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# Microplastics threaten seagrass carbon sinks through microbial changes

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## ABSTRACT

Seagrass beds are key blue carbon ecosystems but their capacity to sequester carbon is threatened by microplastic (MP) pollution in the marine environment. A 28-day mesocosm experiment examined the effect of microplastics and nutrient enrichment (NE) on eelgrass (*Zostera marina*). We tested concentrations of 320 mg MPs per 100 g DW sediment$^{-1}$ and 70 mg of total nitrogen per 100 g DW sediment$^{-1}$ to evaluate impacts on plant performance, microbiome composition and detritus decomposition (after 60-days assay). MPs reduced leaf growth rate (−39 %), net production (−57 %) and rhizome elongation (−35 %), while NE shifted microbial assemblages, increasing phyllosphere and rhizosphere by 1.6-fold. MPs favored the growth of microbial taxa related with the consumption of plant-derived polysaccharides and lignin compounds (1.7-fold higher), accelerating detritus decomposition by 1.5-fold. Critically, MPs produced a notable decrease of bacteria involved in sulfur-cycle (0.45-fold lower under combined MPs + NE vs. NE alone), disrupting REDOX processes essential for seagrass survival in reducing sediments. By reducing plant growth, altering microbial communities and accelerating organic matter turnover, MPs compromise the carbon sequestration capacity of eelgrass meadows. These findings evidence the need for policies addressing plastic pollution to safeguard seagrass ecosystem services while prompt further research on mechanisms of interaction between MPs and biota.

## 1. Introduction

Seagrasses are marine foundation species that form ecologically and socio-economically critical yet threatened coastal habitats. They provide essential services such as carbon sink (Fourqurean et al., 2012), provision of shelter and food for marine fauna (McHenry et al., 2021; Jiménez-Ramos et al., 2021), wave attenuation (Infantes et al., 2011), shoreline stabilization (Infantes et al., 2022), and water quality improvement via particle trapping (Luhar et al., 2017). Despite their ecological importance, seagrass meadows have declined by ~20 % globally since the 19th century (Dunic et al., 2021), primarily due to anthropogenic stressors (eutrophication and climate change) and natural threats (disease, invasive species, among others) (Waycott et al., 2009; Unsworth et al., 2019). These stressors reduce meadow density and cover and disrupt ecosystem functions and services, including carbon cycling (Jiménez-Ramos et al., 2022; Yamuza-Magdaleno et al., 2025), potentially releasing buried carbon through remineralization processes (Egea et al., 2023a; Yamuza-Magdaleno et al., 2024).

Emerging contaminants such as sunscreens (Vilaplana et al., 2025), pharmaceutical residues (Egea and Jiménez-Ramos, 2025a) and microplastics (MPs; 1 μm–5 mm plastic debris; Kershaw, 2015) further threaten seagrasses in recent years. Polyethylene (PE) and polypropylene (PP) –the most abundant polymers in marine environments (Erni-Cassola et al., 2019)– accumulate in seagrass canopies and sediments (Egea et al., 2023b; Dahl et al., 2021). The accumulation of MPs in sediments is particularly favored by epiphytic bacteria via biofilm formation on the surface of MPs, causing them to sink (Zhao et al., 2022). While MPs impacts on marine fauna are well understood (Gall and Thompson, 2015), effects on submerged vegetation remain poorly understood (Li et al., 2023).

Although research indicates that seagrass beds act as a sink for MPs (de los Santos et al., 2021), little attention has been paid to the impact of MPs on the carbon sequestration capacity of this blue carbon ecosystem (Hou et al., 2024). MPs may alter the sediment properties (e.g. grain size, permeability; Wang et al., 2016) indirectly affecting organic carbon (OC) storage, which correlates with sediment characteristics in *Zostera*

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spp. (Serrano et al., 2016). In addition, MPs may alter the seagrass OC stock by alterations of microorganisms associated to these plants. In fact, rather than isolate organisms, animals and plants are viewed as “holobionts” or hosts for a myriad of both, symbiotic and non-symbiotic, microorganisms known as microbiome (Zilber-Rosenberg and Rosenberg, 2008). Seagrasses host a wide variety of microorganisms on their aboveground (i.e., phyllosphere) and belowground (i.e., rhizosphere) biomasses (Ugarelli et al., 2017). Microbiome is fundamental to nearly every aspect of its host and microbe–plant mutualisms have been reported to carry out a broad range of functions that may benefit the host plant, including growth and resistance to environmental stressors (Crump et al., 2018). Furthermore, microbiome seems to be a key component of community primary production by photosynthetic bacteria itself (Zhang et al., 2022) and enhanced nutrient availability and growth of the plant host (Tarquinio et al., 2019). Thus, microbiome represents a key and often overlooked component in the seagrass ecosystem service of carbon sequestration (Zhang et al., 2022, 2025).

Seagrass responses to MPs pollution might be modulated by anthropogenic nutrient load, as it represents a major stressor in coastal systems inhabited by seagrasses (Burkholder et al., 2007). Nutrient enrichment exacerbates seagrass decline by promoting opportunistic algae (Han et al., 2016), ammonium toxicity (Govers et al., 2014) and herbivory (Jiménez-Ramos et al., 2018). At community level, nutrient enrichment shifts meadows from autotrophic (i.e., with higher primary production than community respiration) to heterotrophic (Egea et al., 2020; Jiménez-Ramos et al., 2024a), and reduces sediment OC (Jiang et al., 2022; Zhang et al., 2025). These responses are mediated by the associated community (Jiménez-Ramos et al., 2017) and microbe–plant mutualisms (Zhang et al., 2022; Fuggle et al., 2023). For instance, the narrow oxic microzone surrounding roots is usually dominated by microaerophilic sulfide-oxidizing bacteria, which prevent sulfide accumulation (a potent plant phytotoxin; Lamers et al., 2013) in sediment surrounding the plant. That sulfide-oxidizing bacteria assemblage can be modified under nutrient enrichment condition triggering important consequences for seagrass performance (Fuggle et al., 2023). On the other hand, previous studies reported higher bacteria activity involved in sediment organic carbon (SOC) degradation under nutrient enrichment condition (Liu et al., 2017; Zhang et al., 2022), suggesting that higher nutrient load may reduce seagrass carbon sequestration potential. Therefore, changes in the microbiome of seagrass induced by higher nutrient load lead the response of the community to nutrient enrichment; but, likewise, might alter the resistance or resilience capacity of the plant to MPs pollution.

In this study, a set of laboratory experiments were performed to address the following questions: (1) How MPs and nutrient enrichment interactively affect *Zostera marina* morphology, growth, and production? (2) How these stressors alter the eelgrass microbiome and how this can lead the response of the community? To answer these questions, a 28–days indoor mesocosms containing transplanted *Zostera marina* shoots was conducted to quantify how incidences of MPs, higher nutrient load, or both stressors in combination alter the plant performance, microbiome, and the carbon sequestration capacity of seagrass beds.

## 2. Material and methods

### 2.1. Experimental design

The study was conducted in indoor mesocosms at Kristineberg Center for Marine Research and Innovation (Sweden) during June–September 2024. A full-factorial experiment was designed to test the individual and interactive effects of microplastics pollution and high nutrient enrichment in sediments. Four treatments were designed: control (CT, sediment without additives), nutrient-enriched (NE; 70 mg total nitrogen per 100 g dry weight sediment, using slow-release Osmocote™ fertilizer, N:P:K 22:7:14, based on Peralta et al., 2003), microplastic (MPs; 320 mg of polyethylene and polypropylene particles per 100 g dry weight sediment), and a combined nutrient-microplastic (NE-MPs, sediment with both nutrient and MP additions). Low-density polyethylene (LDPE) and polypropylene (PP) plastic types were selected as they dominate marine plastic pollution and are frequently found in seagrass sediments (Erni-Cassola et al., 2019; Huang et al., 2020). The MPs exposure concentration corresponding to approximately 900 particles per kg DW of sediment, which was in the range of the maximum values found in seagrass sediments (up to 884 particles per kg DW sediment; Huang et al., 2020). However, instead of making a MPs pattern in this experiment that fully match what was observed in seagrass sediments –with fibres (≈38 %) and fragments (≈43 %) as the dominant morphology and sizes below 250 μm; Huang et al., 2020– a commercially available (with similar composition) were used to ensure the reproducibility of the experiments in future research. The MPs were generated from transparent LDPE and PP plastic containers (Rotviksbro Handel AB, Uddevalla, Sweden) using a bullet blender to produce irregular spherical fragments representative of environmentally weathered plastics. Particle size analysis was conducted using an Olympus BX50 microscope coupled with cellSens software (Olympus, Tokyo, Japan) yielded mean diameters of 562 ± 34 μm for LDPE and 856 ± 61 μm for PP, ($n = 5$). These values were well below the upper size limit (5000 μm) for microplastics (Barnes et al., 2009).

Sediment was collected near an established eelgrass bed in Bokevik Bay (58°14′N, 11°26′E) at the Güllmarsfjord in Sweden at 6.3 m depth using a box corer, homogenized, sieved (500 μm) to remove fauna, and distributed into 16 cylindrical pots (10 cm diameter x 12.7 cm height, 1 L) (Fig. 1a). To prevent resuspension, a 5 cm layer of fine sand was placed on top of each pot. Pots were placed in four hydraulic flumes (350 × 80 × 80 cm) equipped with wave makers (0.5 Hz frequency) and dampers, maintaining a 45 cm water level (Infantes et al., 2021) (Fig. 1b and c). Sediment properties were measured by collecting ~60 mL from each sediment type ($n = 10$), using a cut-off syringe and dried at 60 °C for approximately 48 h. Dry bulk density (DBD) was calculated as the dry weight of the sediment divided by the volume of the original sediment sample. The percentage of water content of sediment ($\beta$) was determined as the difference between wet and dry sediment weight with respect wet weight. The average DBD values for mud were 0.61 ± 0.1 g DW $cm^{-3}$ with $\beta = 34 \pm 2$ %, while the fine sand portion had 1 ± 0.1 g DW $cm^{-3}$ and $\beta = 41 \pm 3$ %.

The flumes were preconditioned for five days with flow-through seawater (3–4 L $min^{-1}$, 18.2 °C, salinity 23.9 PSU, pH 8.0). Light conditions simulated natural coastal environments (14:10 light:dark cycle at 140 μmol photons $m^{-2}$ $s^{-1}$). This experimental setup allowed us to examine stressor effects under controlled but environmentally relevant hydrodynamic conditions while minimizing confounding factors. The bottom of the test section was covered with a “pot-bed” consisted of a PVC module with holes (10 cm diameter) distributed equidistantly along the test section to place the pots.

*Zostera marina* shoot were collected from Bokevik between 1 and 2 m depth. Shoots without visible signals of brown or necrotic black lesion area in leaves and intact rhizome-root systems were carefully extracted and transported to the laboratory within 20 min of collection. Plants were processed following techniques that allow successful transplants of eelgrass for experimentation (e.g., Kaldy et al., 2022; Egea et al., 2024a). The rhizomes were standardized to 4 cm (3–4 internodes) and roots to 4 roots × 2 cm in length. Thirty-two uniform shoots (0.69 ± 0.014 g Fresh Weight $shoot^{-1}$; 13.25 ± 0.21 cm of canopy height) were planted in experimental unit (2 shoots/pot).

