top 10 orders including

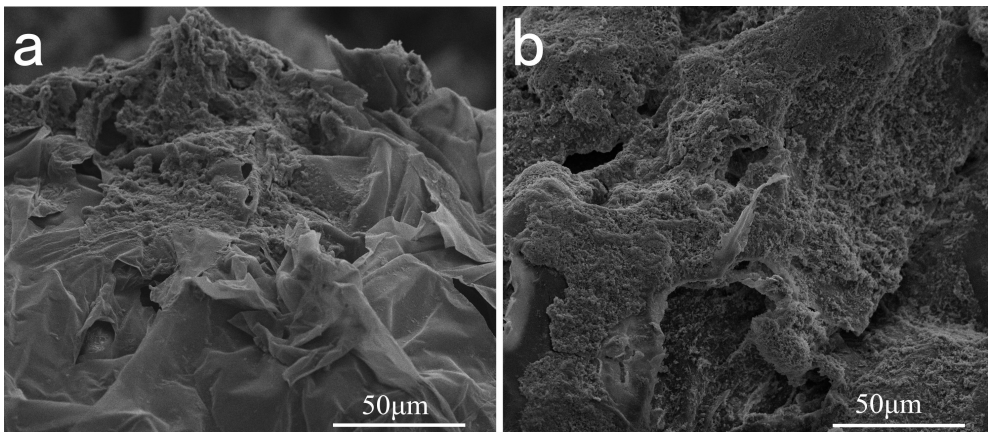


FIGURE 2
Surface micrographs of the in-situ EPSs observed using SEM. Samples were selected randomly from the collections, **(a)** surface of the LPs and **(b)** MPs, respectively.

*Pseudomonadales* (32.35%), *Bacillales* (15.09%), *Legionellales* (12.96%), *Rhodobacterales* (5.66%), *Campylobacterales* (3.97%), *Enterobacterales* (3.81%), *Nitrosococcales* (1.78%), *unclassified_Gammaproteobacteria* (1.6%), *Rickettsiales* (1.38%), and *Rhizobiales* (1.33%). Thus, the microbial diversity in nearshore seawater and sand surface differed significantly from that on EPS, indicating a substantial carrier-mediated selection of microorganisms in the environments. *Rhizobiales*, *Pseudonocardiales, Sphingomonadales*, *Rhodobacterales*, exhibit high relative abundance on both micro- and macro-EPS, making them the dominant component of biofilms. Previous studies have identified *Rhizobiales*, *Rhodobacterales*, *Streptomycetales*, and *Cyanobacteria*, playing a key role in plastic biofilms (Debroas et al., 2017). In the laboratory, mangrove sediments with and without polyethylene terephthalate (PET) particles showed differences in the abundance of *Rhizobiales* after two months (Jiménez et al., 2024a). *Rhodobacteraceae* also exhibited a high relative abundance in microplastic from Yellow Sea (Jiang et al., 2018) and in exposed microplastic from the Yellow Sea and South China Sea (Xu et al., 2019). Moreover, on the EPS biofilms investigated on Xiamen Island, the relative abundance of *Rhodobacteraceae* was 1.9%-18.81% in different seasons (Zhang et al., 2024). In this study, *Rhizobiales* represented the majority at bacterial order level *in-situ* on EPS microplastics, with relative abundance of 22.33%, followed by *Rhodobacterales* of 5.63%. It has also been found that *Rhodobacterales* and *Rhizobiales* were major groups enriched by PE and PS in marine environment (Syranidou et al., 2019). Combined with the above research, we hypothesized that *Rhizobiales* and *Rhodobacterales* may play a key role in marine PS biodegradation.

To analyze relationships among bacterial communities, co-occurrence network analysis was conducted at the OTUs level across all samples. As shown in Figure 3b, the network analysis revealed 303 nodes, an average path length of 2.676, an average clustering coefficient of 0.566, an average modularity of 0.618, a diameter of 6, and 6,255 edges. Among them, 188 OTUs belonged to *Proteobacteria*, 37 for *Actinobacteriota*, and 31, 14, 7, for *Bacteroidota*, *Firmicutes*, and *Bdellovibrionota*, respectively. Especially, *Rhodobacterales* and *Rhizobiales* belong to *Proteobacteria*, have been highlighted in multiple studies as key phyla involved in plastic biodegradation (Debroas et al., 2017; Jiang et al., 2018; Vargas-Suárez et al., 2021). *Rhizobiales* has been designated as a biomarker for microplastic pollution (Rong et al., 2023). Biofilm on floating microplastics in the Mediterranean Sea were found dominated by the key bacterial groups in the biofilm of PS, PE, and PP, including *Flavobacteriales* and *Rhodobacterales* (Vaksmaa et al., 2021). Results in this study combined with the recent findings, propose that *Rhodobacterales* and *Rhizobiales* may play a crucial role in plastic degradation.