The mesocosms system received continuous flow-through seawater from the adjacent fjord, maintaining stable conditions through the experiment: temperature (18.2 ± 1 °C), salinity (23.9 PSU) and pH (8.0). Wave generation at 0.5 Hz frequency produced a gentle oscillatory flow with a mean velocity of 5 cm/s, simulating natural shallow-water hydrodynamic conditions (Infantes et al., 2021). Flow velocities were quantified using an acoustic Doppler velocimeter (Nortek, Vectrino,

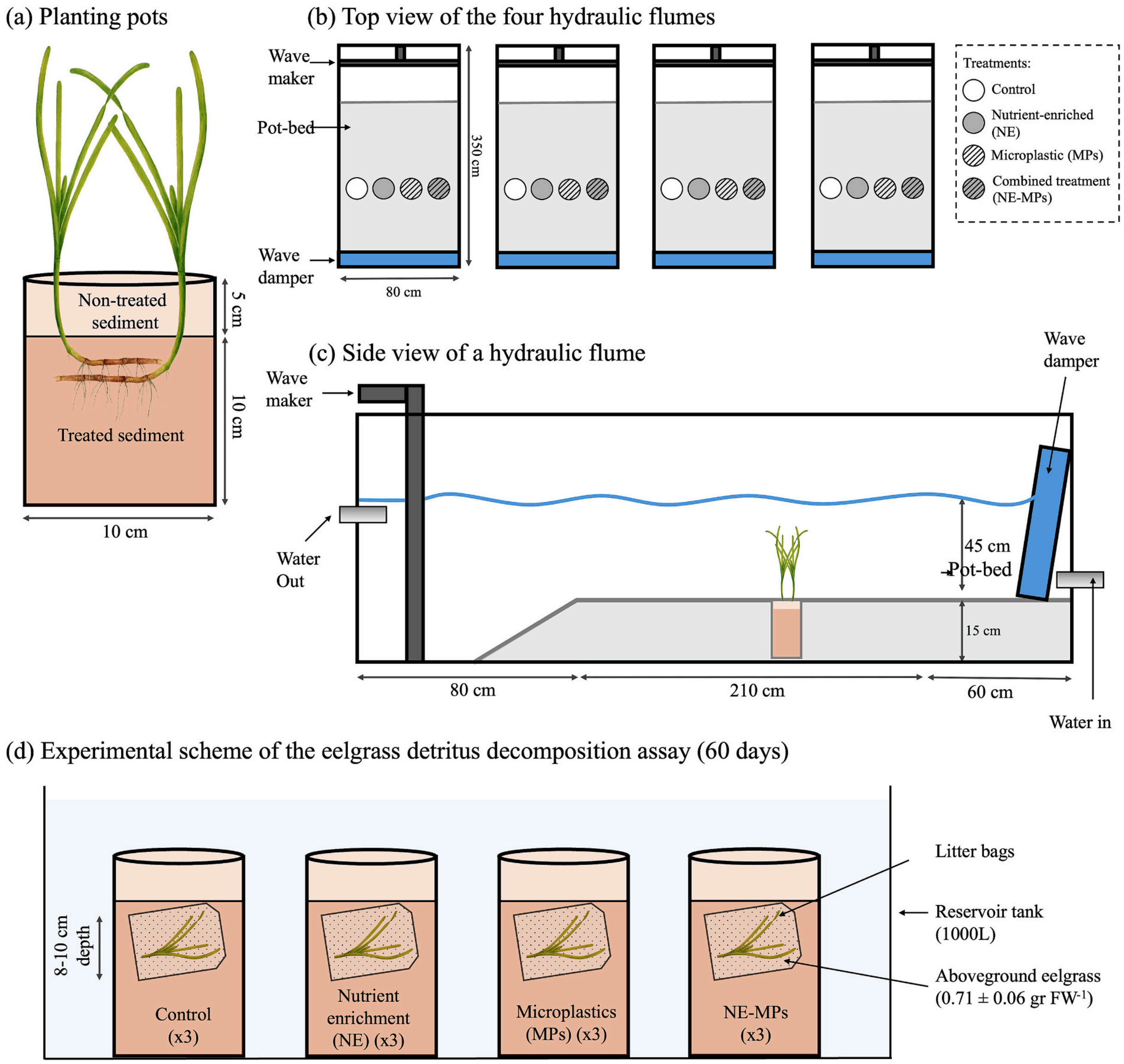

**Fig. 1.** Experimental wave mesocosms system: (a) planting pots, (b) top view, c) side view of hydraulic flume generating 0.5 Hz waves (see Infantes et al. (2021) for details), and (d) experimental scheme of the eelgrass detritus decomposition assay (60 days).

ADV), configured with a 25 Hz sampling rate and 7 mm sampling volume. Flow velocity measurements were performed at 10 cm above the bottom and 5 cm upstream of the experimental pots to avoid interference with seagrass leaves, following previous studies (Luhar et al., 2010). The light system (HelioSpectra lamps) provided 140 μmol photon $m^{-2}$ $s^{-1}$ during 14:10 Light:Dark cycle, with 1-h sunrise/sunset transition (3 steps of ±25 % light adjustment) providing a total daily photon flux of 7.4 mol photon $m^{-2}$ $d^{-1}$ to meet the optimal photosynthetic requirements for eelgrass growth (Olesen and Sand-Jensen, 1993).

### 2.2. Plant response variables

After 28 days of experimental period, plants were collected to estimate production (net production rate based on biomass), aboveground growth (through leaf growth rate, increase in canopy height and photosynthetic surface), belowground growth (through number and length of roots), and potential of expansion of the meadow cover (through new shoots appearance and rhizome length). The net production rate (NPR; mg FW $shoot^{-1}$ $d^{-1}$) was obtained by the difference between the fresh biomass at the end of the experiment and the initial fresh biomass of each shoot, divided by the experimental period. The leaf growth rate (LGR; cm $shoot^{-1}$ $d^{-1}$) was measured using a modified Zieman method widely used to estimate seagrass growth (Jiménez-Ramos et al., 2024b). A hypodermic needle was used to punch a hole just above the ligule in the youngest leaf of all shoots at the start of the experimental period. Marked shoots were collected at the end of the experimental period to estimate the LGR. The number of leaves loss (LL; n° leaves loss $shoot^{-1}$) was obtained by accounting the number of old leaves loss from the marked leaf for each shoot.

The increase in canopy height (Δ canopy height; cm) was calculated as the difference between the maximum leaf length at the end and at the beginning of the experimental period. The increase in leaf photosynthetic area rate (LPR; $cm^{-2}$ $shoot^{-1}$ $d^{-1}$) by using a ruler (± 0.1 cm) and digital caliper (± 0.01 mm) to measure the length and width of all leaves of shoots at the beginning and at the end of the experimental period. The increase in photosynthetic surface (ΔPS; $cm^2$ $shoot^{-1}$ final/initial) was obtained as the $LPR_{final}/LPR_{initial}$. The new shoots appearance (n° new shoots · initial $shoot^{-1}$) was obtained by accounting the number of new shoots per initial shoot. The rhizome elongation (i.e., increase of rhizome length; cm) was calculated as the difference between the rhizome length at the end and at the beginning of the experimental period. All equations used for these estimates of plant growth are provided in the Supplementary material.

The root system was characterised, by scanning the belowground biomass of shoots with a 600 dots per inch (DPI), Epson XP-2200 scanner. The high-resolution images were processed using Image-J software with the SmartRoot plugging. SmartRoot is a semi-automated powerful tracing algorithm to plant roots characterization (Lobet et al., 2011). A calibration image to pixel/mm was made for each image using a ruler scanned along with each root system. Each root was manually traced and automatically measured with SmartRoot where the number of roots (n° roots shoot$^{-1}$) and roots length (cm) were determined.

### 2.3. Sample collection and measurement for microbiome

For the microbiome analysis, three shoots per treatment were aseptically collected using sterile gloves. Shoots were carefully extracted from the sediment to maintain their root structure intact and were placed in sterile 50 mL vials. From each shoot, 1) phyllosphere samples from 8-cm sections of the second youngest leaf from each plant (n = 3), was collected and gently rinsed 3–5 times with sterile seawater, and 2) rhizosphere samples obtained by gently shaking roots to remove loose sediment, followed by washing with 0.2 μm filtered seawater to recover root-adhere microbes (Cúcio et al., 2016). Sterile DNA/RNA Shield preservative (Zymo Research, CA, USA) was used to store all microbiome samples in DNA LoBind tubes at −80 °C.

At Novogene GmbH (Munich, Germany), PCR amplification, library preparation, and sequencing were carried out. First, in accordance with internal corporate procedures, DNA concentrations were standardized across samples. The V4-V5 region of the 16S rRNA gene was then amplified using the primers 515F (GTGCCAGCMGCCGCGGTAA) and 907R (CCGTCAATTCCTTTGAGTTT) (Westermann et al., 2017), and library preparation was performed using the NEBNext® Ultra™ II DNA Library Prep Kit with index adapters synthesized in-house by Novogene. Qubit and real-time PCR were used to quantify the resultant libraries, and a bioanalyzer was used to evaluate the fragment size distribution. Libraries were then sequenced on the Illumina NovaSeq 6000 SP platform (Caporaso et al., 2012) with 150 bp paired-end reads, which yielded 5.04 million read-pairs in plant samples and 1.78 million read-pairs in eelgrass detritus samples. The chimeric sequences in Clean Tags were detected and removed, leaving the Effective Tags which were used for subsequent analysis. Reads were clustered into operational taxonomic units (OTUs) at 97 % similarity using the default Opti clustering method implemented in mothur.

### 2.4. Eelgrass detritus decomposition assay

At the end of 28-day exposure period, a decomposition experiment was conducted using three randomly selected pots per treatment (n = 3) (Fig. 1d). A sample of eelgrass aboveground biomass from each pot was weight (ca. 0.71 ± 0.06 g FW), placed in litter bags and buried at a depth of about 8–10 cm in each pot, respectively. The samples were held in a tank of 1000 L (1.5 × 1.5 m) with similar seawater conditions than used in exposition period. The tank had an open flow-through system (3.6 L min$^{-1}$), 18 °C, salinity of 23.9 PSU and 8 pH. After 60 days of incubation, the biomass was weighed and dried (60 °C for 72 h) to obtain the dry weight. The biomass of the initial and the post incubation elapsed were measured to calculate the percentage of mass remaining after incubation. A part of the plant remains found in the litter bags were used to analyze the microbiota following the method described in the previous section.

### 2.5. Data and statistical analyses

All statistical analyses and visualization were performed using R 4.4.1 (R Core Team, 2024). Differences in response variables among the four treatments (control, NE, MPs and NE-MPs) were tested using generalized linear models (GLMs). Prior to this analysis, normality and homoscedasticity in the response variables were tested using the Shapiro-Wilk and Levene's tests, respectively. All response variables were initially modelled with a Gaussian distribution and identity link, but if the residuals of a Gaussian GLM for a given response variable did not meet the assumption of normality, a GLM with a Gamma error distribution and reciprocal link function was used (which was the case for increase in photosynthetic surface, the number of roots, the maximum root length). The significance level (α) set for all tests was 0.05.

To visualize main changes in microbiota among treatments, OTUs were plotted and grouped into phylum (OTU reads assigned to chloroplast, mitochondria and others rated as low-quality were removed from the plots and the subsequent analyses). Changes in bacterial diversity (i.e., the number of different OTUs observed) and abundance (i.e., the number of reads per OTU) was evaluated through a classification into bacterial families. Rarefaction curves were used to assess differences among treatments through rarefaction and extrapolation implemented in the ‘iNEXT’ R package (Hsieh et al., 2016). Microbiome dissimilarity between the two seagrass compartments (i.e., phyllosphere and rhizosphere) and among treatments were determined using non-metric multidimensional scaling (NMDS) based on the Bray-Curtis distance (Oksanen et al., 2024). Additionally, significant differences among obtained clusters were tested using a permutational multivariate analysis of variance (PERMANOVA) with 999 permutations implemented using the adonis function from the ‘vegan’ package. To explore which taxa most contributed to the observed dissimilarity (observed only in rhizosphere), similarity percentage analysis (SIMPER) with 999 permutations were used. The top-ranked OTUs in this analysis (i.e., those with the highest contribution to dissimilarity) were overlaid on the NMDS graph with the ‘envfit’ function (a list of all OTUs obtained from ‘envfit’ results is provided as Table S1 in the Supplementary material). In addition, to illustrate the differences in the rhizosphere bacterial assemblage among samples, the top 50 OTUs with the highest average difference in relative abundances between the two treatment clusters created by the Bray-Curtis dendrogram analysis was plotted.

## 3. Results

### 3.1. Effects on *Z. marina* plants

Microplastic exposure (MPs) significantly reduced eelgrass growth, reducing leaf growth rate (LGR) by −39 % and aboveground biomass by −35 % compared to control plants (Fig. 2a, b; Table S2 in the Supplementary material). In contrast, nutrient enrichment (NE) alone did not significantly affect these parameters relative to controls (Fig. 2a, b and Table S2). The combined treatment (MP + NE) produced effects comparable to MPs alone, suggesting that MPs dominated the stress response.

Belowground biomass showed a different pattern, with all treatments exhibiting reductions versus controls (NE: −27 %; MPs: −35 %; combined: −20 %), though only the MPs effect reached statistical significance (Fig. 2c). The most comprehensive metric, net production rate (NPR), revealed particularly severe impacts from MPs (−57 %) and the combined treatment (−67 %), indicating that this stressor substantially compromised overall plant productivity (Fig. 2d).

Nutrient enrichment (NE) alone did not significantly affect aboveground tissue production, maintaining photosynthetic surface and canopy height comparable to control. In contrast, microplastic exposure (MPs) showed a non-significant reduction in these parameters (photosynthetic surface: −23.5 %; canopy height: −14.5 %; Fig. 3a, b). However, NE treatment showed the lowest rate of new shoots formation among all groups being the only significantly lower than control (Fig. 3c). While all experimental treatments displayed high leaf loss relative to controls, this effect reached statistical significance only in the

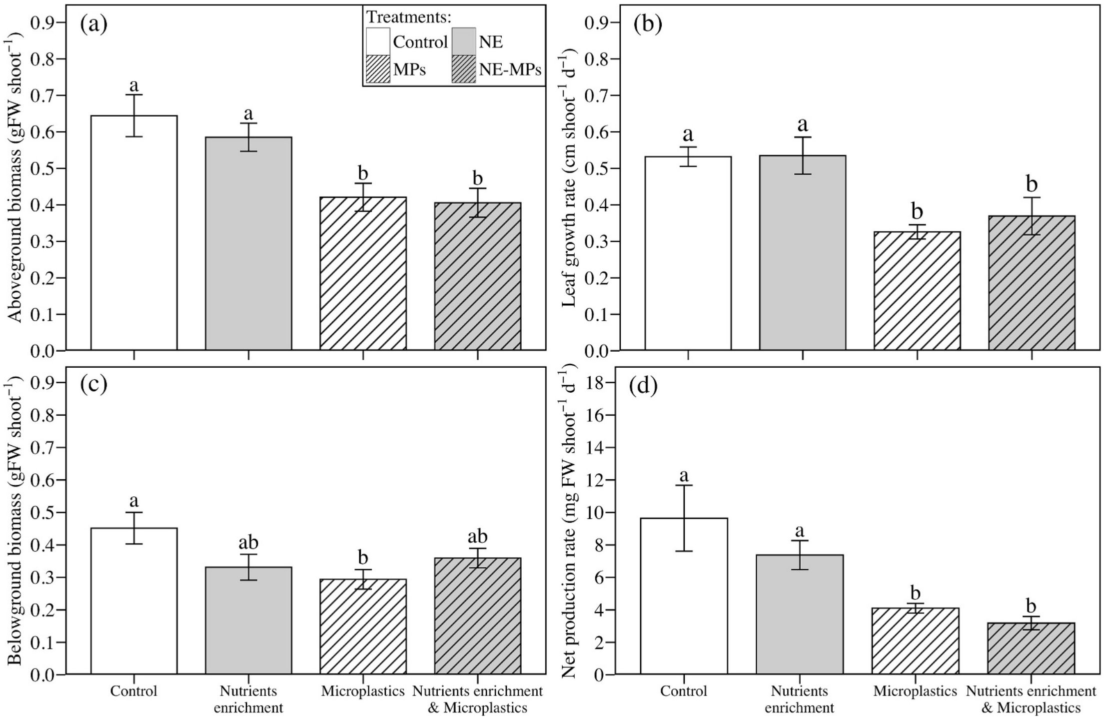

**Fig. 2.** Effect of nutrient enrichment, microplastics and their combinations on (a) aboveground biomass, (b) leaf growth rate (LGR), (c) belowground biomass, and (d) net production rate (NPR) of eelgrass. Letters above SE indicate significant differences among treatments ($p < 0.05$).

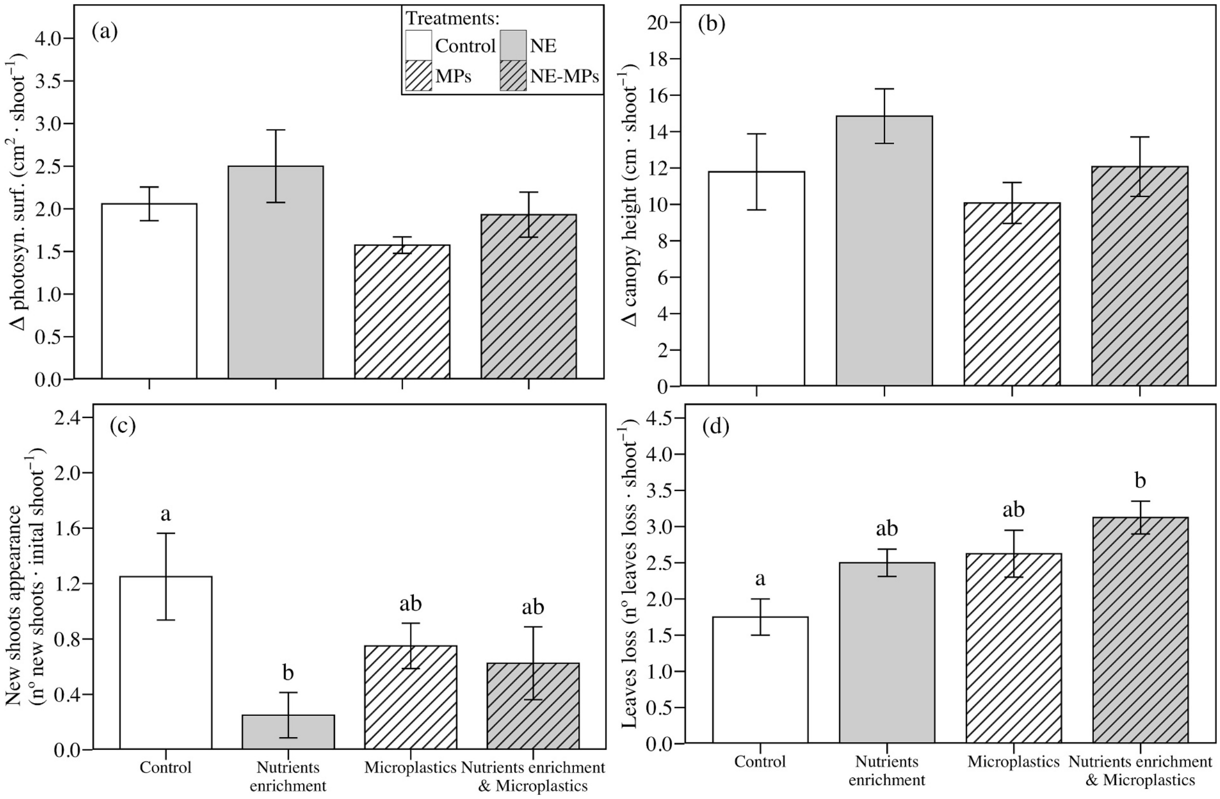

**Fig. 3.** Effect of nutrient enrichment, microplastics and their combinations on (a) the increase in photosynthetic surface, (b) increase in canopy height, (c) new shoots appearance, and (d) number of leaves loss during experimental period. Letters above SE indicate significant differences among treatments ($p < 0.05$).

combined MP + NE treatment (Fig. 3d and Table S3 in the Supplementary material).

Control plants had the greatest rhizome elongation, while microplastics-exposed treatments (MPs and NE-MPs treatments) showed significantly reduced growth, declining by −34.9 % and − 32.8 %, respectively (Fig. 4a). Similarly, both average and maximum root length

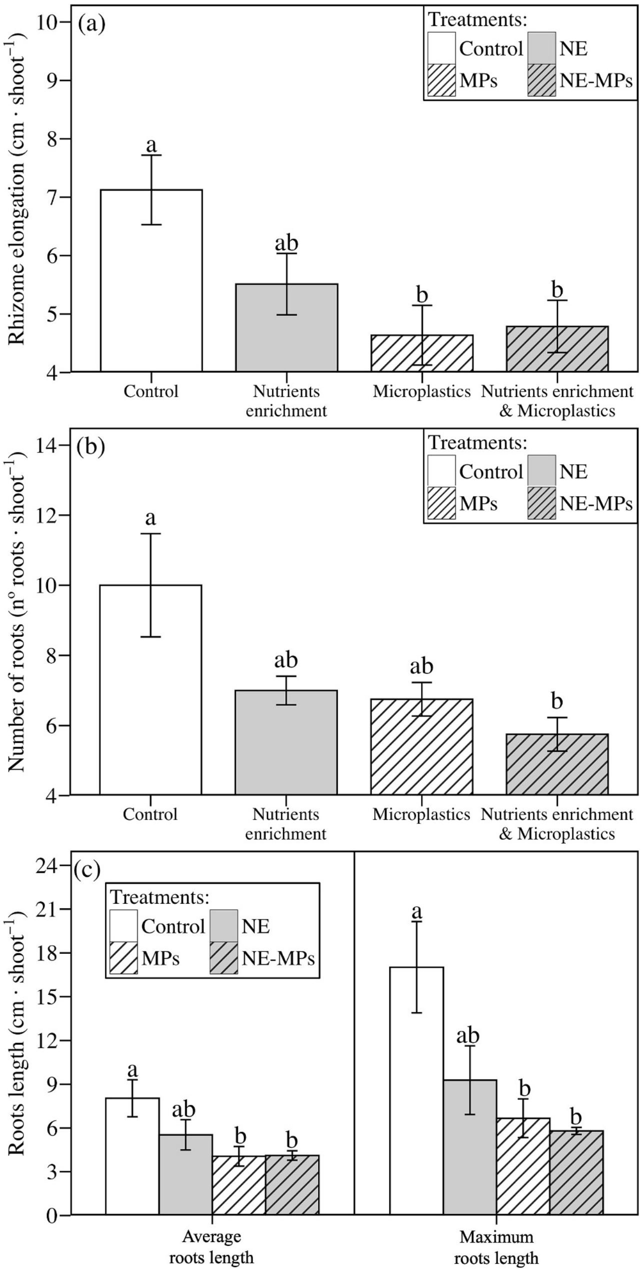

**Fig. 4.** Effect of nutrient enrichment, microplastics and their combinations on (a) final rhizome length, (b) number of roots, and (c) mean (left panel) and maximum (right panel) roots length. Letters above SE indicate significant differences among treatments ($p < 0.05$).

were significantly reduced in MP-exposed treatments (Fig. 4b). The combined NE-MPs treatment had the most pronounced and significant effect, demonstrating the strongest reduction in root number compared to all other groups (Fig. 4c; Table S4 in the Supplementary material).

### *3.2. Effects on the associated microbiome*

After filtering low-quality, unidentified chloroplast, and mitochondria reads, 1,461,222 operational taxonomic units (OTUs) were identified across all samples. The bacterial OTUs were classified into 436 families (see repository dataset at https://doi.org/10.5281/zenodo.15490210). Microbial diversity differed markedly between plant compartments, with 274 families in leaf-associated (phyllosphere) communities compared to 383 in root-associated (rizhosphere) communities. The phyllosphere was dominated by Proteobacteria and Bacteroidota while the rhizosphere showed greater phylogenetic diversity with Proteobacteria, Campylobacterota, Bacteroidota and Desulfobacterota (Fig. 5).

Distance-based analyses show strong compartment-specific clustering of microbial communities, with clear separation between phyllosphere and rhizosphere assemblages (PERMANOVA, F = 22.46, *p*-value < 0.001, and $R^2$ = 0.51, Fig. S1). However, when analyzed separately, rhizosphere microbial communities were clustered based on exposure stressors, particularly among treatments with nutrient enrichment (with NE and NE-MPs treatments forming a separated branch) and control counterparts (PERMANOVA, F = 2.94, *p*-value = 0.0016, and $R^2$ = 0.23) (Fig. 6a and b). By contrast, no such trend was observed in the phyllosphere microbiome. The rarefaction curves indicated that, either in phyllosphere and rhizosphere, the abundance was higher in the NE treatment compared to control counterpart, though difference was only statistically significant for abundance in rhizosphere. This tendency was attenuated when NE is combined with microplastics (i.e., NE-MPs treatment) (Fig. 6c; Table S5 in Supplementary material).

The main drivers of the clustering of the bacterial community in rhizosphere were the higher abundance of some families including groups involved in sulfur metabolism such as Arcobacteraceae, Desulfocapsaceae, Sedimenticolaceae, Desulfobacteraceae and Desulfovibrionaceae and groups involved in remineralization and processing of organic carbon such as Spirochaetaceae, Bacteroidetes BD2-2 and Flavobacteriaceae, among others (Fig. 7). Conversely, Sulfurovaceae, Anaerolineaceae and Thermoanaerobaculaceae showed significant depletion in treatment groups. In addition, a trend toward the enrichment of certain families that are known to degrade complex polymeric substrates such as plant-derived polysaccharides and lignin was observed in samples in MPs treatment. This included families such as Flavobacteriaceae, Marinilabiliaceae, Sandaracinaceae, Bacteroidetes BD2-2, SB-5, Lachnospiraceae, Saprospiraceae and Colwelliaceae –1.7-fold higher by summing, from an average of 16 ± 2.4 % of relative abundance in control to 27.6 ± 3.2 % in MPs treatment.