## 3.3 Isolation of PS-degrading bacteria

To obtain the PS-degrading isolates from the EPS surface, we evaluated the ability of bacteria to degrade PS with PS as the sole carbon source. As shown in Table 1, a total of 51 strains belonging to 23 families were isolated from the EPS surface, which have been reported capable of degrading plastics and various organic compounds, some of which have been reported, such as *Pseudoalteromonadaceae* (Delacuvellerie et al., 2021), *Pseudomonadaceae* (Roberts et al., 2019), *Rhodobacteraceae* (Roager and Sonnenschein, 2019), and *Sphingomonadaceae* (He et al., 2022). Importantly, we identified 36 PS-degraded bacteria species, which not yet previously reported, including *C. kochii*, *F. pelagi*, *P. pseudonitzschiae*, *D. nitrariae*, *C. oceanisediminis*, *N. rotundus, T. cyri, R. antarcticus, A. palladensis, L. soesokkakensis.* They contribute to the diversity of new bacterial strains in the field of PS degradation.

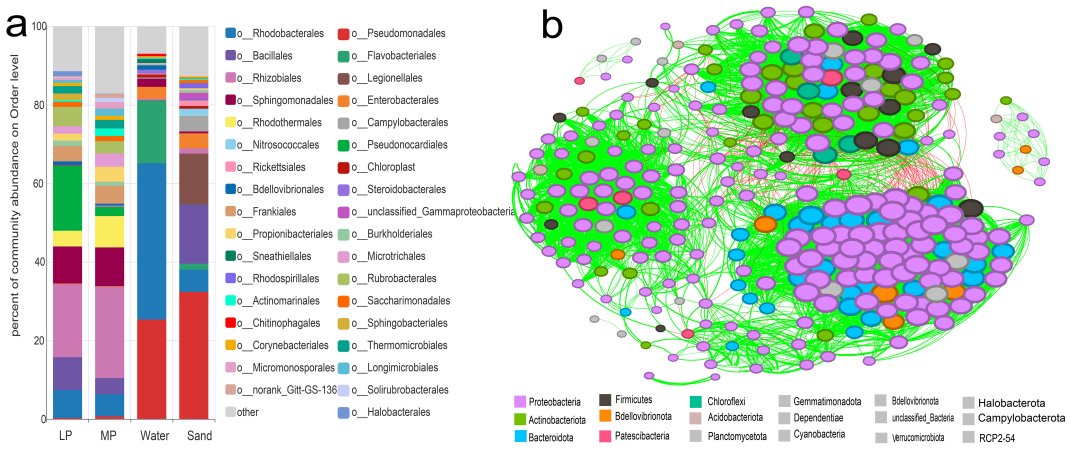


FIGURE 3
Relative abundance of the original bacterial consortia and the co-occurrence network analysis. **(a)**, The original consortium diversity of the samples of LP, MP, seawater, and surface sand at the order level. **(b)**, Network analysis of all the samples. The color of the nodes displays different dominant phyla. Red lines between nodes represent negative correlations, while green lines indicate positive correlations.

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TABLE 1 Isolation and characterization of PS-degrading bacteria from marine EPS detritus.

| Name | Top-hit taxon | Phylum | Similarity (%) | Growth |
|---|---|---|---|---|
| LP1_M20 | *Cytobacillus kochii* WCC 4582(T) | *Firmicutes* | 99.79 | +++ |
| LP1_M1 | *Fulvimarina pelagi* HTCC2506(T) | *Proteobacteria* | 97.92 | +++ |
| LP1_M11 | *Pseudosulfitobacter pseudonitzschiae* H3(T) | *Proteobacteria* | 99.85 | +++ |
| LP1_M3 | *Fictibacillus barbaricus* V2-BIII-A2(T) | *Firmicutes* | 99.57 | +++ |
| MP2_M24 | *Bacillus cereus* ATCC 14579(T) | *Firmicutes* | 99.79 | +++ |
| LP1_M21_1 | *Microbacterium paraoxydans* NBRC 103076(T) | *Proteobacteria* | 100 | ++ |
| MP2_R6 | *Devosia nitrariae* 36-5-1(T) | *Proteobacteria* | 99.14 | ++ |
| LP1_R12 | *Cytobacillus oceanisediminis* H2(T) | *Firmicutes* | 99.42 | ++ |
| LP1_M7_2 | *Rossellomorea oryzaecorticis* R1(T) | *Firmicutes* | 99.28 | ++ |
| LP1_M13 | *Nocardioides rotundus* GY0594(T) | *Actinobacteria* | 97.29 | ++ |
| MP1_M2 | *Bacillus mobilis* 0711P9-1(T) | *Firmicutes* | 99.93 | ++ |
| MP2_M16 | *Thalassobacillus cyri* CCM7597(T) | *Firmicutes* | 99.86 | + |
| MP2_M18_2 | *Roseisalinus antarcticus* CECT 7023(T) | *Proteobacteria* | 94.7 | + |
| LP1_M17 | *Arenibacter palladensis* LMG 21972(T) | *Bacteroidetes* | 99.35 | + |
| LP1_M100 | *Pseudoalteromonas distincta* ATCC 700518(T) | *Proteobacteria* | 99.78 | + |
| LP1_M24 | *Limimaricola soesokkakensis* CECT 8367(T) | *Proteobacteria* | 95.79 | + |
| LP1_M8 | *Sulfitobacter litoralis* DSM 17584(T) | *Proteobacteria* | 99.69 | + |
| LP1_M12 | *Marinobacter lipolyticus* SM19(T) | *Proteobacteria* | 99.28 | + |
| MP2_R4 | *Microbacterium foliorum* DSM 12966(T) | *Actinobacteria* | 99.71 | + |
| MP2_M31 | *Halobacillus sediminis* NGS-2(T) | *Firmicutes* | 99.5 | W |
| LP1_M22 | *Salipiger thiooxidans* DSM 10146(T) | *Proteobacteria* | 99.7 | W |
| LP1_R11_2 | *Novosphingobium fluoreni* HLJ-RS18(T) | *Proteobacteria* | 98.65 | W |
| LP1_R14 | *Paracoccus halotolerans* CFH 90064(T) | *Proteobacteria* | 99.46 | W |
| LP1_R27_6 | *Microbacterium foliorum* DSM 12966(T) | *Actinobacteria* | 99.56 | W |