### *3.3. Effects on eelgrass detritus decomposition*

All experimental treatments significantly enhanced detrital decomposition, as evidenced by reduced remaining biomass relative to controls (Fig. 8a; Table S6 in Supplementary material). Nutrient enrichment (NE) showed the strongest effect (54.6 % mass loss increase), followed by the combined NE-MPs treatment (46 %), and MPs alone (35.8 %). These decomposition patterns corresponded with distinct microbial phylum-level shifts: Desulfobacterota dominated NE treatments, Spirochaetota characterised MPs exposed sediments, while NE-MPs treatments showed co-dominance of Bacteroidota and Desulfobacterota (Fig. 8b). Consequently, the rate of eelgrass detritus decomposition increased in expose treatments by x2.2 (NE), x1.5 (MPs), and x1.9 fold (NW-MPs) compared to control.

## 4. Discussion

This study provides the first comprehensive evidence that microplastic pollution in marine sediments fundamentally alters the carbon sequestration capacity of seagrass meadows through coupled plant-microbial interactions. The innovative mesocosm approach reveals three novel findings: (1) microplastics reduce *Zostera marina*'s carbon storage potential both directly (via impaired growth) and indirectly (via accelerated detritus decomposition); (2) the observed 1.7-fold enrichment of polymer-degrading microbial taxa in MP-exposed sediments demonstrates a previously unrecognized pathway for plastic-induced carbon cycle disruption; and (3) nutrient enrichment exacerbates MP effects on belowground microbial sulfur cycling –a critical ecosystem service for seagrass survival. This mechanistic knowledge advances

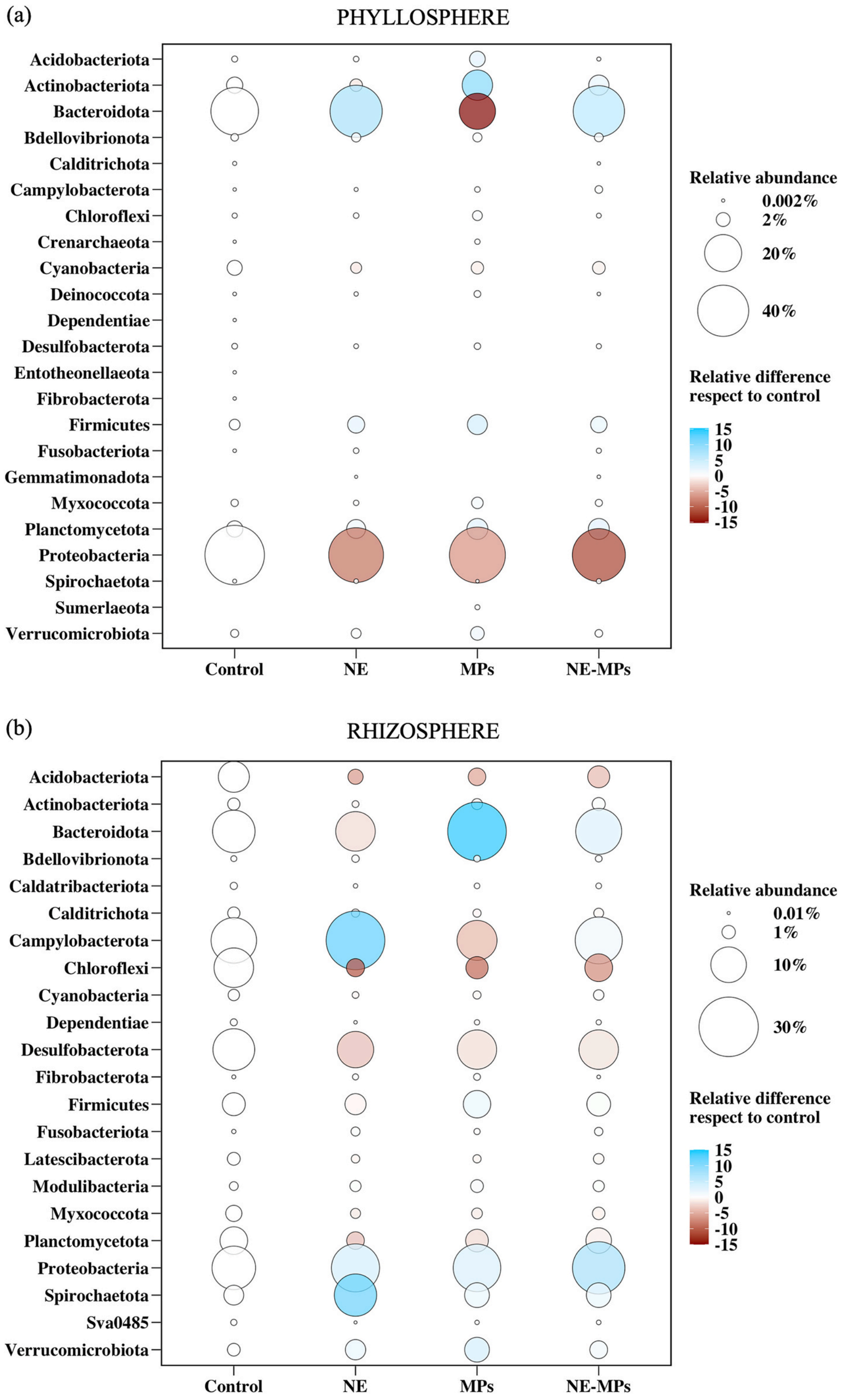

**Fig. 5.** Comparative phylum-level abundance between (a) phyllosphere and (b) rhizosphere microbial communities. Bubble size represents the average OTUs relative abundance (%) across treatments, while colour gradient (blue to red) indicates treatment specific increases or decreases relative to control conditions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

beyond previous toxicity studies by quantifying how microplastics reshape ecosystem-scale functions on blue carbon habitats.

### 4.1. Eelgrass responses to MPs

This study demonstrates that microplastics (MPs) pollution significantly reduces eelgrass productivity, with particularly strong reductions in leaf growth rate (39 %), net production rate (57 %), and rhizome elongation (35 %) after 28 days of exposure. These findings extend previous short-term (<15 day) observations of MPs toxicity in seagrasses (Menicagli et al., 2022; Molin et al., 2023) by showing these stress responses persist through critical vegetative growth periods. For

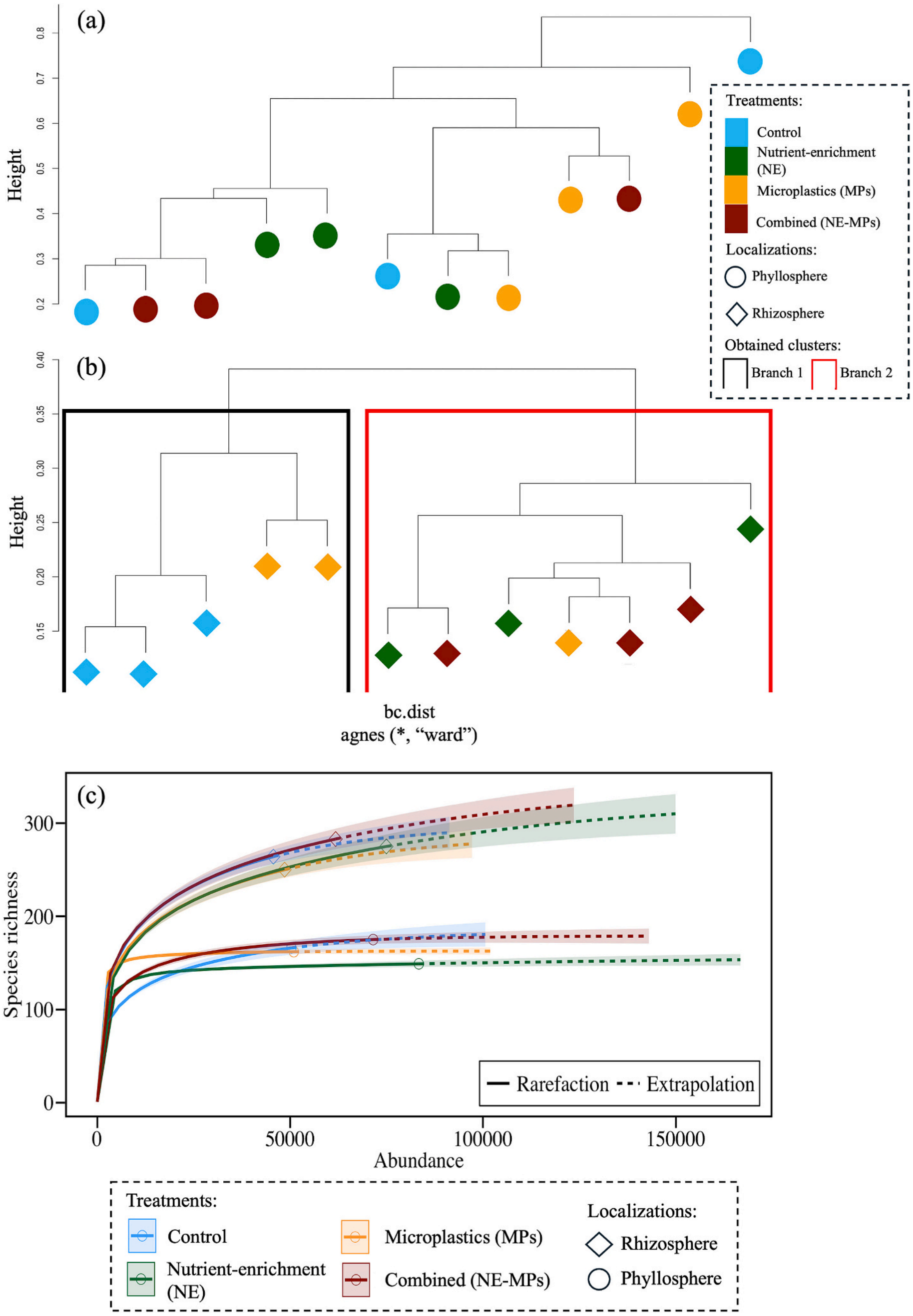

**Fig. 6.** Microbial community analysis showing dendrogram clusters based on Bray–Curtis dissimilarity matrix for (a) phyllosphere and (b) rhizosphere-associated microbes and (c) curves comparing rarefaction (interpolation) and extrapolation (prediction) calculated with the average abundance and family richness of each treatment in phyllosphere and rhizosphere.

instance, Menicagli et al. (2022) reported oxidative stress, higher leaf loss rate and root degeneration during 12 days of polystyrene (PS) exposure in *Cymodocea nodosa*. In addition, Molin et al. (2023) reported lower respiration rate in *Z. marina* leaves exposed during 14 days to PE and PP.

The results demonstrated that microplastics exposure significantly reduced *Zostera marina* root development, reducing both root numbers and length. This observation aligns with documented MP-induced root damage across plant species, including cell viability in terrestrial plants (Kalčíková et al., 2017; Yu et al., 2021) and root degeneration in the seagrass *Cymodocea nodosa* (Menicagli et al., 2022). Such root architecture alterations likely comprise nutrient uptake efficiency, creating a cascade effect that ultimately reduces whole-plant productivity and growth.