*(Continued)*

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TABLE 1 Continued

| Name | Top-hit taxon | Phylum | Similarity (%) | Growth |
|---|---|---|---|---|
| MP1_M12 | *Nesterenkonia alkaliphila* F10(T) | *Actinobacteria* | 97.86 | W |
| MP1_M13 | *Gramella bathymodiolin* BOM4(T) | *Bacteroidetes* | 97.51 | W |
| MP1_R1 | *Limnobacter thiooxidans* CS-K2(T) | *Proteobacteria* | 99.85 | W |
| MP1_R17_2 | *Cytobacillus pseudoceanisediminis* BNO1(T) | *Firmicutes* | 97.99 | W |
| MP2_M15 | *Tsuneonella suprasediminis* Ery12(T) | *Proteobacteria* | 96.73 | W |
| MP2_M18_1 | *Roseisalinus antarcticus* CECT 7023(T) | *Actinobacteria* | 99.19 | W |
| MP2_M2 | *Arenibacter nanhaiticus* NH36A(T) | *Bacteroidetes* | 99.71 | W |
| MP2_M25 | *Bacillus toyonensis* BCT-7112(T) | *Firmicutes* | 99.79 | W |
| MP2_M27 | *Sulfitobacter pontiacus* DSM 10014(T) | *Proteobacteria* | 100 | W |
| MP2_R16_2 | *Lysinibacillus fusiformis* NBRC 15717(T) | *Proteobacteria* | 99.71 | W |
| MP2_R17 | *Erythrobacter sanguineus* DSM 11032(T) | *Proteobacteria* | 99.77 | W |
| MP2_R25 | *Pseudomonas aestusnigri* VGXO14(T) | *Proteobacteria* | 99.93 | W |
| MP2_M23 | *Pseudokineococcus lusitanus* CECT 7306(T) | *Proteobacteria* | 99.14 | – |
| MP2_M29 | *Litchfieldia salsa* A24(T) | *Firmicutes* | 96.64 | – |
| LP1_M15_1 | *Oceanicola granulosus* HTCC2516(T) | *Proteobacteria* | 99.85 | – |
| LP1_M18 | *Alteromonas stellipolaris* LMG 21861(T) | *Proteobacteria* | 99.79 | – |
| LP1_M19 | *Alteromonas naphthalenivorans* SN2(T) | *Actinobacteria* | 99.93 | – |
| LP1_R13 | *Acinetobacter guillouiae* CIP 63.46(T) | *Proteobacteria* | 99.64 | – |
| LP1_R15_1 | *Noviherbaspirillum aurantiacum* SUEMI08(T) | *Proteobacteria* | 98.69 | – |
| LP1_R20 | *Sphingomonas spermidinifaciens* 9NM-10(T) | *Proteobacteria* | 98.12 | – |
| LP1_R21 | *Microbacterium imperial* DSM 20530(T) | *Actinobacteria* | 99.93 | – |
| LP1_R8 | *Demequina activiva* BS-12M(T) | *Actinobacteria* | 99.34 | – |
| LP1_R9_3 | *Blastococcus aggregatus* DSM 4725(T) | *Actinobacteria* | 99.56 | – |
| MP1_M10_2 | *Croceibacterium xixiisoli* S36(T) | *Proteobacteria* | 95.83 | – |
| MP1_M9 | *Afifella pfennigii* DSM 17143(T) | *Proteobacteria* | 92.86 | – |

*(Continued)*

TABLE 1 Continued

| Name | Top-hit taxon | Phylum | Similarity (%) | Growth |
|---|---|---|---|---|
| MP2_M8 | *Psychrobacter nivimaris* 88/2-7(T) | *Proteobacteria* | 99.86 | – |
| MP2_R16_3 | *Pseudomonas oceani* KX 20(T) | *Proteobacteria* | 99.64 | – |

#Bacterial growth with PS as the sole carbon and energy source: "+++", $OD_{600}$ ≥0.5; "++", $OD_{600}$ 0.4 - 0.5; "+", $OD_{600}$ 0.2 - 0.4; "w", $OD_{600}$ 0.1 - 0.2; "-", $OD_{600}$ ≤ 0.1, in 1 week.

## 3.4 Bacterial consortium construction and the dynamic changes of the bacterial composition during PS degradation

Microbiome engineering can be defined as the modification or rearrangement of microbial communities to obtain desired functions, which include the selection, evolution and interaction of species (Jiménez et al., 2024b). Understanding the interactions of bacteria through various biochemical pathways is crucial for the discovery of key degrading bacteria, revealing the role of microbes in the process of plastic degradation. This study considered *in-situ* microbial diversity and degradation ability. Four isolates belonging to *Rhodobacterales* and *Rhizobiales*, including *P. halotolerans*, *F. pelagi*, *p. pseudonitzschiae*, and *O. granulosus*, were chosen for the construction of the PS-degrading consortium. The selection was based on the overall diversity, *in-situ* abundance and co-occurrence, as well as individual capability to degrade PS films. A total of 15 microbial consortia were initially assembled using *P. halotolerans, F. pelagi, P. pseudonitzschiae, and O. granulosus* for preliminary screening. According to bacterial growth with PS, six consortia demonstrating significant growth increases were selected for further investigation, as presented in Table 2. Dynamic changes in their relative abundance of each strain in the course of 45 day-incubation among six consortia their roles in the biodegradation process were displayed by their increase in abundance in the consortium, as shown in Figure 4, as well as the PS degrading efficiency as showed next.

In consortium E, *P. pseudonitzschiae* showed an increase in relative abundance to 82% during a 35-day cultivation, decreasing to 70% on 45th day. *F. pelagi* exhibited an increase from 17% to 30% in relative abundance from day 35 to 45. Consortium F initially included *F. pelagi* and *O. granulosus*, but *P. halotolerans* contamination occurred during the experiment. In consortium F, *O. granulosus* decreased to 6% over time, while *P. halotolerans* increased to 30%. *F. pelagi* initially decreased to 36% by day 35 due to the growth of *O. granulosus*, but rose to 64% by day 45. In consortium G, the relative abundance of *P. halotolerans* increased to 76%, while *F. pelagi* decreased to 24%. In consortium L, relative abundance of *P. pseudonitzschiae* was increasing, with a decrease in *P. halotolerans*, and *F. pelagi* decreased at the early stage and then

TABLE 2 Construction of artificial PS-degrading consortium based on diversity and PS degradation ability.

| Consortium | Bacterial Competition | Single strain | PS degradation |
|---|---|---|---|
| E | *Fulvimarina pelagi*<br>*Pseudosulfitobacter pseudonitzschiae* | +++<br>+++ | ++ |
| F | *Paracoccus halotolerans*<br>*Oceanicola granulosus*<br>*Fulvimarina pelagi* | w<br>–<br> | w |
| G | *Fulvimarina pelagi*<br>*Paracoccus halotolerans* | | w |
| L | *Fulvimarina pelagi*<br>*Pseudosulfitobacter pseudonitzschiae*<br>*Paracoccus halotolerans* | | + |
| M | *Fulvimarina pelagi*<br>*Oceanicola granulosus*<br>*Paracoccus halotolerans* | | +++ |
| O | *Fulvimarina pelagi*<br>*Pseudosulfitobacter pseudonitzschiae*<br>*Oceanicola granulosus*<br>*Paracoccus halotolerans* | | w |