The observed reduction in plant growth can be attributed either the physical impact of microplastic polymers themselves or the leaching of plastic-associated chemical additives, which are incorporated during manufacturing to increase performance and durability (Hermabessiere et al., 2017). Polymers may obstruct root cell wall pores and modify the soil physicochemical properties, thereby impairing nutrient uptake and suppressing plant growth (Kalčíková et al., 2017; Ge et al., 2021). Additionally, direct root uptake of microplastics can induce oxidative stress and root degeneration and further compromising root functionality (Menicagli et al., 2022). Beyond polymer effects, chemical additives leached from microplastics can be absorbed by plants, where they reduce photosynthetic efficiency in both aquatic plants (Gao et al., 2025) and seagrasses such as *Cymodocea nodosa* (Adamakis et al., 2021). These additives may also disrupt associated bacterial communities

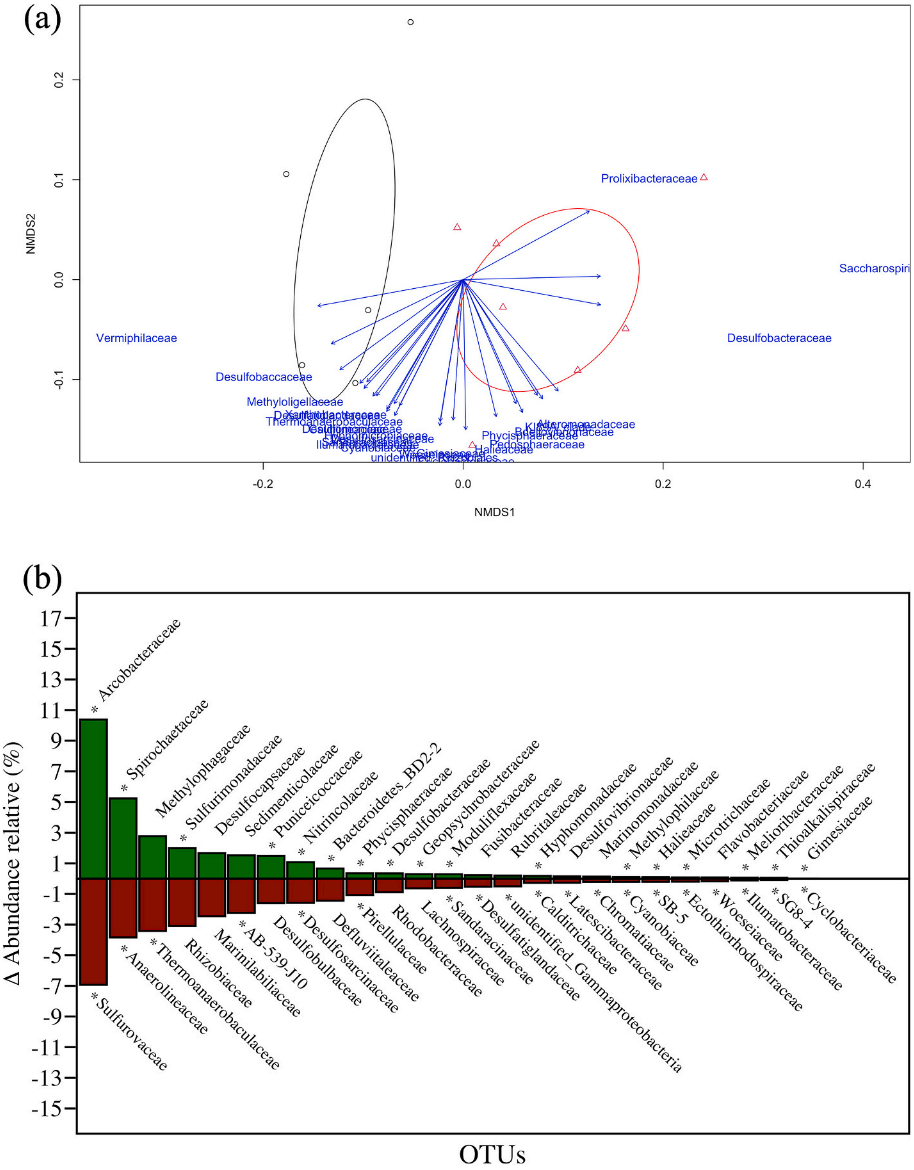

**Fig. 7.** Rhizosphere microbiome response to treatments. (a) Non-metric Multi-dimensional Scaling (NMDS) ordination of rhizosphere microbial communities, with 95 % confidence ellipses for each treatment cluster. Arrows show OTUs with the highest contribution to dissimilarities (*envfit*; $p < 0.001$) based on SIMPER pairwise tests. Full OTUS list obtained from 'envfit' results in Table S1 in Supplementary material. (b) Top 50 OTUs differing most in relative abundances between clusters. Positive/negative values indicate enrichment/reduction between clusters. Asterisks mark significant differences ($p < 0.05$).

(Zhou et al., 2024), indirectly exacerbating impacts on host plants.

Interestingly, while MPs exposure did not significantly alter overall microbial richness or abundance in the rhizosphere, it induced distinct compositional shifts reducing or favoring different taxa. Particularly a 50 % reduction in Rhodobacteraceae was found, which is known by both, attend community carbon fixation (Korlević et al., 2021) and because its role in antioxidant production (Miyamoto et al., 2023). In addition, an enrichment of Flavobacteriaceae, Marinilabiliaceae, and Bacteroidetes BD2-2 families were reported, which are known for their capacity to degrade complex polymeric substrates such as plant-derived polysaccharides and lignin (Wang et al., 2021). Along with these families belonging to the phyla Bacteroidota, a notable increase in Proteobacteria (Fig. 5) was observed in the MPs treatment. Both phyla are usually found as secondary colonizers of the surface of MPs (i.e., once the biofilm around MPs is stabilized; Hou et al., 2025) in the marine systems. These findings suggest that MPs not only physically damage roots but also modify rhizosphere ecology by promoting microbial groups adapted to plastic surfaces, potentially creating feedback loops that further influence plant-microbe interactions and organic matter cycling.

While polypropylene (PP) and low-density polyethylene (LDPE) rank among the least hazardous polymers in some assessments (Lithner et al., 2011) such classifications frequently exclude consideration of chemical additives (Yuan et al., 2022) and are inherently limited by the extremely high diversity of polymers formulations, production methods and environmental contexts (Omidoyin and Jho, 2024). Notably, PP and LDPE contain substantial additive loads (10 % by volume; Murphy, 2001). Environmental factors including UV radiation and temperature can accelerate the leaching of these additives (Do et al., 2022), potentially creating significant risks (Maddela et al., 2023). In this study, these additives may represent a primary mechanism for the observed microplastic-biota interactions. However, as the experimental design did not include pure polymer controls, effects caused by the base polymers versus their chemical additives cannot be definitively distinguish. On the other hand, comparative studies indicate PP may pose a moderately higher environmental risk than LDPE (1.2-fold; Yuan et al.,

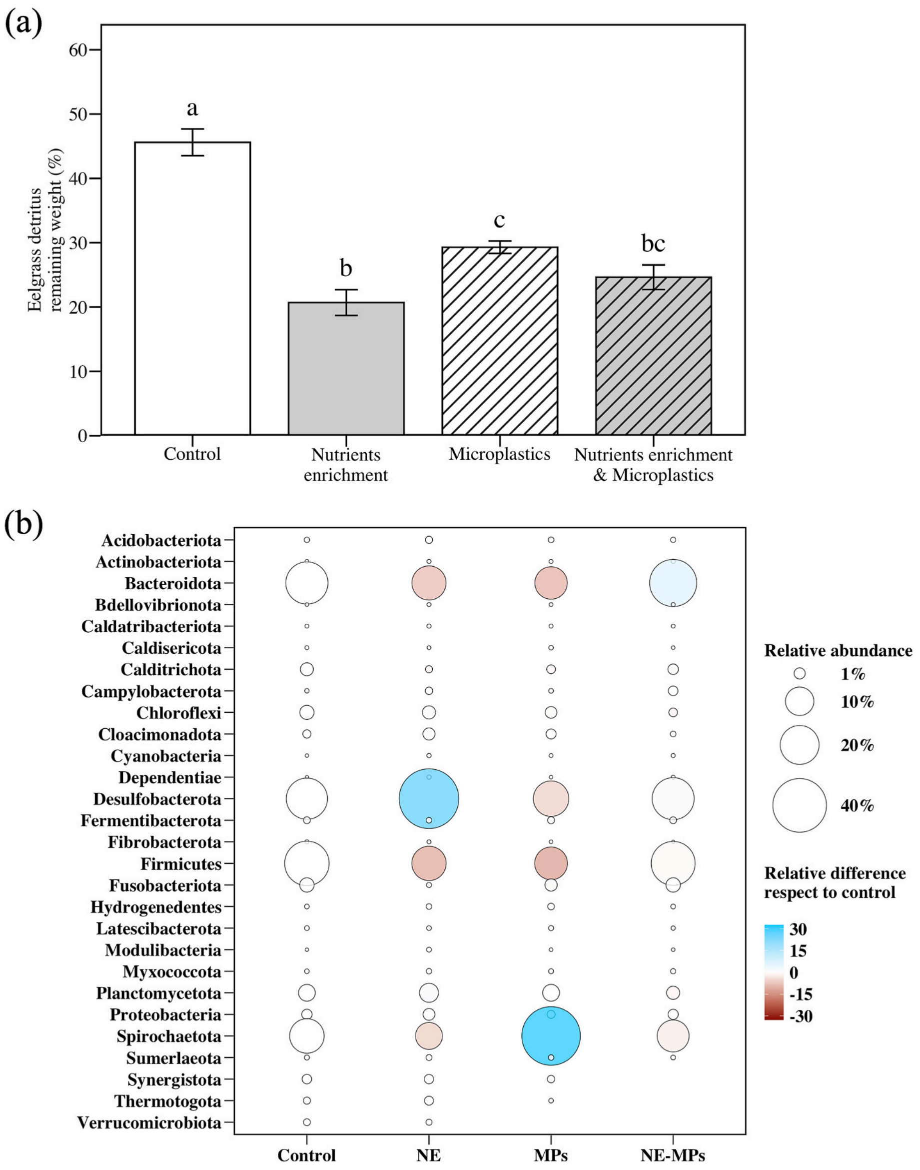

**Fig. 8.** Effect of assessed factors and their combinations on (a) the eelgrass detritus remaining weight (% dry weight) and (b) the phyla assemblage on plant remains. Bubble patterns follow those from Fig. 5 (with relative abundance > 0.01 %).

2022) due to its distinct molecular structure (C-C/C-H bonds with methyl groups; Wu et al., 2023) and greater additive requirements, including UV stabilizers and toxic flame retardants (Zweifel, 2001). In addition, the observed size differences between LDPE (562 ± 34 μm) and PP (856 ± 61 μm) particles used in this study may have further influenced their bioavailability and interactions with seagrass tissues. However, determining the relative contributions of polymer type, particle size, and additive chemistry to the observed growth reductions remains an important research gap that warrants targeted investigation in future studies.

### *4.2. Eelgrass responses to MPs and fertilization*

The combined microplastic with nutrient enrichment (NE-MPs) treatment produced effects largely comparable to MP exposure alone, indicating that microplastics dominated the stress response. This finding contrast with expectation that nutrient enrichment would exacerbate stress responses, since the excess of N and P in sediment can result in reduction of eelgrass weight, leaf growth and leaf turnover rate due to ammonium toxicity (van Katwijk et al., 1997). However, the experimental conditions, characterised by pH (8.1) and high light availability, likely mitigated the toxic effects by facilitating ammonium assimilation into free amino acid compounds (van der Heide et al., 2008; Villazán et al., 2013), thereby preventing the anticipated decline in aboveground productivity. Despite this buffering effect, NE treatment alone still exhibited belowground impacts, including a reduction in new shoots formation and impaired root development. These changes could have long-term consequences for meadow stability, as belowground biomass might reduce anchoring strength, increasing susceptibility to hydrodynamic stress (Infantes et al., 2011). Collectively, these findings highlight that while high-light conditions may temporarily offset nutrient-driven stress, microplastics remain a primary driver of physiological impairment, with potential cascading effects on meadow resilience.

A significant increase in microbial abundance in both the phyllosphere and, especially, rhizosphere in plants that underwent fertilized sediments were found. The main drivers of these differences were due to changes on families mostly involved in sulfur metabolism and organic matter degradation process. Particularly, a stark increase of Arcobacteraceae was found (Fig. 7), a Bacteroidota with a symbiotic relationship with seagrasses to provide their nitrogen requirement to the plants while preventing sulfide toxicity (Crump et al., 2018). However, when fertilized sediments were combined with MPs a notable decrease of bacteria involved in sulfur cycle (0.45-fold lower in combined compared to NE treatment) was observed. Particularly, the abundance of Arcobacteraceae was striking lessened (on average from a relative abundance of 23.1 ± 9 in NE treatment to 2.8 ± 1.2 % in NE-MPs treatment) along with other sulfide-reducing bacteria, which suggests an impact of MPs on sulfur REDOX processes in sediments (Fraser et al., 2023). Previous studies found that MPs like PP and LDPE affect both the soil microbial communities involved in sulfur metabolism and their soil enzyme activities (Dong et al., 2024). The results showed a previous unrecognized pathway in seagrass systems whereby microplastics undermine resilience by disrupting microbial-mediated sulfur cycling, a process critical for plant survival in reducing sediments.

### 4.3. Effects on eelgrass detritus decomposition assay

This study provides the first experimental evidence that microplastics significantly accelerate the rate of detritus decomposition in marine sediments, with decomposition rates increasing by 35–55 % over 60 days. This can be partially attributed to two complementary mechanisms: (1) the selective enrichment of Spirochaetota, a phylum involved in breakdown of complex organic matter in marine sediment such as those from seagrass meadows (Randell et al., 2023), and (2) nutrient-driven stimulation microbial biomass and extracellular enzyme activity associated with carbon cycling, particularly in NE-MPs treatments, which can favor the SOC remineralization (Liu et al., 2017).