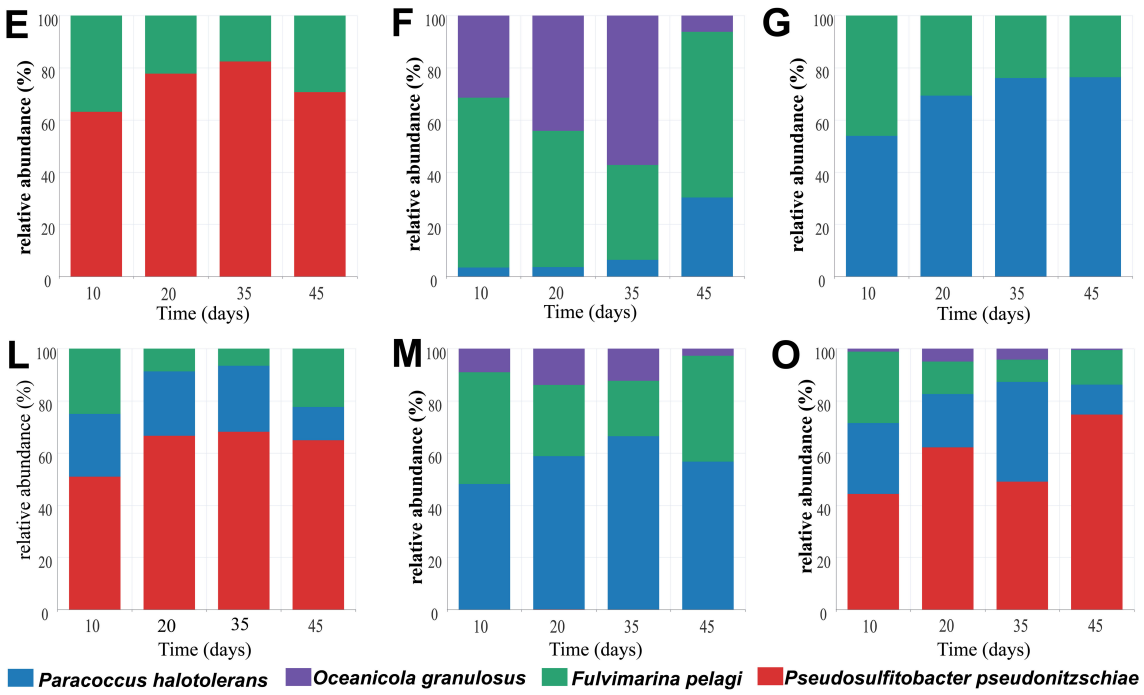


FIGURE 4
Dynamic change of bacterial consortium during PS degradation. After culturing *F. pelagi*, *P. pseudonitzschiae*, *P. halotolerans*, and *O. granulosus*, mixed them in a 1:1 ratio to construction combinations E, F, G, L, M and O containing 2 to 4 species, and observed the changes in relative abundance over 45 days.

increased. In consortium M, during a 45-day culturation, *O. granulosus* decreased to 3% with *P. halotolerans* increased to 57%, and *F. pelagi* was at the same level as in consortium L at 22%. In consortium O, relative abundance of *O. granulosus* decreased to 0.54% as in consortium M, in contrast, *P. pseudonitzschiae* increased to 75%, consistent with the performance in consortium E and L, additionally, *P. halotolerans* decreased to 11% after 45 days of cultivation, while *F. pelagi* decreased to 13%. In consortium E, the relative abundance of *P. pseudonitzschiae* significantly increased from the beginning of cultivation to the 35th day, indicating its potential dominance in the early stages of PS degradation. However, its abundance decreased at 45th day, possibly influenced by metabolic metabolites, whereas *F. pelagi* increased in relative abundance, suggesting a sustained degrading effect. *P. pseudonitzschiae* exhibits remarkable motility (Bartling et al., 2018), and may rapidly attach to plastic surfaces to form biofilms in *in-situ*. Additionally, *F. pelagi* showed increased biomass after 10 days of cultivation, but its proportion decreased when it was co-cultured with *P. halotolerans*. Given the low weight loss rate of 0.43% in consortium G, *P. halotolerans* might adversely affect *F. pelagi*. The consortium F and M showed that *P. halotolerans* also overcome *O. granulosus* by a high abundance.

*F. pelagi* and *P. pseudonitzschiae* showed significant biomass growth in the initial test of single bacterial degradation ability. Combined with the relative abundance of consortium, it can be considered that *F. pelagi* and *P. pseudonitzschiae* as key degraders within bacterial consortium.

## 3.5 Surface morphological and chemical characteristic changes of PS films treated by microbial consortia

With PS as the sole carbon source, different consortia were cultured in liquid MMC medium for 45 days, and SEM observation was performed to assess the biofilm formation and changes on the PS surface. The results showed that all the PS-degrading consortium could form dense biofilms on the PS surface, tightly attached to the PS surface after 45 days of incubation (Figure 5a). After removing the surface biofilm with 2% SDS, significant changes and obvious eroded pits were observed on the PS surface (Figure 5b). SEM observations confirmed the ability of different consortium to degrade PS plastic. Additionally, the hydrophobicity of the PS surface treated by bacterial consortium is decreased. To determine the change in hydrophobicity of PS plastic, the water contact angle was used to analyze the changes in the surface hydrophobicity "after PS degradation by the bacterial consortium for 45 days. After removing the biofilm on the PS surface using 2% SDS and drying overnight at 45°C, the contact angles were measured. As shown in Figure 6, the angles of consortium E, F, G, L, M, and O, were 70.99°, 72.02°, 71.30°, 79.38°, 80.12°, and 84.39°, respectively, which were much lower than the contact angle of the non-incubated control (93.26°). The results indicated that the hydrophobicity of the PS films was decreased due to the bacterial consortium. These results indicate that bacteria degrade PS plastic through extracellular oxidation, consistent with previous studies, wherein PS surfaces