The observed priming effect of microplastics promoting the decomposition of eelgrass litter in sediments can be attributed to their dual role as both microbial substrates and sediment modifiers. MPs can provide more favorable living environments for some microorganisms known for consuming organic compounds in sediments (Fei et al., 2020; Tu et al., 2023). This is because MPs can act as a substrate for heterotrophic microorganisms to colonise (Arias-Andres et al., 2018) and they can alter the sediment mean grain size and permeability, favoring the exchange of nutrients and oxygenation with the surrounding water-column (Wang et al., 2016; Gerstenbacher et al., 2022). The obtained results are consistent with findings from Litchfield et al. (2023) who reported a significant increase of *Zostera muelleri* detritus decomposition in sediments exposed to disposable surgical masks (composed of various plastics, including PP, PE and PS). These authors attributed their result mainly to the size of the filter of the mask (~2.5 μm) that increase area of substrate for heterotrophic microorganisms to colonise.

### 4.4. Ecological implications

Vegetated coastal communities such as seagrasses (Fourqurean et al., 2012), rhizophytic algae (de los Santos et al., 2023), or saltmarshes (Jiménez-Ramos et al., 2025) are among the most effective ecosystems on Earth at sequestering organic carbon. However, this study demonstrates that microplastics pollution directly threatens carbon sequestration capacity of coastal vegetated ecosystems. The reported MP-induced reductions in seagrass biomass and rhizome elongation directly compromise eelgrass carbon storage through dwindling autochthonous carbon inputs (Champenois and Borges, 2021), while the observed acceleration of detritus decomposition further increase carbon remineralization (Yamuza-Magdaleno et al., 2024). Furthermore, low-density or degraded seagrass meadows favor the release of OC stock from upper sediments compared to higher biomass meadows (Egea et al., 2023a), due to increased transfer of dissolved organic carbon (DOC) from the sediment to the water column (Chipman et al., 2010), and by higher degradation of organic matter by sediment bacteria (Jiménez-Ramos et al., 2024a; Ren et al., 2024).

The ecological consequences can be extended beyond carbon cycling. Reduced carbon reserves in MP-exposed plants may diminish their resilience to additional stressors including those related with human-induced impacts such as warming or light limitation (Jiménez-Ramos et al., 2023) or natural impacts such as higher herbivory stress (Egea and Jiménez-Ramos, 2025b), potentially triggering feedback loops that exacerbate meadow degradation. In addition, the lower seagrass biomass and density found in this study may also affect to the food web and biodiversity due to the lower plant biomass for herbivory or shelter (Jiménez-Ramos et al., 2021, 2024b). These findings establish microplastics as a previously underappreciated driver of carbon cycle alteration in coastal vegetated ecosystems, warranting urgent consideration in coastal management strategies. However, this study is not without methodological limitations. While mesocosm experiments may not fully replicate natural field conditions (e.g., sediment heterogeneity, shifts in hydrodynamic forcing, or community interactions), they provide a controlled platform to isolate and mechanistically evaluate stressor impacts on coastal vegetated habitats (Short, 1987; de la Hoz et al., 2025). This is particularly relevant for seagrass-microbiome-carbon feedbacks as critical step toward predicting real-world ecosystem responses. In addition, temperate seagrasses display distinct seasonal dynamics in growth and physiology driven by natural variations in light, temperature, and other environmental factors (Moore and Wetzel, 2000). Importantly, their sensitivity to stressors, including microplastics and nutrient enrichment, can vary significantly across seasons (e.g., Breiter et al., 2024; Egea et al., 2023c). While our study provides critical baseline data under summer conditions (peak growth period), future field experiments should assess these stressor interactions across seasonal cycles to (1) validate our findings under natural environmental variability, (2) identify potential seasonal windows of heightened vulnerability, and (3) improve predictions of long-term impacts on seagrass carbon sequestration capacity.

This study provides novel results into MPs impacts on eelgrass physiology, associated microbiome and ecological functions, however, several important questions remain regarding MPs fate and transformation processes. The experimental design did not specifically track MPs degradation, though we recognize that even during the 28-day exposure period, the incorporated LDPE and PP particles likely underwent initial modifications through three concurrent processes: 1) mechanical degradation through hydrodynamical forces (Chubarenko et al., 2018), 2) environmental conditions such as photo- and chemical-oxidation (Sutkar et al., 2023), and 3) biological degradation through community interactions (Yan et al., 2024). Although MPs degrade on nature at a slow rate (Sutkar et al., 2023), the short-term degradation process can also affect to the community response and the coastal carbon cycle. For instance, the release of dissolved organic carbon (DOC) during the first stages of MPs degradation can trigger a relevant carbon input into the system (Romera-Castillo et al., 2018), exhibits a substantial influence on microbial activity (Egea et al., 2024b) and on the biogeochemical processes within the environment (Liu et al., 2024), resulting in a cascade of effects on the entire community still inadequately understood. Further experimentations are needed not only to validate the obtained results under natural variability but to specifically clarify the mechanism of interactions between MPs and both, seagrass microbiome and plants, and also characterize the degradation of MPs as they impact ecosystems.

## 5. Conclusions

This study demonstrates that microplastics reduces *Zostera marina* growth by disrupting rhizosphere microbiomes, inducing oxidative stress and damaging roots. While high light mitigated nutrient effects, microplastic exposure consistently reduced productivity (39–57 %), rhizome elongation (32–35 %), and root growth (20–35 %), while accelerating detritus decomposition (1.5–2.2×). These impacts, combined with sulfide cycle disruption, threaten seagrass carbon sequestration capacity. Future research would be necessary to assess the mechanisms of the interaction between microplastics and seagrasses (through the impact of polymers themselves or by their chemical additives) and evidence which polymer played the greatest impact in these communities. The findings recommend the need for urgent management actions addressing microplastics pollution in costal ecosystems.

## CRediT authorship contribution statement

**Luis G. Egea:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Rocío Jiménez-Ramos:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Lucía Rodríguez-Arias:** Writing – review & editing, Investigation, Formal analysis. **Eduardo Infantes:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Data curation, 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.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2025.118638.

## Data availability

The dataset for this article is open access in the Zenodo repository: https://doi.org/10.5281/zenodo.15490210.

## References

Adamakis, I.-D.S., Malea, P., Sperdouli, I., Panteris, E., Kokkinidi, D., Moustakas, M., 2021. Evaluation of the spatiotemporal effects of bisphenol A on the leaves of the seagrass Cymodocea nodosa. J. Hazard. Mater. 404, 124001. https://doi.org/10.1016/j.jhazmat.2020.124001.

Arias-Andres, M., Kettner, M.T., Miki, T., Grossart, H.-P., 2018. Microplastics: new substrates for heterotrophic activity contribute to altering organic matter cycles in aquatic ecosystems. Sci. Total Environ. 635, 1152–1159. https://doi.org/10.1016/j.scitotenv.2018.04.199.

Barnes, D.K.A., Galgani, F., Thompson, R.C., Barlaz, M., 2009. Accumulation and fragmentation of plastic debris in global environments. Philos. Trans. R. Soc. B Biol. Sci. 364, 1985–1998. https://doi.org/10.1098/rstb.2008.0205.

Breiter, A.L., Sokoloski, C.T., Yang, S., Gaeckle, J.L., 2024. Effect of prolonged seawater warming on *Zostera marina* ecotypes of the northeast Pacific. J. Exp. Mar. Biol. Ecol. 578, 152036. https://doi.org/10.1016/j.jembe.2024.152036.

Burkholder, J.M., Tomasko, D.A., Touchette, B.W., 2007. Seagrasses and eutrophication. J. Exp. Mar. Biol. Ecol. 350, 46–72. https://doi.org/10.1016/j.jembe.2007.06.024.

Caporaso, J.G., Lauber, C.L., Walters, W.A., Berg-Lyons, D., Huntley, J., Fierer, N., Owens, S.M., et al., 2012. Ultra-high-throughput microbial community analysis on the Illumina HiSeq and MiSeq platforms. ISME J. 6, 1621–1624. https://doi.org/10.1038/ismej.2012.8.

Champenois, W., Borges, A.V., 2021. Net community metabolism of a *Posidonia oceanica* meadow. Limnol. Oceanogr. 66, 2126–2140. https://doi.org/10.1002/lno.11724.

Chipman, L., Podgorski, D., Green, S., Kostka, J., Cooper, W., Huettel, M., 2010. Decomposition of plankton-derived dissolved organic matter in permeable coastal sediments. Limnol. Oceanogr. 55, 857–871. https://doi.org/10.4319/lo.2010.55.2.0857.

Chubarenko, I., Esiukova, E., Bagaev, A., Isachenko, I., Demchenko, N., Zobkov, M., Efimova, I., et al., 2018. Behavior of microplastics in coastal zones. In: Microplastic Contamination in Aquatic Environments. Elsevier, pp. 175–223. https://doi.org/10.1016/B978-0-12-813747-5.00006-0.

Crump, B.C., Wojahn, J.M., Tomas, F., Mueller, R.S., 2018. Metatranscriptomics and amplicon sequencing reveal mutualisms in seagrass microbiomes. Front. Microbiol. 9, 00388. https://doi.org/10.3389/fmicb.2018.00388.

Cúcio, C., Engelen, A.H., Costa, R., Muyzer, G., 2016. Rhizosphere microbiomes of European + seagrasses are selected by the plant, but are not species specific. Front. Microbiol. 7. https://doi.org/10.3389/fmicb.2016.00440.

Dahl, M., Bergman, S., Björk, M., Diaz-Almela, E., Granberg, M., Gullström, M., Leiva-Dueñas, C., et al., 2021. A temporal record of microplastic pollution in Mediterranean seagrass soils. Environ. Pollut. 273, 116451. https://doi.org/10.1016/j.envpol.2021.116451.

de la Hoz, C.F., Brooks, P.R., Coughlan, J., Mazarrasa, I., Ramos, E., Sainz-Villegas, S., Puente, A., et al., 2025. Unveiling growth and carbon composition of macroalgae with different strategies under global change. Mar. Environ. Res. 208, 107128. https://doi.org/10.1016/j.marenvres.2025.107128.

de los Santos, C.B., Krång, A.-S., Infantes, E., 2021. Microplastic retention by marine vegetated canopies: simulations with seagrass meadows in a hydraulic flume. Environ. Pollut. 269, 116050. https://doi.org/10.1016/j.envpol.2020.116050.

de los Santos, C.B., Egea, L.G., Martins, M., Santos, R., Masqué, P., Peralta, G., Brun, F.G., Jiménez-Ramos, R., 2023. Sedimentary organic carbon and nitrogen sequestration across a vertical gradient on a temperate wetland seascape including salt marshes, seagrass meadows and rhizophytic macroalgae beds. Ecosystems 26, 826–842. https://doi.org/10.1007/s10021-022-00801-5.

Do, A.T.N., Ha, Y., Kwon, J.-H., 2022. Leaching of microplastic-associated additives in aquatic environments: a critical review. Environ. Pollut. 305, 119258. https://doi.org/10.1016/j.envpol.2022.119258.

Dong, Y., Gao, M., Cai, Q., Qiu, W., Xiao, L., Chen, Z., Peng, H., et al., 2024. The impact of microplastics on sulfur REDOX processes in different soil types: a mechanism study. J. Hazard. Mater. 465, 133432. https://doi.org/10.1016/j.jhazmat.2024.133432.

Dunic, J.C., Brown, C.J., Connolly, R.M., Turschwell, M.P., Côté, I.M., 2021. Long-term declines and recovery of meadow area across the world's seagrass bioregions. Glob. Chang. Biol. 27, 4096–4109. https://doi.org/10.1111/gcb.15684.

Egea, L.G., Jiménez-Ramos, R., 2025a. Selective herbivory on necrotic tissue can promote tolerance to abiotic disturbances in the seagrass *Cymodocea nodosa*. Mar. Environ. Res. 207, 107064. https://doi.org/10.1016/j.marenvres.2025.107064.

Egea, L.G., Jiménez-Ramos, R., 2025b. Antibiotic pollution alters the microbiome and reduces primary production and growth in the seagrass *Cymodocea nodosa* (Ucria) Ascherson. Mar. Environ. Res. 210, 107242. https://doi.org/10.1016/j.marenvres.2025.107242.

Egea, L.G., Jiménez-Ramos, R., Hernández, I., Brun, F.G., 2020. Differential effects of nutrient enrichment on carbon metabolism and dissolved organic carbon (DOC) fluxes in macrophytic benthic communities. Mar. Environ. Res. 162, 105179. https://doi.org/10.1016/j.marenvres.2020.105179.

Egea, L.G., Infantes, E., Jiménez-Ramos, R., 2023a. Loss of POC and DOC on seagrass sediments by hydrodynamics. Sci. Total Environ. 901, 165976. https://doi.org/10.1016/j.scitotenv.2023.165976.

Egea, L.G., Cavijoli-Bosch, J., Casal-Porras, I., Yamuza-Magdaleno, A., Brun, F.G., Jiménez-Ramos, R., 2023b. Comparison of macroplastics dynamic across a tidal-dominated coastal habitat seascape including seagrasses, salt marshes, rocky bottoms and soft sediments. Mar. Pollut. Bull. 196, 115590. https://doi.org/10.1016/j.marpolbul.2023.115590.