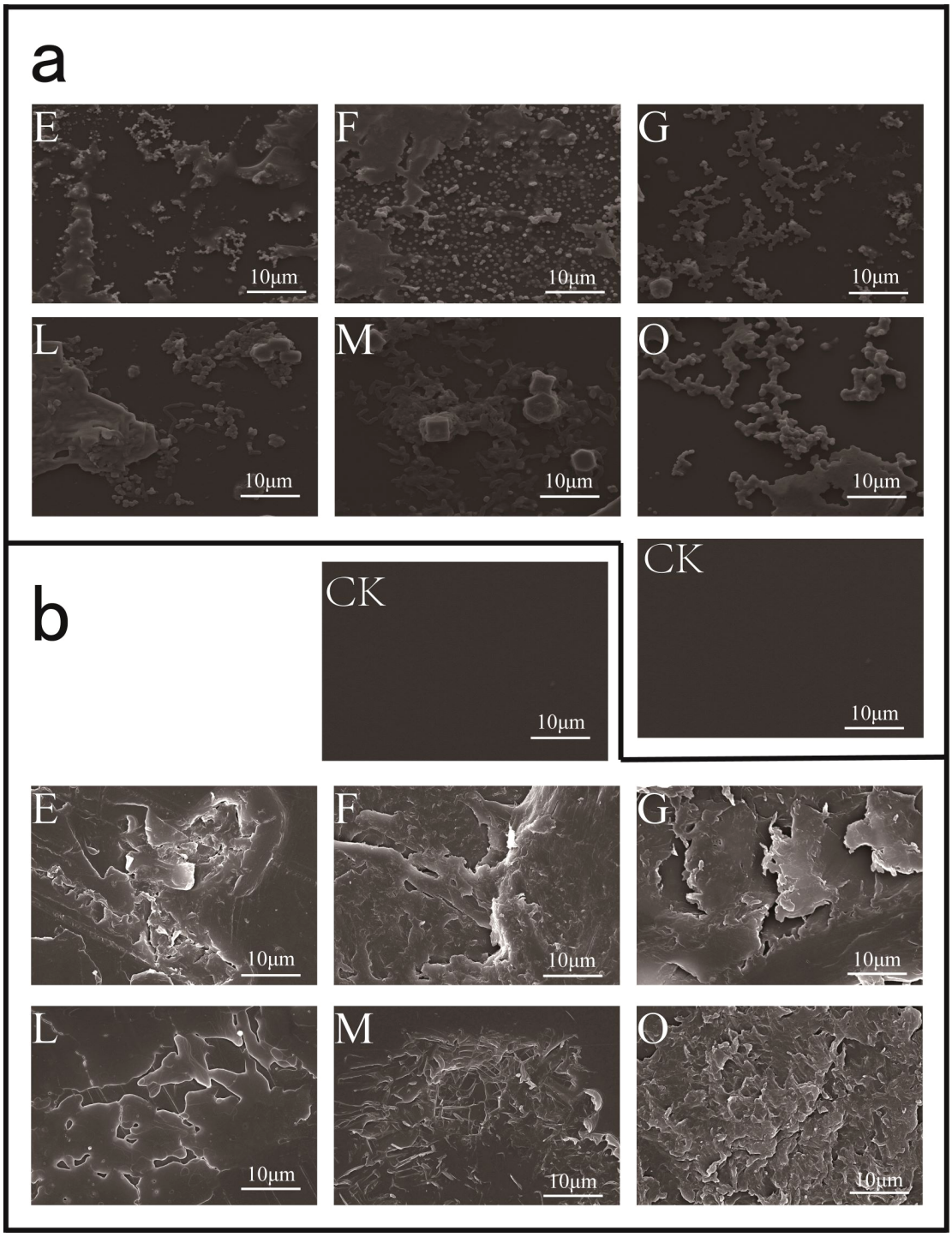


FIGURE 5
Observation of PS degradation by the six consortia for 45 days using SEM. **(a)**, Observation PS film surface treated by consortia E, F, G, L, M, and O compared with the non-inoculated PS (CK); **(b)**, treated by consortia E, F, G, L, M, and O were removed the biofilm with 2% SDS buffer, and evident etch pits were found on the PS surface.

treated by consortium showed hydrophobicity decrease and hydrophilicity increase (Yang et al., 2014). In addition, this reduction in hydrophobicity makes it easier for bacteria to attach to the plastic surface and enhance the degradation ability of plastic (Yang et al., 2015).

## 3.6 Chemical group changes on PS surface revealed by ATR-FTIR analysis

To further elucidate surface changes on PS after consortium treatment, characterization analysis was performed using ATR-


FIGURE 6
Changes in the contact angle between water droplets and the PS surface. On the PS surfaces treated by the consortium E, F, G, L, M, and O, respectively; the contact angle formed between water droplets and PS surface was reduced compared to the control.

FTIR. As shown in Figure 7, new functional groups appeared on the PS after treatment by the bacterial consortium. A new C-O group was detected at 1028 $cm^{-1}$, and a carbonyl group (C=O) was observed at 1601 $cm^{-1}$. These findings indicate that bacterial degradation of PS involves extracellular oxidation, consistent with previous studies on PS biodegradation (Arunrattiyakorn et al., 2022; Kim et al., 2021; Xing et al., 2021). In addition, it was observed that in the infrared spectrum (2800-3100 $cm^{-1}$), the CH vibration intensity was higher than that of the control. The appearance of new oxygen-containing functional groups on the plastic surface provides evidence that PS film degradation primarily occurs through oxidation processes (Dey et al., 2024).