Egea, L.G., Jiménez-Ramos, R., Romera-Castillo, C., Casal-Porras, I., Bonet-Melià, P., Yamuza-Magdaleno, A., et al., 2023c. Effect of marine heat waves on carbon metabolism, optical characterization, and bioavailability of dissolved organic carbon in coastal vegetated communities. Limnol. Oceanogr. 68, 467–482. https://doi.org/10.1002/lno.12286.

Egea, L.G., Jiménez-Ramos, R., English, M.K., Tomas, F., Mueller, R.S., 2024a. Marine heatwaves and disease alter community metabolism and DOC fluxes on a widespread habitat-forming seagrass species (*Zostera marina*). Sci. Total Environ. 957, 177820. https://doi.org/10.1016/j.scitotenv.2024.177820.

Egea, L.G., Brun, F.G., Jiménez-Ramos, R., 2024b. Dissolved organic carbon leaching from microplastics and bioavailability in coastal ecosystems. Sci. Total Environ. 909, 168673. https://doi.org/10.1016/j.scitotenv.2023.168673.

Erni-Cassola, G., Zadjelovic, V., Gibson, M.I., Christie-Oleza, J.A., 2019. Distribution of plastic polymer types in the marine environment; a meta-analysis. J. Hazard. Mater. 369, 691–698. https://doi.org/10.1016/j.jhazmat.2019.02.067.

Fei, Y., Huang, S., Zhang, H., Tong, Y., Wen, D., Xia, X., Wang, H., et al., 2020. Response of soil enzyme activities and bacterial communities to the accumulation of microplastics in an acid cropped soil. Sci. Total Environ. 707, 135634. https://doi.org/10.1016/j.scitotenv.2019.135634.

Fourqurean, J.W., Duarte, C.M., Kennedy, H., Marbà, N., Holmer, M., Mateo, M.A., Apostolaki, E.T., et al., 2012. Seagrass ecosystems as a globally significant carbon stock. Nat. Geosci. 5, 505–509. https://doi.org/10.1038/ngeo1477.

Fraser, M.W., Martin, B.C., Wong, H.L., Burns, B.P., Kendrick, G.A., 2023. Sulfide intrusion in a habitat forming seagrass can be predicted from relative abundance of sulfur cycling genes in sediments. Sci. Total Environ. 864, 161144. https://doi.org/10.1016/j.scitotenv.2022.161144.

Fuggle, R.E., Gribben, P.E., Marzinelli, E.M., 2023. Experimental evidence root-associated microbes mediate seagrass response to environmental stress. J. Ecol. 111, 1079–1093. https://doi.org/10.1111/1365-2745.14081.

Gall, S.C., Thompson, R.C., 2015. The impact of debris on marine life. Mar. Pollut. Bull. 92, 170–179. https://doi.org/10.1016/j.marpolbul.2014.12.041.

Gao, S., Huang, G., Han, D., 2025. Ecotoxicity of plastic leachates on aquatic plants: multi-factor multi-effect meta-analysis. Water Res. 268, 122577. https://doi.org/10.1016/j.watres.2024.122577.

Ge, J., Li, H., Liu, P., Zhang, Z., Ouyang, Z., Guo, X., 2021. Review of the toxic effect of microplastics on terrestrial and aquatic plants. Sci. Total Environ. 791, 148333. https://doi.org/10.1016/j.scitotenv.2021.148333.

Gerstenbacher, C.M., Finzi, A.C., Rotjan, R.D., Novak, A.B., 2022. A review of microplastic impacts on seagrasses, epiphytes, and associated sediment communities. Environ. Pollut. 303, 119108. https://doi.org/10.1016/j.envpol.2022.119108.

Govers, L.L., de Brouwer, J.H.F., Suykerbuyk, W., Bouma, T.J., Lamers, L.P.M., Smolders, A.J.P., van Katwijk, M.M., 2014. Toxic effects of increased sediment nutrient and organic matter loading on the seagrass *Zostera noltii*. Aquat. Toxicol. 155, 253–260. https://doi.org/10.1016/j.aquatox.2014.07.005.

Han, Q., Soissons, L.M., Bouma, T.J., van Katwijk, M.M., Liu, D., 2016. Combined nutrient and macroalgae loads lead to response in seagrass indicator properties. Mar. Pollut. Bull. 106, 174–182. https://doi.org/10.1016/j.marpolbul.2016.03.004.

Hermabessiere, L., Dehaut, A., Paul-Pont, I., Lacroix, C., Jezequel, R., Soudant, P., Duflos, G., 2017. Occurrence and effects of plastic additives on marine environments and organisms: a review. Chemosphere 182, 781–793. https://doi.org/10.1016/j.chemosphere.2017.05.096.

Hou, X., Li, C., Zhao, Y., He, Y., Li, W., Wang, X., Liu, X., 2024. Distinct impacts of microplastics on the carbon sequestration capacity of coastal blue carbon ecosystems: a case of seagrass beds. Mar. Environ. Res. 202, 106793. https://doi.org/10.1016/j.marenvres.2024.106793.

Hou, X., Li, X., Lin, Y., Li, C., Jing, R., Zhang, L., Li, J., Jiang, Z., Wang, S., et al., 2025. Plastisphere provides a unique ecological niche for microorganisms in Zostera marina seagrass meadows. Commun. Earth Environ. 6, 632. https://doi.org/10.1038/s43247-025-02619-0.

Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol. Evol. 7, 1451–1456. https://doi.org/10.1111/2041-210X.12613.

Huang, Y., Xiao, X., Xu, C., Perianen, Y.D., Hu, J., Holmer, M., 2020. Seagrass beds acting as a trap of microplastics - emerging hotspot in the coastal region? Environ. Pollut. 257, 113450. https://doi.org/10.1016/j.envpol.2019.113450.

Infantes, E., Orfila, A., Bouma, T.J., Simarro, G., Terrados, J., 2011. *Posidonia oceanica* and *Cymodocea nodosa* seedling tolerance to wave exposure. Limnol. Oceanogr. 56, 2223–2232. https://doi.org/10.4319/lo.2011.56.6.2223.

Infantes, E., de Smit, J.C., Tamarit, E., Bouma, T.J., 2021. Making realistic wave climates in low-cost wave mesocosms: a new tool for experimental ecology and biogeomorphology. Limnol. Oceanogr. Methods 19, 317–330. https://doi.org/10.1002/lom3.10425.

Infantes, E., Hoeks, S., Adams, M., van der Heide, T., van Katwijk, M., Bouma, T., 2022. Seagrass roots strongly reduce cliff erosion rates in sandy sediments. Mar. Ecol. Prog. Ser. 700, 1–12. https://doi.org/10.3354/meps14196.

Jiang, Z., Li, L., Fang, Y., Lin, J., Liu, S., Wu, Y., Huang, X., 2022. Eutrophication reduced the release of dissolved organic carbon from tropical seagrass roots through exudation and decomposition. Mar. Environ. Res. 179, 105703. https://doi.org/10.1016/j.marenvres.2022.105703.

Jiménez-Ramos, R., Mancilla, M., Villazán, B., Egea, L.G., González-Ortiz, V., Vergara, J. J., et al., 2017. Resistance to nutrient enrichment varies among components in the *Cymodocea nodosa* community. J. Exp. Mar. Biol. Ecol. 497, 41–49. https://doi.org/10.1016/j.jembe.2017.09.008.

Jiménez-Ramos, R., Egea, L.G., Vergara, J.J., Brun, F.G., 2018. Nutrient load and epiphytes are drivers of increased herbivory in seagrass communities. Mar. Ecol. Prog. Ser. 599, 49–64. https://doi.org/10.3354/meps12622.

Jiménez-Ramos, R., Egea, L.G., Vergara, J.J., Brun, F.G., 2021. Factors modulating herbivory patterns in *Cymodocea nodosa* meadows. Limnol. Oceanogr. 66, 2218–2233. https://doi.org/10.1002/lno.11749.

Jiménez-Ramos, R., Tomas, F., Reynés, X., Romera-Castillo, C., Pérez-Lloréns, J.L., Egea, L.G., 2022. Carbon metabolism and bioavailability of dissolved organic carbon (DOC) fluxes in seagrass communities are altered under the presence of the tropical invasive alga Halimeda incrassata. Sci. Total Environ. 839, 156325. https://doi.org/10.1016/j.scitotenv.2022.156325.

Jiménez-Ramos, R., Brun, F.G., Pérez-Lloréns, J.L., Vergara, J.J., Delgado-Cabezas, F., Sena-Soria, N., Egea, L.G., 2023. Resistance and recovery of benthic marine macrophyte communities to light reduction: insights from carbon metabolism and dissolved organic carbon (DOC) fluxes, and implications for resilience. Mar. Pollut. Bull. 188, 114630. https://doi.org/10.1016/j.marpolbul.2023.114630.

Jiménez-Ramos, R., Brun, F.G., Vergara, J.J., Hernández, I., Pérez-Lloréns, J.L., Egea, L. G., 2024a. Nutrient enrichment and herbivory alter carbon balance in temperate seagrass communities. Mar. Pollut. Bull. 206, 116784. https://doi.org/10.1016/j.marpolbul.2024.116784.

Jiménez-Ramos, R., Egea, L.G., Pérez-Estrada, C.J., Balart, E.F., Vergara, J.J., Brun, F.G., 2024b. Patch age alters seagrass response mechanisms to herbivory damage. Mar. Environ. Res. 197, 106443. https://doi.org/10.1016/j.marenvres.2024.106443.

Jiménez-Ramos, R., Egea, L.G., D'Agostino, V.C., Degrati, M., Loizaga, R., 2025. Carbon and nitrogen stocks in sediment at Península Valdés Biosphere Reserve: novel insights into the potential contribution of large marine vertebrates to carbon sequestration. Front. Mar. Sci. 12, 1500594. https://doi.org/10.3389/fmars.2025.1500594.

Kalčíková, G., Žgajnar Gotvajn, A., Kladnik, A., Jemec, A., 2017. Impact of polyethylene microbeads on the floating freshwater plant duckweed Lemna minor. Environ. Pollut. 230, 1108–1115. https://doi.org/10.1016/j.envpol.2017.07.050.

Kaldy, J., Brown, C., Pacella, S., 2022. Carbon limitation in response to nutrient loading in an eelgrass mesocosm: influence of water residence time. Mar. Ecol. Prog. Ser. 689, 1–17. https://doi.org/10.3354/meps14061.

Kershaw, P., 2015. Sources, Fate and Effects of Microplastics in the Marine Environment: A Global Assessment. UNESCO: United Nations Educational, Scientific and Cultural Organisation, France. Retrieved from. https://coilink.org/20.500.12592/63vw7s (on 19 Jan 2025, COI: 20.500.12592/63vw7s).

Korlević, M., Markovski, M., Zhao, Z., Herndl, G.J., Najdek, M., 2021. Seasonal dynamics of epiphytic microbial communities on marine macrophyte surfaces. Front. Microbiol. 12, 671342. https://doi.org/10.3389/fmicb.2021.671342.

Lamers, L.P.M., Govers, L.L., Janssen, I.C.J.M., Geurts, J.J.M., Van der Welle, M.E.W., Van Katwijk, M.M., et al., 2013. Sulfide as a soil phytotoxin—a review. Front. Plant Sci. 4, 00268. https://doi.org/10.3389/fpls.2013.00268.

Li, C., Zhu, L., Li, W.-T., Li, D., 2023. Microplastics in the seagrass ecosystems: a critical review. Sci. Total Environ. 902, 166152. https://doi.org/10.1016/j.scitotenv.2023.166152.

Litchfield, S.G., Tan, M., Schulz, K.G., Kelaher, B.P., 2023. Disposable surgical masks affect the decomposition of *Zostera muelleri*. Mar. Pollut. Bull. 188, 114695. https://doi.org/10.1016/j.marpolbul.2023.114695.

Lithner, D., Larsson, Å., Dave, G., 2011. Environmental and health hazard ranking and assessment of plastic polymers based on chemical composition. Sci. Total Environ. 409, 3309–3324. https://doi.org/10.1016/j.scitotenv.2011.04.038.

Liu, S., Jiang, Z., Wu, Y., Zhang, J., Arbi, I., Ye, F., et al., 2017. Effects of nutrient load on microbial activities within a seagrass-dominated ecosystem: implications of changes in seagrass blue carbon. Mar. Pollut. Bull. 117, 214–221. https://doi.org/10.1016/j.marpolbul.2017.01.056.