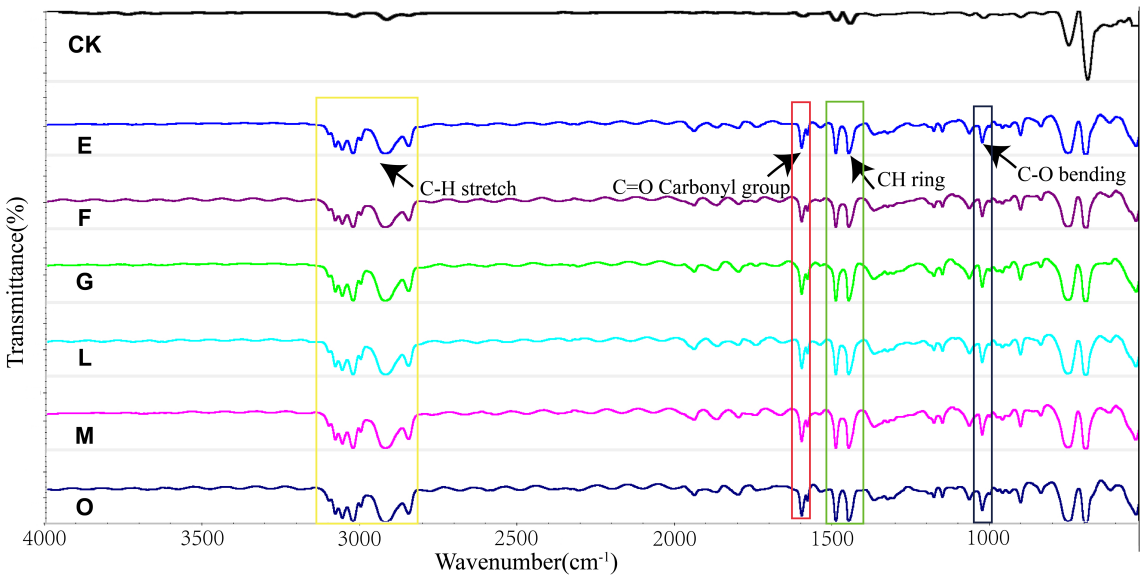


FIGURE 7
Characterization of biodegradation and oxidation of PS polymers by the six consortia using ATR-FTIR. Detection of C-O at 1028 $cm^{-1}$, C=O carbonyl group at 1601 $cm^{-1}$, and C-H vibrations at 2800-3100 $cm^{-1}$ higher than CK for the consortium E, F, G, L, M, and O.

## 3.7 Weight loss evaluation of PS films after degradation by bacterial consortium

To evaluate PS biodegradability of the consortium, the weight loss of PS film was measured after 45 days' cultivation with PS as the sole carbon and energy source in MMC medium. An independent-sample t-test was performed to assess the statistical significance of weight loss rate of PS (n = 3), evaluating biodegradation efficiency. The results showed that weight loss was statistically significant ($P < 0.05$) in all consortia. As depicted in Figure 8, consortium E exhibited a weight loss rate of 12.14%, however, *P. halotolerans* was added to consortium L, the weight loss rate decreased to 9.18%. The weight loss rate of consortium F was 3.91%, while consortium M was 18.9%, which was the same composition but in different proportions with consortium F. Furthermore, consortium G and O displayed extremely low weight loss rates, 0.43% and 1.57%, respectively.

Overall, *P. pseudonitzschiae* exhibited high relative abundance in all consortia, indicating its importance in the PS-degradation. In contrast, *O. granulosus* could not degrade PS, and in consortium F, a high initial proportion of *O. granulosus* correlated with poor degradation effects, but its sharp decrease over time suggests degradation occurred between days 35 and 45. Conversely, the consortium M showed an increased weight loss rate to 18.9% with the relative abundance of *O. granulosus* decreasing from 9% to 3% during a 45-day cultivation.

The notable efficiency of consortium comprising *F. pelagi*, *O. granulosus*, and *P. halotolerans*, may be attributed to impressive denitrification capabilities of the genus *Paracoccus* (Li et al., 2023), which has been reported as a typical S-oxidizing bacterium (Zhao et al., 2017). Studies indicate that endogenous microorganisms mainly including *Rhizobiales* significantly contribute to nitrogen cycling in coral reefs, particularly in coral skeletons (Moynihan et al., 2022). In plants, *Rhizobium* belonging to *Rhizobiales* forms symbiotic relationships with leguminous plants, which are crucial for nitrogen fixation processes (Lemos et al., 2021). The SoxB gene is detected in all investigated phototrophic and chemotrophic species (Meyer et al., 2007), primarily sourced from *Alphaproteobacteria* with *Rhizobiales* as the dominant group (Santana et al., 2021). Bacteria rich in sulfur-oxidizing genes encode and highly express genes for sulfur metabolism, carbon fixation, and nitrogen fixation (NifHDK) in a variety of conditions, demonstrating the connection between sulfur oxidation and nitrogen cycle mechanisms (Rolando et al., 2024). *Oceanicola* could produce poly-β-hydroxybutyrate (PHB), converting poly (butylene succinate) (PBS) into a more available internal carbon source, PHB, thereby enhancing denitrification activity (Ruan et al., 2016). Hence, the higher weight loss rate observed in consortium M might be attributed to the mutual promotion between sulfur-oxidation and denitrification.