Liu, X., Fang, L., Gardea-Torresdey, J.L., Zhou, X., Yan, B., 2024. Microplastic-derived dissolved organic matter: generation, characterization, and environmental behaviors. Sci. Total Environ. 948, 174811. https://doi.org/10.1016/j.scitotenv.2024.174811.

Lobet, G., Pagès, L., Draye, X., 2011. A novel image-analysis toolbox enabling quantitative analysis of root system architecture. Plant Physiol. 157, 29–39. https://doi.org/10.1104/pp.111.179895.

Luhar, M., Coutu, S., Infantes, E., Fox, S., Nepf, H., 2010. Wave-induced velocities inside a model seagrass bed. J. Geophys. Res. Oceans 115. https://doi.org/10.1029/2010JC006345.

Luhar, M., Infantes, E., Nepf, H., 2017. Seagrass blade motion under waves and its impact on wave decay. J. Geophys. Res. Oceans 122, 3736–3752. https://doi.org/10.1002/2017JC012731.

Maddela, N.R., Kakarla, D., Venkateswarlu, K., Megharaj, M., 2023. Additives of plastics: entry into the environment and potential risks to human and ecological health. J. Environ. Manag. 348, 119364. https://doi.org/10.1016/j.jenvman.2023.119364.

McHenry, J., Rassweiler, A., Hernan, G., Uejio, C.K., Pau, S., Dubel, A.K., Lester, S.E., 2021. Modelling the biodiversity enhancement value of seagrass beds. Divers. Distrib. 27, 2036–2049. https://doi.org/10.1111/ddi.13379.

Menicagli, V., Castiglione, M.R., Balestri, E., Giorgetti, L., Bottega, S., Sorce, C., et al., 2022. Early evidence of the impacts of microplastic and nanoplastic pollution on the growth and physiology of the seagrass *Cymodocea nodosa*. Sci. Total Environ. 838, 156514. https://doi.org/10.1016/j.scitotenv.2022.156514.

Miyamoto, H., Kawachi, N., Kurotani, A., Moriya, S., Suda, W., Suzuki, K., et al., 2023. Computational estimation of sediment symbiotic bacterial structures of seagrasses overgrowing downstream of onshore aquaculture. Environ. Res. 219, 115130. https://doi.org/10.1016/j.envres.2022.115130.

Molin, J.M., Groth-Andersen, W.E., Hansen, P.J., Kühl, M., Brodersen, K.E., 2023. Microplastic pollution associated with reduced respiration in seagrass (*Zostera marina* L.) and associated epiphytes. Front. Mar. Sci. 10, 1216299. https://doi.org/10.3389/fmars.2023.1216299.

Moore, K.A., Wetzel, R.L., 2000. Seasonal variations in eelgrass (*Zostera marina* L.) responses to nutrient enrichment and reduced light availability in experimental ecosystems. J. Exp. Mar. Biol. Ecol. 244, 1–28. https://doi.org/10.1016/S0022-0981(99)00135-5.

Murphy, J., 2001. Additives for Plastics Handbook. Elsevier Science Ltd, Oxford.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'hara, R.B., et al., 2024. Package 'vegan'. Community Ecology Package, Version, 2(9), pp. 1–295.

Olesen, B., Sand-Jensen, K., 1993. Seasonal acclimatization of eelgrass *Zostera marina* growth to light. Mar. Ecol. Prog. Ser. 94, 91–99. https://doi.org/10.3354/meps094091.

Omidoyin, K.C., Jho, E.H., 2024. Environmental occurrence and ecotoxicological risks of plastic leachates in aquatic and terrestrial environments. Sci. Total Environ. 954, 176728. https://doi.org/10.1016/j.scitotenv.2024.176728.

Peralta, G., Bouma, T.J., van Soelen, J., Pérez-Lloréns, J.L., Hernández, I., 2003. On the use of sediment fertilization for seagrass restoration: a mesocosm study on *Zostera marina* L. Aquat. Bot. 75, 95–110. https://doi.org/10.1016/S0304-3770(02)00168-7.

R Core Team, 2024. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Randell, A.S., Tanner, J.E., Wos-Oxley, M.L., Catalano, S.R., Keppel, G., Oxley, A.P.A., 2023. The root of influence: root-associated bacterial communities alter resource allocation in seagrass seedlings. Front. Mar. Sci. 10. https://doi.org/10.3389/fmars.2023.1278837.

Ren, Y., Liu, S., Luo, H., Jiang, Z., Liang, J., Wu, Y., Huang, X., Macreadie, P.I., 2024. Seagrass decline weakens sediment organic carbon stability. Sci. Total Environ. 937, 173523. https://doi.org/10.1016/j.scitotenv.2024.173523.

Romera-Castillo, C., Pinto, M., Langer, T.M., Álvarez-Salgado, X.A., Herndl, G.J., 2018. Dissolved organic carbon leaching from plastics stimulates microbial activity in the ocean. Nat. Commun. 9, 1430. https://doi.org/10.1038/s41467-018-03798-5.

Serrano, O., Lavery, P.S., Duarte, C.M., Kendrick, G.A., Calafat, A., York, P.H., et al., 2016. Can mud (silt and clay) concentration be used to predict soil organic carbon content within seagrass ecosystems? Biogeosciences 13, 4915–4926. https://doi.org/10.5194/bg-13-4915-2016.

Short, F.T., 1987. Effects of sediment nutrients on seagrasses: literature review and mesocosm experiment. Aquat. Bot. 27, 41–57. https://doi.org/10.1016/0304-3770(87)90085-4.

Sutkar, P.R., Gadewar, R.D., Dhulap, V.P., 2023. Recent trends in degradation of microplastics in the environment: a state-of-the-art review. J. Hazard. Mater. Adv. 11, 100343. https://doi.org/10.1016/j.hazadv.2023.100343.

Tarquinio, F., Hyndes, G.A., Laverock, B., Koenders, A., Säwström, C., 2019. The seagrass holobiont: understanding seagrass-bacteria interactions and their role in seagrass ecosystem functioning. FEMS Microbiol. Lett. 366. https://doi.org/10.1093/femsle/fnz057.

Tu, C., Yang, Y., Wang, J., Su, H., Guo, J., Cao, D., Lian, J., Wang, D., 2023. In situ effects of microplastics on the decomposition of aquatic macrophyte litter in eutrophic shallow lake sediments, China. Environ. Pollut. 337, 122543. https://doi.org/10.1016/j.envpol.2023.122543.

Ugarelli, K., Chakrabarti, S., Laas, P., Stingl, U., 2017. The seagrass holobiont and its microbiome. Microorganisms 5, 81. https://doi.org/10.3390/microorganisms5040081.

Unsworth, R.K.F., McKenzie, L.J., Collier, C.J., Cullen-Unsworth, L.C., Duarte, C.M., Eklöf, J.S., Jarvis, J.C., et al., 2019. Global challenges for seagrass conservation. Ambio 48, 801–815. https://doi.org/10.1007/s13280-018-1115-y.

van der Heide, T., Smolders, A.J.P., Rijkens, B.G.A., van Nes, E.H., van Katwijk, M.M., Roelofs, J.G.M., 2008. Toxicity of reduced nitrogen in eelgrass (*Zostera marina*) is highly dependent on shoot density and pH. Oecologia 158, 411–419. https://doi.org/10.1007/s00442-008-1155-2.

van Katwijk, M., Vergeer, L., Schmitz, G., Roelofs, J., 1997. Ammonium toxicity in eelgrass *Zostera marina*. Mar. Ecol. Prog. Ser. 157, 159–173. https://doi.org/10.3354/meps157159.

Vilaplana, M.I., Egea, L.G., Bautista-Chamizo, E., Rodríguez-Romero, A., Tollardo, R., Brun, F.G., Vergara, J.J., Jiménez-Ramos, R., 2025. The temperate seagrass species *Cymodocea nodosa* and the associated bacteria co-response to sunscreen pollution. Mar. Environ. Res. 208, 107115. https://doi.org/10.1016/j.marenvres.2025.107115.

Villazán, B., Brun, F., Jiménez-Ramos, R., Pérez-Lloréns, J., Vergara, J., 2013. Interaction between ammonium and phosphate uptake rates in the seagrass *Zostera noltii*. Mar. Ecol. Prog. Ser. 488, 133–143. https://doi.org/10.3354/meps10395.

Wang, J., Tan, Z., Peng, J., Qiu, Q., Li, M., 2016. The behaviors of microplastics in the marine environment. Mar. Environ. Res. 113, 7–17. https://doi.org/10.1016/j.marenvres.2015.10.014.

Wang, L., English, M.K., Tomas, F., Mueller, R.S., 2021. Recovery and community succession of the *Zostera marina* rhizobiome after transplantation. Appl. Environ. Microbiol. 87. https://doi.org/10.1128/AEM.02326-20.

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., et al., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. 106, 12377–12381. https://doi.org/10.1073/pnas.0905620106.

Westermann, A.J., Barquist, L., Vogel, J., 2017. Resolving host-pathogen interactions by dual RNA-seq. PLoS Pathog. 16, e1006033. https://doi.org/10.1371/journal.ppat.1006033.

Wu, Z., Shi, W., Valencak, T.G., Zhang, Y., Liu, G., Ren, D., 2023. Biodegradation of conventional plastics: candidate organisms and potential mechanisms. Sci. Total Environ. 885, 163908. https://doi.org/10.1016/j.scitotenv.2023.163908.

Yamuza-Magdaleno, A., Jiménez-Ramos, R., Casal-Porras, I., Brun, F.G., Egea, L.G., 2024. Long-term sediment organic carbon remineralization in different seagrass and macroalgae habitats: implication for blue carbon storage. Front. Mar. Sci. 11, 1370768. https://doi.org/10.3389/fmars.2024.1370768.

Yamuza-Magdaleno, A., Jiménez-Ramos, R., Cavijoli-Bosch, J., Brun, F.G., Egea, L.G., 2025. Ocean acidification and global warming may favor blue carbon service in a *Cymodocea nodosa* community by modifying carbon metabolism and dissolved organic carbon fluxes. Mar. Pollut. Bull. 212, 117501. https://doi.org/10.1016/j.marpolbul.2024.117501.

Yan, X., Chio, C., Li, H., Zhu, Y., Chen, X., Qin, W., 2024. Colonization characteristics and surface effects of microplastic biofilms: implications for environmental behavior of typical pollutants. Sci. Total Environ. 937, 173141. https://doi.org/10.1016/j.scitotenv.2024.173141.

Yu, H., Peng, J., Cao, X., Wang, Y., Zhang, Z., Xu, Y., Qi, W., 2021. Effects of microplastics and glyphosate on growth rate, morphological plasticity, photosynthesis, and oxidative stress in the aquatic species *Salvinia cucullata*. Environ. Pollut. 279, 116900. https://doi.org/10.1016/j.envpol.2021.116900.

Yuan, Z., Nag, R., Cummins, E., 2022. Ranking of potential hazards from microplastics polymers in the marine environment. J. Hazard. Mater. 429, 128399. https://doi.org/10.1016/j.jhazmat.2022.128399.

Zhang, X., Liu, S., Li, J., Wu, Y., Luo, H., Jiang, Z., Huang, X., 2022. Nutrient enrichment decreases dissolved organic carbon sequestration potential of tropical seagrass meadows by mediating bacterial activity. Ecol. Indic. 145, 109576. https://doi.org/10.1016/j.ecolind.2022.109576.

Zhang, X., Liu, S., Wu, Y., Luo, H., Ren, Y., Liang, J., et al., 2025. Nutrient loading accelerates breakdown of refractory dissolved organic carbon in seagrass ecosystem waters. Water Res. 273, 123017. https://doi.org/10.1016/j.watres.2024.123017.

Zhao, L., Ru, S., He, J., Zhang, Z., Song, X., Wang, D., et al., 2022. Eelgrass (*Zostera marina*) and its epiphytic bacteria facilitate the sinking of microplastics in the seawater. Environ. Pollut. 292, 118337. https://doi.org/10.1016/j.envpol.2021.118337.

Zhou, Z., Hua, J., Xue, J., Yu, C., 2024. Differential impacts of polyethylene microplastic and additives on soil nitrogen cycling: a deeper dive into microbial interactions and transformation mechanisms. Sci. Total Environ. 942, 173771. https://doi.org/10.1016/j.scitotenv.2024.173771.

Zilber-Rosenberg, I., Rosenberg, E., 2008. Role of microorganisms in the evolution of animals and plants: the hologenome theory of evolution. FEMS Microbiol. Rev. 32, 723–735. https://doi.org/10.1111/j.1574-6976.2008.00123.x.

Zweifel, H., 2001. Plastics Additives Handbook, 5th ed. Carl Hanser Verlag, Munich.