*P. pseudonitzschiae* exhibited a high relative abundance across all reconstructed consortia, underscoring its significant role in PS

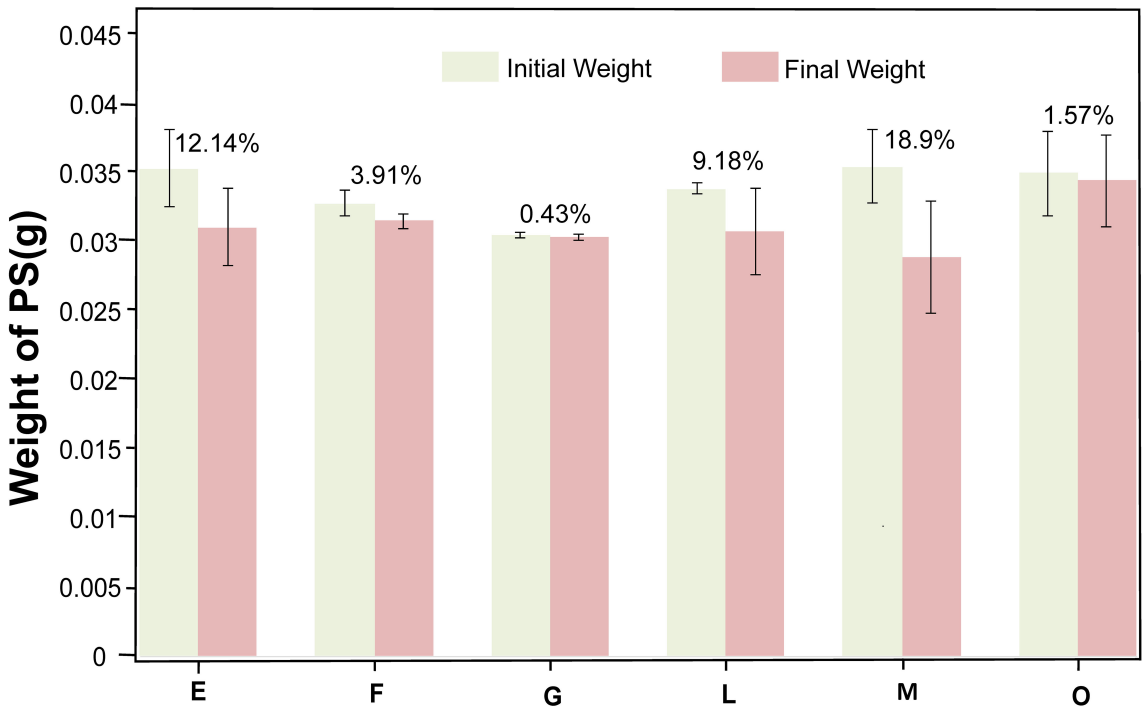


FIGURE 8
Weight loss of the PS film after being cultured for 45 days in consortia E, F, G, L, M, and O. After culturing the PS membrane as the sole carbon and energy source for 45 days, the biofilm was removed, and the weight loss of PS degraded by consortia E (12.14%), F (3.91%), G (0.43%), L (9.18%), M (18.9%), and O (1.57%) was measured, with three replicates per consortia.

degradation. However, *P. pseudonitzschiae* was excluded from the most efficient consortium, may be attributed to the production of certain metabolic byproducts by this bacterium, which inhibit the growth and degradation capabilities of other strains, a phenomenon frequently observed in microbial communities (Contreras-Salgado et al., 2024). Additionally, *P. pseudonitzschiae* possesses strong motility and biofilm formation capabilities, enabling it to rapidly attach to plastic surfaces and form biofilms in the early stages (Fei et al., 2020). This early attachment allows it to occupy advantageous positions, thereby inhibiting the attachment and growth of other strains. Results indicate that efficient degradation consortium is not merely a mixture of efficient PS degradation strains; non-degradation strains also play a crucial role within the consortium.

## 4 Conclusion

This study extended the bacterial diversity associated with EPS plastic wastes in the subtropical estuary coast of Xiamen Island, and obtained an engineered bacterial consortium constituted of *F. pelagi*, *P. halotolerans*. and *O. granulosus* showing a high weight loss by 18.9% in 45 days. The microorganisms enriched on EPS debris were exhibited differences from those in seawater and sandy sediments, and varied between microplastics and macroplastics. Co-occurrence network and bacterial characterization revealed that *Rhodobacterales* and *Rhizobiales* play important roles in PS degradation. The results expanded the diversity of PS-degrading bacteria, identifying several newly recognized bacterial taxa as PS degraders for the first time. Moreover, the non-degrading bacteria of *Oceanicola* also contribute to PS degradation, imply their role and interactions with PS-degraders in biofilms on plastic debris during plastic fragmentation and further breakdown in environments. The construction of a highly efficient consortium revokes further investigations in artificial consortia for plastic pollution remediation and recycling.

## Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: https://www.cncb.ac.cn/search/specific?dbId=bioproject&q=cra018003, CRA018003.

## Author contributions

JW: Conceptualization, Data curation, Formal Analysis, Methodology, Visualization, Writing – original draft. RL: Conceptualization, Methodology, Resources, Visualization, Writing – original draft. SZ: Conceptualization, Methodology, Validation, Writing – original draft. ZB: Conceptualization, Validation, Writing – original draft. ZS: Conceptualization, Funding acquisition, Resources, Supervision, Writing – review & editing.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The author(s) declared that they were an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

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